acta

Phytopathologica et Entomologica Hungarica

Acta Phytopathologica et Entomologica Hungarica

Volume 25

CONTENTS

SYSTEMATICS

PHYLOGENY

GENETICS

PHYSIOLOGY

DISTRIBUTION

APPLIED APHIDOLOGY

CONTENTS

SYSTEMATICS

PHYLOGENY

GENETICS

PHYSIOLOGY

DISTRIBUTION

APPLIED APHIDOLOGY

III   INTERNATIONAL SYMPOSIUM ON APHIDS

KECSKEMÉT, HUNGARY 14-19 August, 1989.

Edited by   Z. Basky

A.F.G. Dixon

M.B. Stoetzel

1 Nawrocka	16 Binazzi	31 Lampel
2 Carter	17 Kidd	32 Hansen
3 Cichocka	18 Szalay-Marzsó	33 Guldemond
4 J. Holman	19 Mier Durante	34 Jorg
5 Mrs. Holman	20 Abdel Karem Nasser	35 Aoki
6 Aal Yehia	21 Hardie	36 Volkl
7 Ponsen	22 Polgar	37 Kurosu
8 Van Oosten	23 Prinsen	38 Clement
9 Basky	24 Dixon	39 Gianni
10 Harrington	25 Stadler	40 Halbert
11 Harrewijn	26 Mackenzie	41 Ghosh
12 Stoetzel	27 Nieto Nafria	42 Foottit
13 Roversi	28 Wood-Baker	43 von Dohlen
14 Ruszkowska	29 Heie	44 Danielson
15 Shaposhnikov	30 Blackman	45 Loxdale
		46 Ward

III. INTERNATIONAL SYMPOSIUM ON APHIDS

14-19 August 1989

Kecskemét, Hungary

LIST OF PARTICIPANTS

Aal Yehia, Abdel; Plant Protection Department, College of Agri-
culture, Assuit University, 71516 Assiut, Egypt

Abdel Karem Nasser, Mohamed; Vegetable Crops Research Institute,
Mészöly Gyula, ut. 6, 6000 Kecskemét, Hungary

Ali, Mohamed; Plant Protection Department, Faculty of Agriculture,
Al-Azhar University, Resr City, Cairo, Egypt

Andrásfalvy, Pál; Zenit Kft, Ciba-Geigy, Képviselet, Belgrad
RKP 25, 1056 Budapest, Hungary

Aoki, Shigeyuki; Laboratory of Biology, College of General
Education, Rissho University, Magechi 1700, Kumagaya,
Saitama, 360-01, Japan

Basky, Zsuzsa; Institute of Crop Protection and Soil Conservation
Service, P.O.Box 250, Vizpart KRT 32, 5000 Szolnok, Hungary

Binazzi, Andrea; Instituto Sperimentale per la Zoologia Agraria,
Via Lanciola 12/A, Cascine del Riccio, 50125 Florence, Italy

Blackman, Roger L.; Department of Entomology, British Museum
/Natural History/ Cromwell Road, London, SW7 5BD, United
Kingdom

Carter, Clive; Forest Research Station, Alice Holt Lodge, Farnham,
Surrey, GU10 4 LH, United Kingdom

Cichocka, Elzbieta; Department of Applied Entomology, Warszaw
Agricultural University, Nowoursynowska 166, Warszaw, 02 766
Poland

Clement, Stephen L.; USDA, ARS, Washington State University,Pullman,
    Washington 99164, USA

Van Oosten, Adrian Mearten; Department of Biology, MT-TNO, P.O.Box
    217, 2600 AE Delft, The Netherlands

Danielsson, Roy; Department of Systematic Zoology, Lund University,
    Helgonavogen 3, 62 Lund, Sweden

Dixon, Anthony (Tony) F.G.; School of Biological Sciences,University
    of East Anglia, Norwich, NB4 7TJ, United Kingdom

Von Dohlen, Carol D.; Department of Zoology, University of Maryland,
    College Park, Maryland 20742, USA

El-Bassiouny, Suzan A.; Plant Protection Institute, Hungarian
    Academy of Sciences, P.O.Box 102, 1525 Budapest, Hungary

Foottit, Robert; Biosystematics Research Institute, Agricultural
    Canada, K.W. Neatby Building, C.E.F.,Ottawa, Ontario,KíA OC6,Canada

Ghosh, Asish K.; Zoological Survey of India, Jawharlal Nehru Road,
    Calcutta 700 016, India

Cianni, Coceano P.; Centro Regionale Sperimentazione, Agraria, Via
    Sabbadini 5, Pozzholo del Friuli, Udine, Italy

González Funes, Pilar; Department of Zoology, University of Valencia,
    46100 Burjassot, Valencia, Spain

Guldemond, J.Adriaan; Agricultural University of Wageningen,
    Binnenhaven 7, 6709 PD, Wageningen, The Netherlands

Halbert, Suzan; Idaho Research and Education Center,
    603 University of Idaho Lane, Parma, Idaho 83660, USA

Hansen, Lars M.; Research Centre for Plant Protection, Institute of
    Plant Pathology, Lottenbortvej 2, DK-2800, LYNGBY, Denmark

Hardie, R.Jim; Agriculture and Food Research Couwal, Imperial
    College at Silwood Park, Ascot, Berkshire, SL5 7DE,United Kingdom

Harrewijn, Paul; Research Institute for Plant Protection, P.O.Box
    9060, 6700 GW Wageningen, The Netherlands

Harrington, Richard; Department of Entomology, Rothamsted Experimental
    Station, Harpenden, Hertfordshire, AL 5 2JQ, United Kingdom

Hegab, Aly; Plant Protection Department, Faculty of Agriculture,
    Zagazig University, Zagazig, Egypt

Heie, Ole E.; Institute of Biology, DLH, Emdrupvej 101, DK-2400,
    Copenhagen NV, Denmark

Holman, Jaroslav; Czechoslovak Academy of Sciences, Institute of
    Entomology, Branisovska 31, 370 05 Ceske Budejovice, Czecho-
    slovakia

Jörg, Erwin; Department of Entomology, Zoological Institute,
    University of Freibourg, Rue du Musee, CH-1700 Freibourg,
    Switzerland

Kalmár, G.; Plant Production System of Kisalfold, Győr, Pásztor
    u. 17. H-9024, Hungary

Kidd, Neil A.C.; School of Pure Applied Biology, University of
    Wales, P.O. Box 915, Cardiff, CFl 3TL, United Kingdom

Kindlmann, Pavel; Czechoslovas Academy of Sciences, Department of
    Biomatematics, Branisovska 31, 370 05 Ceske Budejovice,
    Czechoslovakia

Kurosu, Utako; Faculty of Agriculture, Tokyo University of
    Agriculture and Technology, Fuchu, Tokyo, 183, Japan

Lampel, Gerolf; Department of Entomology, Zoological Institute,
    University of Freiburg, Rue de Musee, CH-1700 Freiburg,
    Switzerland

Loxdale, Hugh D.; Department of Entomology, Rothamsted Experimental
    Station, Harpenden, Hertfordshire, AL 5 2JQ, United Kingdom

Mackenzie, Aulay; School of Biological Sciences, University of East
    Anglia, Norwich, NR4 7TJ, United Kingdom

Mier Durante, Milagros Pilar; Department of Zoology, Faculty of
    Biology, University of León, 24071, León, Spain

Nawrocka, Bozena; Research Institute of Vegetable Crops, Department
    of Plant Protection, 96-100 Skierniewice,ul.22 Lipca 1/3,Poland

Nieto Narfía, Juan M.; Department of Zoology, Faculty of Biology,
    University of León, 24071, León, Spain

Polgár,László; Plant Protection Institute, Hungarian Academy of
    Sciences, P.O.Box 102, 1525 Budapest, Hungary

Ponsen, Mattheus B.; Department of Entomology, Postbus 8031,
    6700 EH Wageningen, The Netherlands

Prinsen, Jacomijn D.; Desearch Institute for Plant Protection,
    P.O. Box 9060, 6700 GW Wageningen, The Netherlands

Roversi, Pio Federico; Instituto Sperimentale per la Zoologia
    Agraria, Via Lanciola 12/A, Cascine del Riccio,50125 Florence
    Italy

Ruszkowska, Maria; Institut of Plant Protection, ul.Miczurina 20,
    60-318, Poznan, Poland

Seco Fernandez, Victoria; Faculty of Biology, University of León,
    Campus of Vegazana, 24071 León, Spain

Shaposhnikov, George Ch.; Zoological Institute, Academy of Sciences,
    Leningrad B 164, USSR

Stadler, Bernhard; Lehrstuhl fur Tierokologie I., University of
    Bayreuth, P.O.Box 101251, D-8580 Bayreuth, GFR

Stoetzel, Manya B.; Systematic Entomology Laboratory, Rm 6, Bldg
     004, BARC-West, ARS, USDA, Beltsville, Maryland 20705, USA

Szalay-Marzsó, László; Department of Plant Protection, University
     of Agriculture, 2103 Gödöllő, Hungary

Tomiuk, Jürgen: Institute of Anthropology and Humaugenétics,
     University of Tubingen, Wilhelm Str. 27., 7400 Tubingen, GFR

Turak, Eren; School of Biological Sciences, Marguarie University,
     New South Wales 2109, Australia

Völkl, Wolfgang; Department of Animal Ecology, University of
     Bayreuth, Universitat Str., D-858 Bayreuth, GFR

Ward, Seamus A.; Department of Theoretical Pro Ecology,Agricultural
     University, P.O.Box 430, 6700 AK Wageningen, The Netherlands

Wood-Baker, Cyril S.; Tyngwndwn Cilcennin Lampeter, Dyfed, SA48 8RS,
     United Kingdom

PREFACE

In 1981 the late Professor Henryk Szelegiewicz organised a symposium on Evolution and Biosystematics of Aphids at Jablonna, Poland. In so doing he started a series of symposia on aphids, the second of which "Population Structure and Genetics of Aphids" was organised by Dr Jaroslav Holman and held at Smolenice, Czechoslovakia in 1985.

The following proceedings are the result of the third such meeting, which was organised by Dr Zsuzsa Basky and held in August 1989 at Kecskemet, Hungary. The meeting was attended by 52 participants from 18 countries. All of the lectures presented at the meeting and summaries of most of the posters are included in the present volume. As editors we have offered advice to authors, where appropriate, concerning changes to the presentation and scientific content of their papers. However, as we have not made these changes mandatory, the authors retain full responsibility for their papers.

We take this opportunity to thank Dr Zsuzsa Basky and her colleagues for organising this symposium and to the participants for responding so rapidly to our demands for their manuscripts. We look forward to the next meeting which will be organised by Dr Pavel Kindlmann and held in Czechoslovakia in 1993.

The Editors:
Z. Basky
A.F.G. Dixon
M.B. Stoetzel

Akadémiai Kiadó, Budapest

IN MEMORY OF DR. FRITZ PAUL MÜLLER

(25 May 1913 - 21 July 1989)

Dr. sc.phil.Fritz Paul Müller was born in Meerane (Saxony) as the son of a master baker. He began nis university studies in 1932 at the Leipzig University. Following a period of keen interest in botany he has become especially interested in entomology and zoosystematics. In 1935 he continued his studies at the Rostock University where he obtained also his doctor's degree. From 1939 until the end of 1941 he worked as leader of the laboratory of the Plant Protection Service of Meiningen (Thuringia).

After the conclusion of the Second World War F. P. Müller became employed as research worker at the Institute of Agricultural Zoology of the Biologische Reichsanstalt (Berlin-Dahlem) where he treated various subjects of agricultural entomology and parasitology.

His work has brought him into close scientific contact with Prof.
Dr.A.HASE, one of the eminent German scholars of that period.Between
1948 and 1955 F.P.Müller became head of the Entomological Department
of the Institute of Phytopathology (Naumburg/Saale) and worked in
insecticide screening and in beeding of plants resistant to insect
pests. His interest in aphidology was aroused in Naumburg where h
met Dr.C. BÖRNER, one of the most outstanding aphidologists of our
time. His first studies on the taxonomy and biology of aphids date
back to this period.

In 1955 F.P.Müller was invited as lecturer to the Agricultural
Faculty of the Rostock University. Here he became then qualified
as lecturer; his thesis dealt with the biology of aphid vectors of
potato viruses. In 1959 he was promoted to the status of full
professor and in 1964 was appointed to head of the Institute of
Zoology and Entomology. Later he became also head of the Department
of Applied Entomology of the Phytopathological and Plant Protection
Institute and head of the Zoological Department in the Institute
of Agricultural Biology of the Rostock University. During his
educational activity F.P.Müller attached always great importance
to help his students to acquire the knowledge of systematics and
taxonomy.

In course of the reform of higher education in the GDR F.P.
Müller became transferred to the Biology Section of the Rostock
University and was named head of the Research Group of Phyto-Entomo-
logy. In spite of the enormous educational engagements he was able
to follow with the highest zeal, consistency and diligence his ori-
ginal research subject. While at the begin of his scientific career
he had dealt with different groups of insects (Coleoptera,Lepidoptera,
Anoplura), from 1953 his activity has been directed towards Aphids.

Studies on their taxonomy, their relationships to host plants, the connections between their morphological characteristics and biological properties were always completed with laboratory and field experiments. His long-range autecological experiments that were conducted with the creative mind of a natural philosopher brought valuable contributions to evolutionary genetics. In course of his work he conducted detailed studies in the Aphis fabae and Aphis gossypii-frangulae groups and dealt with the alternation of generations, formation of morphs, host specificity and evolution. The results of these activities were published in 189 publications; F.P.Müller verified the presence of 628 aphid species in the GDR of which 101 were new for the fauna of Germany. His taxonomical works contained the detailed descriptions of 21 new aphid species.

Both his experimental results and the productive cooperation with numerous research institutions brought F.P.Müller high international recognition; he became among others honorary member of the Hungarian Entomological Society and of the Entomological Society of Sudan.

In spite of his grave illness in 1980 F.P. Müller continued his valuable aphidological studies and worked on his publications until the last hours of his rich life. It was a great schock for all participants of the III. International Symposium of Aphids to get the sad news of the decease of F.P. Müller, one of the leading aphidologists of our time and the Symposium paid proper respect to the memory of this humane teacher, diligent researcher and outstanding scientist.

PUBLICATIONS OF PROFESSOR FRITZ PAUL MÜLLER

1. 1938: Die Verdauung bei nahe verwandten Käfern mit
         verschiedener Ernährungsweise. Versuche an Carabiden
         und Silphiden. Zool. Jb. Syst., Ökol.u.Geogr. 71.
         291-318.

2. 1939: Sterblichkeit und Wachstum der Kiefernspannerraupe bei
         Futter aus Reinbestanden und aus Mischwald. Z.ang.Ent.
         26, 359-367.

3. 1939: Nachwirkungen des Berührungsstäubemittels "Lipan" auf
         die bei der Begiftung überlebenden Kiefernspanner.
         Forstwiss. Zentralbl. 61, 538-544.

4. 1949: Erdraupenschäden durch Agrotis (Feltia) ypsilon ROTT.
         Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 3,
         10-13.

5. 1949: Die Überwinterung der Grünen Pfirsichblattlaus (Myzodes
         persicae SULZ.) als Virginogenia an Zier- und Gewächs-
         hauspflanzen. Nachrichtenbl. Deutsch. Pflanzenschutzd.
         Berlin 3, 41-44, 100-104.

6. 1949: Stärke und Dichte der Besiedelung durch die Blatt-
         gallenreblaus auf der Europäerrebe bei Freilandversuchen.
         Der Weinbau, Wiss. Beihefte 3, 276-286.

7. 1949: Das Zahlenverhältnis der Geschlechter in Zuchtpopu-
         lationen der Kleiderlaus (Pediculus corporis DE GEER,
         Anoplura). Z. Parasitenkunde 14, 285-299.

8. 1949: Versuche über die Wirksamkeit von Hexa- und Estermitteln
         gegen wurzelbesaugende Insekten. Nachrichtenbl. Deutsch.
         Pflanzenschutzd. Berlin 3, 151-158.

9. 1950: Über Schadauftreten und Biologie von Colaphellus sophiae
         SCHALL. (Chrysomel.). Z.ang.Ent. 31, 591-508.

10. 1950: Über das Zahlenverhältnis der Geschlechter beim
          Kartoffelkäfer (Leptinotarsa decemlineata SAY) im Frei-
          land. Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 4.
          141-145.

11. 1950: Die Verminderung der Gaswirkung von Hexa- und Ester-
          mitteln im Boden im Hinblick auf die direkte Bekämpfung
          der Wurzelreblaus. Der Weinbau, Wiss. Beihefte 4,
          Nr. 3. 90-95.

12. 1951: Die Wirkung von Hexa- und Estermitteln auf Reblauseier.
    Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 5,
    203-206.

13. 1952: Der jahreszeitliche Massenwechsel der Grünen
    Pfirsichblattlaus (Myzodes persicae SULZ.). Nach-
    richtenbl. Deutsch. Pflanzenschutzd. Berlin 6, 28-32.

14. 1952: Die San José-Schildlaus. Biolog. Zentralanstalt, Flugbl.
    Nr. 7, 22 Seiten. 2. Aufl. 1958.

15. 1953: Die Zwiebellaus, Rhopalomyzus ascalonicus (DONCASTER),
    Vorkommen in Deutschland und Lebensweise. Z.ang.Ent.35.
    187-196.

16. 1953: Noctuidae. In: Handbuch der Pflanzenkrankheiten, begr.
    von P. SORAUER, Bd. IV, 5. Aufl., 2. Lieferung,
    p. 367-413. Berlin und Hamburg (Verlag PAUL PAREY).

17. 1953: Die Gewächshausüberwinterung der Grünen Pfirsich-
    blattlaus. In: Querschnitt durch den neuen Gartenbau,
    herausg. von J. REINHOLD, Band 2, p. 275-285. Berlin
    (Deutscher Bauernverlag).

18. 1953: Die San José-Schildlaus. In: Querschnitt durch den
    neuen Gartenbau, herausg. von J.REINHOLD, Band 2,
    p. 286-300. Berlin (Deutscher Bauernverlag).

19. 1954: Quadraspidiotus schneideri BACHMANN (= marani ZAHRADNIK),
    eine der San José-Schildlaus ähnliche Deckelschildlaus.
    Nachrichtenbl. Deutsch.Pflanzenschutzd. Berlin 8,
    151-153. /Mit H. EISENSCHMIDT/.

20. 1954: Prognose des Massenauftretens von Blattläusen bei
    Berücksichtigung des Wirtswechsels. Nachrichtenbl.
    Deutsch. Pflanzenschutzd. Berlin 8, 206-209.

21. 1954: Holozyklie und Anholozyklie bei der Grünen Pfirsich-
    blattlaus, Myzodes persicae (SULZ.) Z.ang. Ent. 36,
    369-380.

22. 1954: Die Populationsdynamik der Grünen Pfirsichblattlaus
    Myzodes persicae (SULZ.) Wiss.Z.Univ.Rostock 3,
    Math.-naturw. Reihe Heft 5, 379-385.

23. 1954: Winterspritzung und Winterpflege der Obstkulturen.
    Biolog. Zentralanstalt, Flugbl. Nr. 19. 11 pp.

24. 1954: Die wichtigsten Blattlausarten in Landwirtschaft und
    Gartenbau. Biolog. Zentralanstalt, Flugbl. Nr.18. 26 pp.

25. 1955: Blattläuse. Die Neue BREHM-Bücherei, Heft 149, 144 pp.
    Wittenberg Lutherstadt (A. ZIEMSEN Verlag.).

26. 1955. Brachycaudus lucifugus n. sp., eine Wurzellaus am
    Spitzwegerich (Plantago lanceolata L.) Beitr. Ent.5,
    84-88.

27. 1955: Blattläuse in Mieten, Lagerraumen und Kellern. Nach-
    richtenbl. Deutsch. Pflanzenschutzd. Berlin 9, 81-86.

28. 1955: Beschädigungen in einer Wohnung durch Wespen. Anz.
    Schädlingsk. 28, 74-75. /Mit C. HOFMANN/.

29. 1955: Holozyklische Überwinterung von Myzus persicae (SULZ.)
    an Lycium halimifolium. Nachrichtenbl. Deutsch.
    Pflanzenschutzd. Berlin 9, 109-110.

30. 1955: Lipaphis erysimi (KALT.) ssp. alliariae n. ssp.
    (Homoptera, Aphididae), eine Blattlaus an Alliaria
    officinalis. Zool. Anz. 155, 190-195.

31. 1955/1956: Erstfunde und starkes Auftreten der Gallen von
    Gilletteella cooleyi (GILL.) in Mecklenburg. Arch.
    Freunde Naturg. Mecklenb. 2, 281-289./Mit J.KRUMBHOLZ/.

32. 1956: Zwei neue Blattlausarten aus Norddeutschland
    (Homoptera: Aphididae). Beitr. Ent. 6, 501-510.

33. 1957: Die Hauptwirte von Myzus persicae (SULZ.) und von
    Aphis fabae SCOP. Nachrichtenbl. Deutsch.Pflanzen-
    schutzd. Berlin 11, 21-26.

34. 1957: Die Futterpflanzen in der Blattlaus-Systematik
    (Hom., Aphididae). Ber. 100-Jahrfeier Deutsche Ent.
    Ges. 1956, p. 93-99 . Berlin (Akademie-Verlag).

35. 1958: Zwei weitere neue Blattlausarten aus Norddeutschland
    und ein neues Genus (Homoptera: Aphididae). Beitr.
    Ent. 8, 84-98.

36. 1958: Wirtswahlversuche mit Gynoparen von Myzus persicae
    (SULZ.) und Aphis fabae SCOP. Z. Pflanzenkrankh.65,
    405-411.

37. 1958: Some notes on the aphid fauna of South Africa.J.Ent.
    Soc. South Africa 21, 382-414./Mit S.E.SCHÖLL/.

38. 1958: Zur Biologie der Egel. Arch. Freunde Naturg.Mecklenb.
    4, 301.

39. 1958: Bionomische Rassen der Grünen Pfirsichblattlaus Myzus
    persicae (SULZ.) Arch. Freunde Naturg.Mecklenb. 4,
    200-233.

40. 1959: Die Männchen einiger Blattlausarten mit vorwiegend
    permanenter Parthenogenese. Deutsch. Ent.Z.6, 51-64.

41. 1959: Zwei neue Sitobion-Arten aus Südafrika (Homoptera: Aphididae). J.Ent. Soc. South Africa 22, 409-419.

42. 1960: Die Apfelgraslaus Rhopalosiphum insertum (WALK.) - ein bisher mit der Grünen Apfelblattlaus Aphis pomi DE GEER verwechselter Schädling. Nachrichtenbl.Deutsch. Pflanzenschutzd. 14, 74-79.

43. 1960: Auswirkungen des Dürresommers 1959 auf das Auftreten von Blattläusen. Mitteilungsbl. f.Insektenkunde, herausg. vom Kulturbund der DDR, Berlin, 4, Heft 2/3, 1960.

44. 1960: Die Wirtspflanzenwahl phytophager Insekten in Beziehung zur Artenbildung. Biolog. Ges. der DDR, Arbeitstagung zu Fragen der Evolution 1959 in Jena, p. 159-165. Jena (VEB GUSTAV FISCHER Verlag).

45. 1961: Die wissenschaftlichen Namen von wirtschaftlich wichtigen Blattlausen der Landwirtschaft und des Gartenbaues. Nachrichtenbl. Deutsch. Pflanzenschutzd. 15, 46-53.

46. 1961: Die Maisblattlaus erstmalig in Mitteleuropa. Die Deutsche Landwirtschaft 12, 181-182. /Mit G.FREITAG/.

47. 1961: Aphis spiraephaga n.sp., eine in Mitteleuropa häufig an Spiraea auftretende Blattlaus (Homoptera:Aphididae(. Beitr. Ent. 11, 414-425.

48. 1961: Über das Auftreten von Gynandern in Zuchten der Grünen Pfirsichblattlaus Myzus persicae (SULZ.) Z.ang. Ent. 48, 294-300.

49. 1961: Blattläuse an Mais. Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 15, 181-184.

50. 1961: Auftreten der Schwarzen Bohnenlaus an Mais. Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 15, 218.

51. 1961: Ergänzungen zur Blattlausfauna von Mitteleuropa. Mitt.Deutsch. Ent.Ges. 20, 69-70.

52. 1961: Der fakultative Wirtswechsel der Blattlause (Homoptera: Aphididae). Verh. XI. Internat. Kongr. Entomologie Wien 1960, Bd.II, 100-102.

53. 1961: Stabilität und Veränderlichkeit der Färbung bei Blattläusen. Arch. Freunde Naturg. Mecklenb. 7, 228-239.

54. 1961: Eine neue nichtwirtswechselnde Dysaphis-Art (Homoptera: Aphididae) an den Wurzeln von Valeriana officinalis. Arch. Freunde Naturg. Mecklenb. 7, 281-297.

55. 1962: Biotypen und Unterarten der "Erbsenlaus" Acyrthosiphon
    pisum (HARRIS). Z. Pflanzenkrankh. 69, 129-136.

56. 1962. Celochloral nach OSSIAN NILSSON, ein Einschlussmittel
    für die mikroskopische Untersuchung kleiner Arthropoden.
    Wiss.Z.Univ. Rostock 11, Math.-naturw. Reihe Heft 1,
    69-73.

57. 1962: Der Speisebohnenkäfer. Biolog. Zentralanstalt, Flugbl.
    Nr. 31, 14 pp.

58. 1962: Aphididae. In: South African Animal Life, Results of
    the Lund University Expedition in 1950-1951, Vol.9,
    p. 319-323. Stockholm.

59. 1963: Wybor roslin-zywicieli u niektórych szkodliwych gatunków
    mszyc. Biuletyn Inst. Ochrony Róslin 19, 19-35. Poznan.

60. 1964: Faunistische und ökologische Untersuchungen über
    Blattläuse im Naturschutzgebiet Ostufer der Müritz.
    (Homoptera, Aphididae). Faun. Abh. Mus. Tierk. Dresden 4,
    133-147.

61. 1964: Merkmale der in Mitteleuropa an Gramineen lebenden
    Blattläuse (Homoptera: Aphididae). Wiss. Z. Univ. Rostock
    13, Math.-naturw. Reihe Heft 2/3, 269-278.

62. 1965: Hyadaphis tataricae (AIZENBERG), ein neuer Schädling
    in Mitteleuropa an Lonicera tatarica L. und einigen
    anderen Lonicera-Ziersträuchern (Homoptera: Aphididae).
    Anz. Schädlingsk. 38, 69-72. /Mit H.J.BUHR/.

63. 1965: Blattläuse (Homoptera: Aphididae) von den Azoren und von
    Madeira. Boletim de Museu Municipal de Fuchal Nr. 19,
    Art. 76, p. 5-15.

64. 1965: Schutz pflanzlicher Vorräte. In: Phytopathologie und
    Pflanzenschutz, herausg. von M. KLINKOWSKI, E.MÜHLE
    und E. REINMUTH, Bd. I, p. 536-559. Berlin (Akademie-
    Verlag).

65. 1966: Geflügelte Blattläuse in Gelbschalen. Wiss.Z. Univ.
    Rostock 15, Math.-naturw. Reihe Heft 2, p.295-313.

66. 1966: Schädliche Blattläuse in den Tropen und Subtropen unter
    besonderer Berücksichtigung von Rassendifferenzierungen.
    Z. ang. Ent. 58, 76-82.

67. 1966: Formen des Wirtswechsels der Blattläuse.Forschungen u.
    Fortschritte 40, 353-357.

68. 1966. Zwei neue Blattlausarten (Homoptera: Aphididae) aus
    Mecklenburg. Arch. Freunde Naturg. Mecklenb. 12, 149-172.

69. 1957: Die Abteilung Angewandte Entomologie des Instituts für
Phytopathologie und Pflanzenschutz der Universitat
Rostock. Entomologische Forschungsstätten der Deutschen
Demokratischen Republik, IV. Entomologische Berichte
1957, p. 107-111.

70. 1958: Eine rote holozyklische Rasse von Metopolophium festucae
(THEOBALD 1917) (Homoptera: Aphididae). Z.ang Ent. 51,
131-141.

71. 1968: Ein Fund der Blattlaus Dysaphis (Pomaphis) gallica
(HILLE RIS LAMBERS 1955) in Mitteleuropa, mit Wirtswahl-
versuchen und Beschreibung des oviparen Weibchens. Ent.
Nachr. 12, 25-29.

72. 1958: Mszyce trafiajace do zoltych szalek. Instytut Ochrony
Roslin, Poznan, 49 pp.

73. 1958: Weitere Ergänzungen zur Blattlausfauna von Mitteleuropa
(Homoptera, Aphidina). Reichenbachia, Mus. Tierk.Dresden
2, Nr. 14, 101-106.

74. 1958: Eine neue Subspecies zu Therioaphis trifolii (MONELL
1882) (Homoptera, Aphidina). Reichenbachia, Mus. Tierk.
Dresden 10, Nr. 35, 261-265.

75. 1958: Zwei neue Aphiden aus dem Gebiet des Bezirkes Halle.
Beitr. Ent. 18, 625-640.

76. 1958: Beiträge zur Kenntnis der Blattlausfauna von Kuba.
Wiss. Z. Univ. Rostock 17, Math.naturw. Reihe Heft 4/5,
439-448. /Mit M. SEIDEL/.

77. 1968: Ein bemerkenswertes Massenauftreten von Myzus ascalonicus
DONCASTER (Homoptera: Aphididae) im Freiland. Arch.
Freunde Naturg. Mecklenb. 14, 44-55.

78. 1969: Ein besonderes ungeflügeltes vivipares Weibchen im
Adultenstadium als Überwinterungsmorphe bei Ovatomyzus
calaminthae (MACCHIATI 1885) (Homoptera: Aphididae).
Ent. Nachr. 13, 25-30.

79. 1969: Herstellung mikroskopischer Präparate und Sammeln von
kleinen Insekten. Entomologische Berichte 1969, p. 4-11.

80. 1969: Bastardierungsversuche zur Feststellung von Isolierungs-
mechanismen zwischen nahe verwandten Formen der Gattung
Myzus PASSERINI (Homoptera: Aphididae). Biol.Zentralbl.
88, 147-164.

81. 1969: Eine bionomische Rasse von Aphis nasturtii KALTENBACH,
welche die Kartoffel meidet. Arch. Pflanzenschutz 5,
179-188.

82. 1969: Kratkoe metoditscheskoe posobie po utschetu tlej na
         posalkach kartofelia. Nautschno-issledowatelskij insti-
         tut kartofelnowo chosjajstwa, Moskwa, 47 pp.

83. 1969: Eine neue, wirtswechselnde Unterart der Getreideblatt-
         laus Macrosiphum (Sitobion) avenae (F.). Wiss.Z.Univ.
         Rostock 18, Math.-naturw. Reihe Heft 3/4, 409-415.

84. 1969: Aphidina - Blattläuse, Aphiden. In: Exkursionsfauna von
         Deutschland, herausg. von E. STRESEMANN, Bd. II/2,
         p. 51-141. Berlin (Verlag Volk und Wissen). 2.Aufl.1974.

85. 1970: Zur Kenntnis der Schwarzen Bohnen- oder Rübenblattlaus
         vom Gesichtspunkt der Prognose und des Warndienstes.
         Nachrichtenbl. Deutsch. Pflanzenschutzd. Berlin 14, 96-100.

86. 1970: Zucht- und Übertragungsversuche mit Populationen und
         Klonen der Grünfleckigen Kartoffelblattlaus Aulacorthum
         solani (KALTENBACH, 1843) (Homoptera: Aphididae).
         Deutsch. Ent. Z. 17, 259-270.

87. 1970: Einschlussmittel für die Herstellung von mikroskopischen
         Präparaten. Amt für Erfindungs- und Patentwesen der DDR.
         Patentschrift 73577 (WP451) 134935. Ausgabetag: O5.VI.
         1970. 2 pp.

88. 1970: Blattlausbiologie, Faunistik und Evolution. Polskie
         Pismo Entomologiczne 40 (3(, 435-466.

89. 1970: Klucz de oznaczania mszyc (Homoptera: Aphididae)
         wystepujacych na graminae w Europie srodkowej. Instytut
         Ochrony Roslin, Poznan, 41 pp.

90. 1970: Was ist Aulacorthum prasinum BÖRNER 1950? Arch. Pflan-
         zenschutz 6, 487-497.

91. 1971: Isolationsmechanismen zwischen sympatrischen bionomischen
         Rassen am Beispiel der Erbsenblattlaus Acyrthosiphon
         pisum (HARRIS) (Homoptera, Aphididae). Zool. Jahrb.
         Syst. 98, 131-152.

92. 1971: Vorläufige Ergebnisse nach langjähriger zwangsweiser
         parthenogenetischer Dauerzuchthaltung von Aphiden.
         Beitr. Ent. 21, 165-178.

93. 1971: Bisher unbekannte Überwinterungsformen bei anholozyklischen
         Aphiden. Wiss, Z.Univ. Rostock 20, Math.-naturw.Reihe
         Heft 1, 91-95.

94. 1972: Eine neue, auf Hieracium lebende Art von Pleotrichopho-
         rus BÖRNER (Homoptera, Aphididae). Ann. Zool, Warszawa,
         29, Nr. 11, 349-359.

95. 1972: Beziehungen der Blattläuse des Formenkreises Acyrtho-
siphon pelargonii (KALTENBACH) zur Erdbeere. Tag.-Ber.
Akad. Landwirtsch.-Wiss. DDR, Nr. 121, p. 41-47.

96. 1972: Starkes Auftreten und Beschreibung der Fundatrix der
Blattlaus Hyadaphis tataricae (AIZENBERG). Ent. Nachr.
16, 105-109.

97. 1972: Eine nordamerikanische Blattlausart als neuer Bestandteil
der mitteleuropäischen Fauna. Wiss. Z.Univ. Rostock 21,
Math.-naturw. Reihe Heft 6/7, 697-700.

98. 1973: Übertragung des Enationenvirus der Erbse durch verschie-
dene Unterarten und Biotypen der Grünfleckigen Kartoffel-
blattlaus Aulacorthum solani (KALTENBACH). Zbl. Bakt.,
Abt. II, 128, 72-80. /Mit B.HINZ und F.W. MÖLLER/.

99. 1973: Defractosiphon rugosus n. sp. (Homoptera: Aphididae)
von Peucedanum officinale L. Mitt. Zool. Museum Berlin
49, 69-79.

100. 1973: Aphiden an Moosen (Homoptera, Aphididae). Entom Abh.
Mus. Tierk. Dresden 39, Nr. 3, 205-247.

101. 1973: Wirtspflanzen und Überwinterung eines an Erbse lebenden
Biotyps von Acyrthosiphon pisum (HARRIS) (Homoptera:
Aphididae). Deutsch. Ent. Z. 20, 321-328. /Mit M. L.
HUBERT-DAHL/.

102. 1973: Möglichkeiten der parthenogenetischen Überwinterung von
Aphiden unter den klimatischen Bedingungen des Bezirkes
Rostock. Wiss. Z. Univ. Rostock 22, Math.-naturw.Reihe
Heft 6/7, Teil II, 799-804. /Mit F.W.MÖLLER/.

103. 1973: Zur Morphologie von Blattläusen (Aphiden). Wiss.Z.Univ.
Rostock 22, Math.-naturw. Reihe Heft 6/7, Teil II,
805-813.

104. 1973: Zur Biologie der Getreideblattläuse. Wiss. Z.Univ.Rostock
22, Math.-naturw. Reihe Heft 10, 1185-1191.

105. 1974: Unterscheidungsmerkmale der Larvenstadien der Grünstrei-
figen Kartoffelblattlaus Macrosiphum euphorbiae (THOMAS)
und der Erbsenblattlaus Acyrthosiphon pisum (HARRIS). Arch.
Phytopathologie u. Pflanzenschutz 10, 197-209. /Mit U.
KABISCH und H. REIHER/.

106. 1974: Paraschizaphis typhae (Laing, 1923) und eine neue
Subspecies von Paraschizaphis scirpi (PASSERINI, 1874)
(Homoptera: Aphididae). Beitr. Ent. 24, 59-66.

107. 1974: DARWINS Entdeckung unter dem Gesichtspunkt der Mannig-
faltigkeit tierischer Organismen. Biol. Rundschau 12,
335-340.

108. 1974: Aphis oenotherae OESTLUND, 1887, Erstfunde in Europa
           und als potentieller Zierpflanzenschädling. Ent.Nachr.
           18, 129-133.

109. 1974: Die modernen Aufgaben der Faunistik für die angewandte
           Entomologie und die Biosphärenforschung. Fol. Ent. Hung.
           27 - Suppl., 15-28.

110. 1974: Versuche über das Ansiedelungsverhalten zweier Rassen
           der Blattlaus Acyrthosiphon pisum (HARRIS) auf Vicia
           faba L. Biol. Zentralbl. 93, 675-686. /Mit I.BERGER
           und A. HERRMANN/.

111. 1974: Häufige Vorratsschädlinge des Getreides. In: Phytopa-
           thologie und Pflanzenschutz, herausg. von M. KLINKOWSKI,
           E. MÜHLE, E. REINMUTH und H. BOCHOW, Bd.II, 2. Aufl.,
           p. 263-271. Berlin (Akademie-Verlag).

112. 1974: Blattläuse, Aphiden, im Feldbau. In: Phytopathologie
           und Pflanzenschutz, herausg. von M. KLINKOWSKI, E.MÜHLE,
           E. REINMUTH und H. BOCHOW, Bd.II, 2. Aufl., p. 70-84.
           Berlin (Akademie-Verlag).

113. 1975: Bestimmungsschlüssel für geflügelte Blattläuse in
           Gelbschalen. Arch. Phytopathol. u. Pflanzenschutz 11,
           49-77.

114. 1975: Untersuchungen zur Biologie von Aphis evonymi F.
           (Homoptera: Aphididae) im Freiland-Insektarium. Arch.
           Freunde Naturg. Mecklenb. 15, 90-99.

115. 1975: Weitere Ergänzungen und ökologische Untersuchungen zur
           Blattlausfauna von Mitteleuropa mit Beschreibungen bisher
           nicht bekannter Morphen. Faun. Abh. Mus. Tierk. Dresden
           5, Nr. 12, 265-287.

116. 1975: Incidence of the aphid Acyrthosiphon gossypii MORDVILKO
           on legumes and on cotton (Homoptera: Aphididae).
           Beitr. Ent. 15, 257-260.

117. 1975: Aphidologische Beobachtungen im Botanischen Garten der
           Universität Rostock. Wiss. Z. Univ. Rostock 24, Math.-
           naturw. Reihe Heft 6, 811-815.

118. 1976: Mszyce-szkodniki roslin. Warszawa (Panstwowe Wydaw-
           nictwo Naukowe). 119 pp.

119. 1976: Hosts and non-hosts in subspecies of Aulacorthum solani
           (KALTENBACH) and intraspecific hybridizations (Homoptera:
           Aphididae). Symp. Biol. Hung. 16, 187-190.

120. 1976: Faunistisch-ökologische Beobachtungen über Aphiden
           (Homoptera:Aphididae) im Küstenbereich des Bezirkes
           Rostock. Wiss. Z. WILHELM-PIECK-Univ.Rostock 25, Math.-
           naturw. Reihe Heft 3, 283-286.

121. 1976: Beitrag zur Kenntnis der Bionomie und Morphologie der
           Hanfblattlaus Phorodon cannabis PASSERINI, 1860
           (Homoptera: Aphididae). Beitr. Ent. 26, 455-463.
           /Mit E. KARL/.

122. 1976: Blattläuse an Gemüsepflanzen. In: Phytopathologie und
           Pflanzenschutz, herausg. von M. KLINKOWVSKI, E. MÜHLE,
           E. REINMUTH und H. BOCHOW, Bd. III, 2. Aufl., p.65-67.
           Berlin (Akademie-Verlag).

123. 1976: Schildläuse an Obstgewächsen. In: Phytopathologie und
           Pflanzenschutz, herausg. von M. KLINKOWSKI, E. MÜHLE,
           E. REINMUTH und H. BOCHOW, Bd. III, 2. Aufl., p.420-423.
           Berlin (Akademie-Verlag).

124. 1976: Blattläuse an Obstgewächsen. In: Phytopaghologie und
           Pflanzenschutz, herausg. von M. KLINKOWSKI, E. Mühle,
           E. REINMUTH und H. BOCHOW, Bd. III, 2. Aufl.,p. 423-425.
           Berlin (Akademie-Verlag).

125. 1977: Verbreitung und Biologie der submersen Blattlaus Aspi-
           daphium cuspidati STROYAN, 1955, und anderer Wasser-
           pflanzen-Aphiden. Verh. des Sechsten Int. Symp. über
           Entomofaunistik in Mitteleuropa Lunz 1975, p. 47-53.
           Den Haag (Verlag JUNK).

126. 1977: Vergleich einer tropischen mit einer mitteleuropäischen
           Population von Aphis craccivora KOCH (Homoptera: Aphi-
           didae). Deutsch. Ent. Z. 24, 251-260.

127. 1977: Polymorphismus, Wirtswechsel und genetische Divergenz
           bei Aphiden. Probleme der Taxonomie in der Zoologie.
           Vorträge aus der Sektion Spezielle Zoologie der Bio-
           logischen Gesellschaft der DDR anlässlich der 8.
           Generalversammlung 1976 in Dresden, p. 68-73. Leipzig.

128. 1977: A preliminary simplified key for the aphids hitherto
           recorded from the Democratic Republic of the Sudan.
           Wiss. Z. WILHELM-PIECK-Univ. Rostock 26, Math.-naturw.
           Reihe Heft 2, 245-249. /Mit EL TIGANI M. EL AMIN und
           KHALID MUDDATHIR/.

129. 1977: Report on an aphidological survey in the Democratic
           Republic of the Sudan. Agricultural Research Corporation,
           Wad Medani, D.R. Sudan, 17 pp.

130. 1977: Überwinterung und Fundatrix der Getreideblattlaus
           Macrosiphum (Sitobion) avenae (F.). Arch. Phytopathol.
           u. Pflanzenschutz 13, 347-353.

131. 1977: Morphen und Biologie von Paramyzus heraclei BÖRNER
           1933 (Homoptera, Aphididae). Reichenbachia, Mus.Tierk.
           Dresden 16, Nr. 25, 233-240.

132. 1977: Fortpflanzungsisolation einer Population der Schwarzen
           Bohnen- oder Rübenblattlaus Aphis fabae SCOPOLI bei
           Versuchen im Freiland-Insektarium. Arch. Freunde Naturg.
           Mecklenb. 17, 53-59.

133. 1978: Sympatrische autökologische Divergenz als Evolutions-
           faktor. Wiss. Z. WILHELM-PIECK-Univ. Rostock 27, Math.-
           naturw. Reihe, Heft 4, 467-472.

134. 1979: Quantitative und qualitative Veränderungen der Aphiden-
           fauna der DDR im intraspezifischen Bereich. VII. Inter-
           nationales Symposium über Entomofaunistik in Mittel-
           europa,Leningrad, 19.-24. September 1977, Verhandlungen
           S. 136-139.

135. 1979: Brachícaudus cardui lateralis (WALKER, 1848), Erstfund
           in Österreich und Generationenfolge (Homoptera, Aphidi-
           dae). Mitt. naturwiss. Ver. Steiermark, Graz, 109,
           309-316. /Mit A. HORATSCHEK/.

136. 1979: Eine gelbe Mutante der Schwarzen Blattlaus Aphis fabae
           cirsiiacanthoides SCOPOLI und Bastardierungsversuche.
           Biol. Zbl. 98, 449-457.

137. 1979: Advice for aphid flight monitoring methods in the
           Democratic Republic of the Sudan. Agricultural Research
           Corporation, Wad Medani, D. R. Sudan, 25 pp.

138. 1979: Morphologie und Biologie von Aulucorthum speyeri BORNER
           1939, Vergleich mit Aulacorthum watanabei (MIYAZAKI
           1971). Reichenbachia, Mus. Tierk. Dresden 17, Nr. 17,
           129-141.

139. 1980: Eine neue Protophis-Art von Sonchus aus dem Sudan.
           (Homoptera: Aphididae). Beitr. Ent 30-39. /Mit EL
           TIGANI M. EL AMIN/.

140. 1980: Ein roter Biotyp von Acyrthosiphon pisum (HARRIS) an
           Erbse. Beitr. Ent. 31, 1981.

141. 1980: Beschreibung der Fundatrix, des oviparen Weibchens und
           des Männchens von Aphis urticata GMELIN, mit Angaben
           über die Bionomie der Blattlaus. Arch. Freunde Naturg.
           Mecklenb. 18, 43-47.

142. 1980: Untersuchungen über Blattläuse (Homoptera: Aphididae)
           mecklenburgischer Hochmoore. Arch. Freunde Naturg.
           Mecklenb. 18, 31-41.

143. 1980: Wirtswechsel, Generationenfolge und reproduktive Isola-
           tion von Ovatus crataegarius (WALKER, 1850) und O.insi-
           tus (WALKER, 1849) (Homoptera: Aphididae). Deutsch.Ent.
           241-253. /Mit M.L. DAHL/.

144. 1980: Identification of the alatae of common and economically
           important aphids in the Democratic Republic of the Sudan.
           Wiss. Z. WILHELM-PIECK-Univ. Rostock, 28. Math.-naturw.
           Reihe, Heft 6, 609-614.

145. 1980: Ovatus cataegarius (WALKER, 1850) und O. insitus (WALKER,
           1849) als Modell für sympatrische Speziation ohne
           Inanspruchnahme von ökologischen Nischen. Deutsch.Ent.Z.
           27, 199-217.

146. 1980: Beitrag zur Kenntnis der Blattlausfauna Österreichs,
           speziell der Steiermark (Homoptera, Aphidina). Mitt.
           naturwiss. Ver. Steiermark, Graz, 110, 157-161. /Mit
           A.HORATSCHEK/.

147. 1980: Zur Taxonomie der Blattlaus Aphis veratri (WALKER,1852)
           Mitt.-naturwiss. Ver. Steiermark, Graz, 110, 163-170.
           /Mit A. HORATSCHEK/.

148. 1980: Wirtspflanzen, Generationenfolge und reproduktive Iso-
           lation infraspezifischer Formen von Acyrthosiphon pisum.
           Entomogolia experimentalis et applicata, Amsterdam, 18,
           145-157.

149. 1980: Moos-Blattläuse, Sammel- und Untersuchungsmethoden.
           Acta Musei Reginaehradensis Série A Supplementum 1980,
           Hradec Kralove, S. 73-74.

150. 1982: Das Problem Aphis fabae. Z.ang.Ent. 94, 432-446.

151. 1982: Sitobion paludum n.sp., mit Wirtswechsel von Vaccinium
           uliginosum zu Gramineen. Entom.Abh. Mus. Tierk. Dresden
           46, Nr. 5, 99-108.

152. 1983: Transmission of the pea enation mosaic virus by Acyrtho-
           siphon gossypii (Homoptera: Aphididae). Beitr. trop.
           Landwirtsch. Veterinärmed., Leipzig, 21, 73-77. /Mit
           B. HINZ und EL TIGANI M. EL AMIN/.

153. 1983: Untersuchungen über Blattläuse der Gruppe Acyrthosiphon
           pelargonii im Freiland-Insektarium.
           Zschr. angew. Zool. (West-Berlin) 70, 351-367.

154. 1983: Differential alarm pheromone response between strains
           of the aphid Acyrthosiphon pisum. Entomologia experi-
           mentalis et applicata, Amsterdam, 34, 347-348.

155. 1984: Aphidina - Blattläuse, Aphiden. In: Exkursionsfauna für
           die Gebiete der DDR und der BRD Bd. II/2 4. Aufl.,
           p. 51-141, Berlin, Volk u. Wissen Volkseig. Verlag.

156. 1980: Erstfund von Myzus varians DAVIDSON, 1912, in der DDR
           (Homoptera, Aphididae). Entom. Nachrichten, Dresden, 24,
           Nr. 12, 177-180.

157. 1984: Bindung an die Wirtspflanze oder an den Biotop bei
           Aphiden. Verh. SIEEC X. Budapest, 1983, S. 102-104.

158. 1984: Die Rolle des Lichtes bei dem Ansiedelungsverhalten
           zweier Rassen der Blattlaus Acyrthosiphon pisum (HAR-
           RIS) (Homoptera, Aphididae). Deutsch. Ent.Z., N.F. 31,
           Heft 4-5, 201-214.

159. 1984: Host alternation in Aphididae using perennial herbs as
           winter host. Aphidologists' Newsletter, Christchurch
           N.Z., 19, No. 2, p. 6.

160. 1984: Observations on occurrence and host plants of Cleth-
           robius comes (WALK). Aphidologists' Newsletter,
           Christchurch N.Z., 19, No. 2, p. 12.

161. 1984: Obituary Prof. V. MOERICKE. Aphidologists' Newsletter
           19, No. 2, p. 21.

162. 1985: Biotype formation and sympatric speciation in aphids.
           In: Evolution and Biosystematics of Aphids. Proceedings
           of the Internat. Aphidological Symp. at Jablonna 1981,
           pp. 135-154, Warszawa.

163. 1985: Genetic and evolutionary aspects of host choice in
           phytophagous insects, especially aphids. Biol.Zentralbl.,
           Leipzig, 104, 225-237.

164. 1985: Das Problem Acyrthosiphon pisum (Homoptera: Aphididae).
           Zschr. angew. Zool., West-Berlin, 72, Heft 3, 317-334.
           /Mit H. STEINER/.

165.   Further notes on Sudanese aphids inclusive the desciption
           of a new Brachyunguis (Homoptera: Aphididae). Deutsch.
           Ent. Z., N.F. 33, H. 1-2, S. 1-9. /Mit EL TIGANI M. EL
           AMIN/.

166. 1985: Biotype formation and sympatric speciation in aphids.
           (Homoptera: Aphididae). Entom. Gener. Stuttgart, 10,
           (3/4), 161-181.

167. 1986: Faunistisch-ökologische Untersuchungen über Aphiden im
           Kyffhäuser-Gebiet. Hercynia N.F.Leipzig 23, H.1,94-108.

168. 1986: The role of subspecies in aphids for affairs of applied
           entomology. Z.ang.Ent. 101, H. 3, 295-303.

169. 1986: Morphologische Unterschiede und Variation der Geflügel-
           ten im Formenkreis Aphis fabae (Homoptera:Aphididae).
           Beitr. Ent., Berlin, 36, Heft 2, 209-215. /Mit H.STEINER/.

170. ú986: Eine neue Aphis-Art von Astragalus cicer. Deutsch.Ent.
           Z., N.F. 33, H. 3-5, 129-135.

171. 1986: Beitrag zur vergleichenden Morphologie und Bionomie
          von Aphis evonymi F. (Homoptera: Aphididae).
          Deutsch. Ent.Z., N.F. 33, H. 3-5, 257-262. /Mit H.
          STEINER/.

172.   Im Druck: Urbanogene Ursachen für das Auftreten von
          Aphiden innerhalb und ausserhalb von Städten. Verh.
          XI. SIEEC.

173. 1987: Faunistisch-ökologische Untersuchungen über Aphiden
          im westlichen Erzgebirge und Vogtland. Faun. Abh. Mus.
          Tierk. Dresden 14, Nr. 8, 105-129.

174. 1986: Unterordnung Aphidina - Blattläuse, Aphiden. In:
          Exkursionsfauna für die Gebiete der DDR und der BRD
          Bd. 2/2, 5. Aufl., p. 87-167, Berlin, Verlag Volk u.
          Wissen.

175. 1987: Die Arten der Gattung Aphis L. an Dipsacaceae.
          (Insecta, Homoptera, Aphididae).   Entom Abh. Mus.
          Tierk. Dresden 51, Nr. 2, 17-24.

176. 1988. Was ist Brachycaudus semisubterraneus BÖRNER? (Homop-
          tera, Aphididae). Deutsch. Ent. Z. Berlin, N.F. 35,
          H. 4-5, 249-255. /Mit H. STEINER/.

177. 1988: Occurrence of the aphid Rhodobium porosum in Central
          Europe (Homoptera, Aphidina, Apihidae). Entomol.Gener.,
          Stuttgart 13 (3/4), 255-260. /Mit H. STEINER/.

178. 1988: Simpatric and allopatric variation in aphids. Zool.
          Jb. Syst. Ökol., Jena, 115, 129-142.

179. 1987: Einfluss von Biotop und Biotopveränderungen auf die
          Aphidenfauna (Homoptera, Aphididae) im Küstenstreifen
          der DDR. Wiss. Z. WILHELM-PIECK-Univ. Rostock 26, Math.-
          naturw. Reihe, H. 2, 81-83.

180. 1989: Ausbreitung der Pflanze Telekia speciosa und der
          Blattlaus Uroleucon telekiae (HOLM.). Beitr. Ent.
          Berlin 39, 169-173. /Mit H. STEINER/.

181. 1989: Holozyklie und Anholozyklie bei der Schwarzen Rüben-
          oder Bohnenblattlaus Aphis fabae SCOP., im Vergleich
          mit anderen Aphididae. Beitr. Ent., Berlin 39, 163-168.
          /Mit I. JENNERJAHN/.

182. 1988: Flugverhalten und Aktivitäten geflügelter Aphiden
          speziell im Ostseeraum. Arch. Freunde Naturg. Mecklen-
          burg, Rostock, 27, 1-9.

183. 1988: Bestimmungsschlüssel Unterordnung Aphidina - Blattläuse,
          Aphiden. In: Exkursionsfauna für die Gebiete der DDR
          der BRD, Bd. 2/2, 6, Aufl., S. 87-167. Verlag Volk u.
          Wissen, Berlin

184. 1988: Revision of Börner's black Naumburg Aphis species
          (Homoptera: Aphidinea: Aphididae). Entom. Gener.,
          Stuttgart 13 (3/4), 263-268.

185. Im Druck: Zwei wenig bekannte Macrosiphum-Arten (Homop-
          tera: Aphididae). Deutsch. Ent. Z., Berlin

186. Im Druck: Aphis armata HAUSMANN, 1802, ein Doppelgänger
          der Schwarzen Rüben- oder Bohnenblattlaus Aphis fa-
          bae SCOP. (Insecta, Homoptera, Aphididae).
          Reichenbachia, Mus. Tierk. Dresden 27 (1). /Mit
          HANNA STEINER/.

187. Im Druck: Mutual influences between aphids on a joint host
          plant. Beitr. Ent. /Mit HANNA STEINER/.

188. Im Druck: Eindringen und Ausbreitung der Lupinenblattlaus
          Macrosiphum albifrons Essig in Mitteleuropa.
          Arch Phytopathol. Pflanzenschutz. /Mit H. STEINER
          und H. DUBNIK/.

189. Im Druck: Is there a kind of allelopathy between aphids
          feeding on the same host plant. Aphidologists'
          Newsletter.

190. Im Druck: Vermehrtes und verstärktes Auftreten von Blatt-
          läusen innerhalb und ausserhalb von Stadten durch
          urbanogene Ursachen. Arch. Freunde Natur.

191. Im Druck: Vortragsanmeldung zum III. Internetionalen
          Symposium in Ungarn: Conjectural evolution of
          aphids on Pteridophyta.

192. Im Druck: Vortragsanmeldung zum III. Internetionalen
          Symposium in Ungarn: Overlooked members of the
          Black Bean and Beet aphid complex.
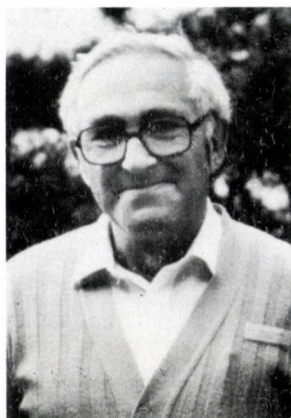
IN MEMORY OF Dr. ALBERT PINTERA

(4 April 1929 - 30 June 1989)

Albert Pintera was born in Bratislava, Czechoslovakia in 1929. His mother died when he was only a few months old and he was brought up and received his early education from his grandparents. In 1938 his father had to leave Slovakia and he took his son with him to Prague where Albert spent the next two years in an orphanage. He then spent 5 years in Bučovice, Moravia with his uncle. In 1945 he returned to Prague where he received education in a gymnasium until 1948 when he enrolled in the Faculty of Education of Charles University. His interest in biology caused him to quickly transfer to the Biological Faculty from which he graduated in 1952.

His first employment /1952-68) was with the Department of
Phytopathology of the Biological Institute of the Czechoslovak
Academy of Sciences, Prague, where he mainly worked on the role
of aphids as vectors of plant viruses. From 1968 until his death
he worked in the Institute of Entomology of the Czechoslovak
Academy of Sciences, also in Prague. His main research interest
was always the biology and taxonomy of aphids, especially tree
dwelling aphids - Callaphidids, Chaitophorids and Lachnids. In
addition he made significant contributions to the Bulgarian,
Hungarian and Romanian aphid faunas. In 1978/79 he spent 18
months in Cuba at the Botanical Institute of the Cuban Academy
of Sciences. During this and several subsequent shorter visits
he worked on the leaf cutter ant, Atta insularis, and Psyllids.

His other great interest was cats. He was a very active
member of the Central Committee of the Union of Cat Breeders
and the Czechoslovakian representative in the International Cat
Jury. In the latter capacity he used his taxonomical skill to
judge feline quality at many international cat shows. This
interest culminated in his book "Cats, tomcats and kittens",
which was published only 10 days before his death.

With his death we have lost a keen aphidologist who made
highly significant contributions to both aphid faunistics and
taxonomy. More importantly we have lost a modest colleague who was
both cooperative and helpful, and above all a good friend.

Publications of Dr. Albert Pintera (entomology)

1. 1952. The aphids on rice. Fol. Zool. Ent. 2: 73-74.
(in Czech, summary in Russian)

2. 1952. Hoplocallis ruperti gen. n. sp. n., a new aphid
on oak. Folia Zool. Ent. 3: 151-157 (in Czech,
summary in English).

3. 1954. The woolly apple aphid. Vesmír 33, 2: 66-7 (in Czech).

4. 1955. Aphids of the family Callaphididae in Czechoslovakia.
Čas. Nár. musea, odd. přírod., 124: 202-230.

5. 1956. Aphids sg. Tuberculaphis Börner new for Slovakia.
Acta Faun. Ent. Mus. Nat. Pragae 1: 39-42.

6. 1957. The aphids on Seseli. Acta Soc. Ent. Čechoslov.
54: 379-384 (in Czech, summary in German).

7. 1957. A monograph of the European species of the subfamily
Therioaphidinae. Acta Soc.ent. Čechoslov.
53: 115-142. (in. Czech, summary in German).

8. 1957. The influence of feeding either only during the day
or the night on the development of parthenogenetic
aphids. Biologie 6: 457-461 (in Czech, summary in
German and Russian).

9. 1957. The causes of the development of alate and apterous
forms of the aphids. Rozpravy ČSAV 67: 1-46.
(in Czech, summary in German).

10. 1959. (Pintera A., Ulrychová M.): Der Einfluss der
Wirtspflanzenwuchsphase auf die Entwicklung der
Blattlausart Myzodes persicae (Sulz). The Ontogeny
of Insects: 333-338.

11. 1959. Faunistic contribution to the knowledge of Bulgarian
aphids (Hom., Aphid.). Acta Soc.ent.Čechoslov.
56: 69-80.

12. 1962. Die Wurzelläuse der Gramineen mit besonderer
Berücksichtigung der Anoecia corni F. Schriftenreihe
der Karl-Marx-Univ. Leipzig. 8: 85-89.

13. 1962. (Pintera A., Szalay Marzsó L.): Neuere Angaben zur
           Kenntnis der Blattlausfauna Ungarns (Aphidoidea).
           Acta Zool. Acad. Sci. Hung.: 127-133.

14. 1962. (Pintera A., Čech M., Blattný C.): Symptoms of the
           growth asymetry by aphids and their relaticon to the
           presence of virus particles, ascertained by means
           of electron microscopy. Plant virology, Proc. 5th
           Conf. Czechoslov. plant virologists, Prague, 296-298.

15. 1965. New aphid species from Pannonian region (Homoptera).
           Acta Entomol. Bohemoslov. 62: 283-286.

16. 1965. Two new species of Lachnidae in collection of the
           British Museum (Hemiptera, Aphidoidea). Entomologist
           98: 60-63.

17. 1965. The effect of various substances on the development
           of aphids. Proc. XII. Int. Congr. Ent., London 1964.
           546.

18. 1966. Revizision of the genus Cinara Curt. (Aphidoidea,
           Lachnidae) in Middle Europe. Acta Entomol. Bohemoslov.
           63: 281-321.

19. 1966. Physiological regularities of the bionomy of aphids
           and their economical importance. Studijni informace
           UVTI Základní a pom. vědy v zemedelství 76 pp.
           (in Czech, summary in German and English).

20. 1968. Aphids from the subtribe Schizolachnina (Aphidoidea,
           Lachninae) in Middle Europe. Acta Entomol. Bohemoslov.
           65: 100-111.

21. 1969. Über die Verbreitung der Gattunk Chaitophorus Koch
           (Aphidoidea, Aphidae). Abh. Ber. Naturkundemus.
           Görlitz, 44: 207-209.

22. 1969. Evaluation of some recent classification systems in
           aphidology (Homoptera). Acta Entomol. Bohemoslov.
           66: 122-124.

23. 1970. A new species of the genus Aphidura Hille Ris Lambers
           (Homoptera, Aphidoidea) from Bulgaria. Acta Entomol.
           Bohemoslov 67: 241-244.

24. 1971. Some observations on mealy plum aphid, Hyalopterus
           pruni Geoffr.,occuring on reed. Hidrobiologia (Bucu-
           resti) 12: 293-295.

25. 1973. Seasonal dynamics of the mealy plum aphid population
           on reed at the Opatoviczký pond (1968-1971) Czech.
           IBP (PT-PP Report no. 3, Třeboň)1973: 231-232.

26. 1976. Selección de especies de árboles maderables para
    plantaciones y cortinas rompevientos, desde el punto
    de vista de las posibilidades de propagación de plagas
    de insectos. Baracoa 4: 53-56.

27. 1977. (Holman J., Pintera A.): Enumeratio insectorum Bohemo-
    sloveniae (Aphidoidea). Acta Faun. Entom. Mus. Nat.
    Pragae 15 (suppl. 4) 101-116.

28. 1981. (Holman J., Pintera A.): Übersicht der Blattläuse der
    Rumänischen Sozialistischen Republik. Studie ČSAV
    15: 125 pp.

29. 1983. Europäische und paläarktische Verbretung einiger an
    Salix lebenden Chaitophorus-Arten (Homoptera, Aphido-
    idea). Verh. SIEEC X. Budapest, pp. 115-118.

30. 1984. Aphids of the tribes Therioaphidina and Saltusaphidina
    and their relation to the host plants. Práce Slov.
    ent. spol. SAV, Bratislava 4: 153-158.

31. 1986. The spreading of aphid species in the past and at the
    present. Živa 5: 182-183 (in Czech).

32. 1987. Ecological and taxonomical relationship of some
    palearctic species of the genus Chaitophorus.In Holman
    et al. (eds): Popul. Structure, Genetics and Taxonomy
    of Aphids and Thysanoptera. Int. Symposium Smolenice,
    1985: 389-390.

33. 1987. (Pintera A., V. Lapáček): Aphids on the Orchids.
    Živa 6: 221.

34. 1988. Taxonomic revision of the species of genus Chaitophorus
    Koch in Palearctic (Homoptera, Aphidoidea) Dtsch. Ent.
    Z. N. F. 34 (4-5): 219-340.

35. in press:

    - Aphids of the tribe Thripsaphidini in Middle Europe.
      Acta Univ. Carolinae, Praha.

EVOLUTIONARY ASPECTS OF PARTHENOGENETIC
REPRODUCTION IN APHIDS

A.F.G. Dixon,
School of Biological Sciences, University of East Anglia,
Norwich, NR4 7TJ, U.K.

ABSTRACT

The ancestors of aphids possibly evolved parthenogenesis
over 200 million years ago. Since then further increases in
reproductive potential have been achieved by the telescoping of
generations and the development of alary polymorphism. As a
consequence, the virginoparae of many modern aphids have
prodigious rates of increase.

The objective of this paper is to identify the factors that
have constrained the evolutionary development of the
reproductive potential in aphids and to discuss how the
telescoping of generations and alary polymorphism may be seen as
ways of overcoming developmental and physiological constraints.
In addition, a possible ecological reason will be offered for
the absence of alary polymorphism in the virginoparae of many
genera and species of Drepanosiphinae.

INTRODUCTION

Most aphid species reproduce both asexually and sexually,
with several generations of parthenogenesis between each period
of sexual reproduction. This is known as cyclical partheno-
genesis. As it is common to all the Aphidoidea it is likely to
have developed early in the history of the group, before the
three families, Adelgidae, Aphididae and Phylloxeridae evolved
200 million years ago. It seems likely that continuous

parthenogenesis evolved first from sexual reproduction, and the
sexual/parthenogenetic cycle evolved subsequently. Whether
parthenogenesis was initially automictic or apomictic is not
easily deduced. Automixis is a common phenonenon in many animal
species (White, 1973), but is thought to confer lower fitness
than sexuality in most situations (Templeton, 1982; Uyenoyama,
1984). Cuellar (1977) favours an accumulation of genetic
modifiers causing endomitosis and apomixis as the likely
scenario. The two-fold reproductive advantage that follows from
producing only female offspring was followed by the telescoping
of generations and alary polymorphism that resulted in even
higher rates of increase.

This paper will consider the possible adaptive significance
of parthenogenetic reproduction for aphids and then review the
factors that have constrained further increase in their
reproductive potential.

ADAPTIVE SIGNIFICANCE OF PARTHENOGENETIC REPRODUCTION

Parthenogenesis is relatively rare in both plants and
animals (Maynard Smith 1984) and predominates in climax
situations (disclimax) that are maintained by disturbance, i.e.,
by drought, fire, flooding, glaciation or grazing, which tend
temporarily to denude an area of its animals and plants
(Cuellar, 1977), or more specifically for aphids, it is claimed
they exploit ephemeral, fluctuating and wholly unstable habitats
(Clarke, 1973). The high rate of increase of parthenogens and
the ability of an individual to establish a colony gives them a
considerable advantage over sexual species when colonizng such
habitats. The idea that parthenogenesis is associated with the
colonisation of temporarily denuded or ephemeral habitats is
based mainly on studies of earthworms, flies, grasshoppers,
isopods, lizards, plants and weevils (Jaenike & Selander, 1979;
Cuellar, 1977). What evidence is there that aphids generally
exploit habitats that are often devoid of aphids or contain
aphids at levels well below the carrying capacity?

Taylor & Taylor's (1979) maps of the aerial densities of

various species of aphids indicate that there are dramatic
seasonal and year-to-year changes in the spatial distribution of
aphids. These maps are highly suggestive of a continually
shifting mosaic of relatively under-utilized habitats.
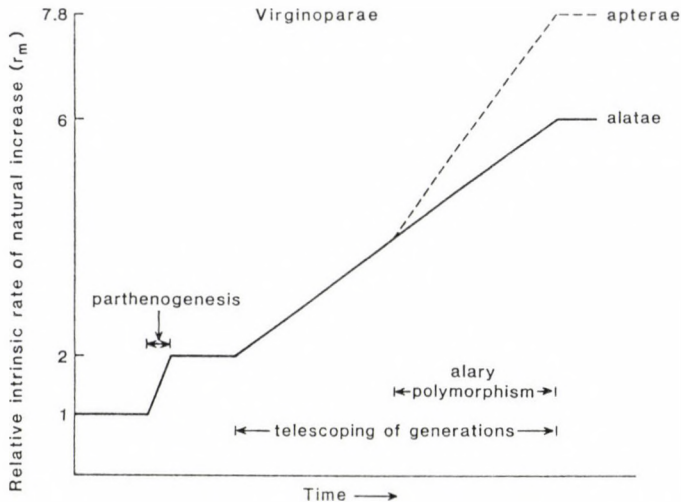
Fig. 1.The relative increase in the intrinsic rate of natural
        increase that accompanied the evolution of partheno-
        genesis, telescoping of generations and alary
        polymorphism in aphids.

Taxonomists have also noted that aphid species often disappear
from an area or remain at very low densities for long periods
(Eastop, 1978). Similarly, studies of aphid populations have
revealed that plants frequently lack aphids or are infested at
low levels. In addition, egg mortality is high and few of the
aphids that hatch from the eggs reach maturity. Thus at egg
hatch most host plants are lightly infested or devoid of
aphids. The leaves of sycamore (Acer pseudoplatanus), for
example, can support more than 100 sycamore aphids and yet at
bud burst there can be fewer than one per leaf, and there is a
very short period in which conditions remain favourable for
reproduction. This applies to all aphids, whether they live on
herbaceous plants, shrubs or trees. Thus the very high rate of

increase associated with parthenogenesis (Fig. 1) is likely to be of considerable advantage in such ephemeral habitats (Dixon, 1987.

TELESCOPING OF GENERATIONS

The life cycle of most animal and plant species is divided into two parts. In the first the growth and development of the body is of primaryimportance, while the second is devoted to reproduction., i.e. they have what is called a bang-bang repro- ductive strategy. A theoretical explanation of this strategy for univoltine organisms based on the optimal allocation of energy between growth and reproduction in order to maximise their rate of increase has been proposedby Cohen (1971), King & Roughgarden (1982) and Ziolko & Kozlowski (1983). A similar approach was used by Sibly & Calow (1986) for organisms with overlapping generations.
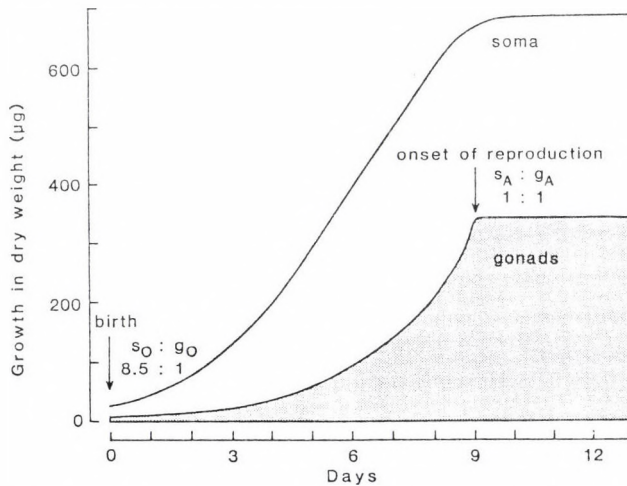
Fig. 2.The growth of the gonads and soma from birth, to shortly after the onset of reproduction in apterae of Megoura viciae.

However, many plants and animals have another strategy. They continue to grow after breeding is initiated (e.g. some fish and molluscs). Sibly & Calow (1986) show that this

intermediate strategy is a consequence of the slopes of the
relationships between both fecundity and mortality rate, and the
fraction of energy devoted to growth. Parthenogenetic aphids
show a third type of strategy, which is a combination of the
previous two. They invest in both somatic and gonadal growth
during their larval development with soma growing logistically
and the gonads exponentially (Brough et al., 1990) (Fig. 2).
At birth aphids already have embryos developing in their gonads
and their most advanced embryos have also started to develop
gonads (Fig. 3). This telescoping of generations is charac-
teristic of aphids. That is, throughout larval development
aphids simultaneously invest in growth of soma and gonads such
that on becoming adult, most aphids are ready to give birth,
i.e., they do not indulge in a bang-bang reproductive strategy.
What favours the simultaneous commitment to growth and reproduc-
tion during larval development?
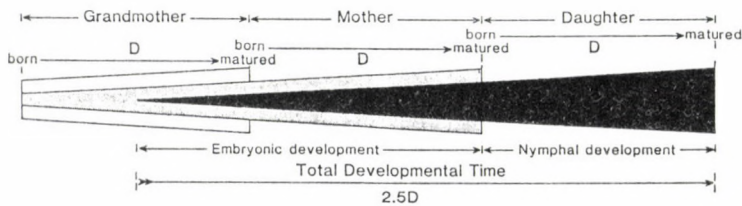
Fig. 3.Diagrammatic representation of the telescoping of
generations, with each individual starting its
development inside its grandmother. (D = the time from
birth to the onset of reproduction).

If there is no constraint on the relative growth rate of the
gonads, then the best strategy is a bang-bang one (Sibly &
Calow, 1986). Kindlmann & Dixon (1989) argue for a constraint on
the relative growth rate of the gonads. Fecundity is the
conversion of gonadal tissue into offspring containing their own
gonads. Gonads are crucial for the future, while soma only
assimilates and then dies. The best strategy for maximising
growth rate is to use all the energy gained from the soma to

keep the gonadal growth rate maximal. After moulting to the
adult stage aphids usually do not grow any more and all the
energy assimilated is utilised for reproduction. Thus there
must be an optimal somatic (s_A) to gonadal (g_A) ratio for an
adult. If the ratio were bigger, there would be a surplus of
energy as the gonads would be unable to utilise all of the
energy (because of the constraint on the growth of the gonads,
R) and the soma has ceased to grow. If the ratio were smaller,
then there would be insufficient energy to ensure the maximum
rate of growth of the gonads (R). Therefore, either energy
would be wasted or gonadal growth rate would be submaximal
during the adult stage if s_A/g_A is not optimal.

An embryo is unlikely to develop faster if it consisted of
only soma, as the assimilation of nutrients occurs over the
whole body surface (Brough & Dixon, 1989a). Therefore, the
prenatal developmental time (i.e. the period from ovulation to
birth) is unlikely to be affected by the size of the gonads of
the embryo. The size of an egg at ovulation can be denoted by
m_E and of an aphid at birth by $m_O = s_O + g_O$. Then, if the maximum
rateof growth of the gonads, R, applies to both eggs and embryos
and $m_E e^{RD} < m_O$, then an egg cannot achieve the size m_O during the
larval development (period equal to D) of its mother, even if
ovulated at the time of its mother's birth. That is, it cannot
grow quicker than at the rate R. Thus, all the embryos would
have to complete their development after their mother
became adult, this would lead to further increase in size of the
mother's gonads during adulthood and break the optimal balance
between s_A/g_A. Therefore, it would be advantageous if
ovulation occurred T time units before a mother's birth, where T
satisfies $m_E e^{R(D+T)} = m_O$. Then a mother can give birth just
after reaching maturity. After birth of offspring the mother's
gonads are smaller, the optimal balance between s_A/g_A is broken
and there is now surplus energy to support further exponential
growth of the gonads, allowing maturation of other embryos and
ovulation. Thus the incorporation of a constraint on the rate
of growth of the gonads makes telescoping of generations

advantageous.

What evidence is there for such a constraint? Under congenial conditions aphids generally take approximately a week to develop from birth to maturity. In contrast many other insects take approximately 3 weeks. However, if one takes into consideration that an aphid starts developing inside its grandmother, then the actual development time is 2.5 times longer than it takes an aphid to develop from birth to maturity, i.e., approximately 3 weeks (Fig. 3). Therefore, there appears to be a minimum 'time' required for development, which for the convenience of modelling can also be framed in terms of growth.

Iteroparity versus semelparity

Some aphids like the emigrants and sexuparae of Pemphiginae are semelparous. Instead of staggering the development of their embryos their development is synchronized and they are born together. For example, the migrants and sexuparae of Eriosoma ulmi (L) give birth to 26 and 5 offspring in 17 and 10 minutes, respectively, and then die within a few minutes of giving birth (Parker, 1976). This implies that factors other than the optimal utilization of energy have been important in shaping the reproductive strategies of these species. Time available to exploit a resource (Walters et al., 1984) and a high risk of adult mortality before larviposition is complete could be two such factors.

Most aphids, however, produce their offspring singly (iteroparous), rather than in clutches (semelparous). This can be explained in terms of the advantage of keeping the gonads approximately the same size throughoutearly adult life. Maximum gonad size (g_A) is achieved at the instant of reproductive maturity and s_A remains constant throughout adult life. This quantity of soma provides enough energy to cover the respiration costs of a body of size s_A+g_A and the Rg_A needed for the growth of the gonads. However if there is a constraint on the gonadal growth rate, R, then on giving birth gonad size decreases to g where $g<g_A$ and only requires sufficient energy to support Rg

where $Rg < Rg_A$. Thus a certain amount of energy is unused until the gonads reach the size g_A again (Fig.4). Therefore, it is advantageous to keep the size of the gonads as close to g_A as possible in order to use most of the energy assimilated by the soma. This is achieved by the anterior germaria ovulating first and ovulation occurring over a prolonged period so that there are big differences in the developmental status of embryos both within and between ovarioles (Brough & Dixon, 1989b). In this way aphids are able to produce offspring continuously and maintain the size of their gonads close to g_A.
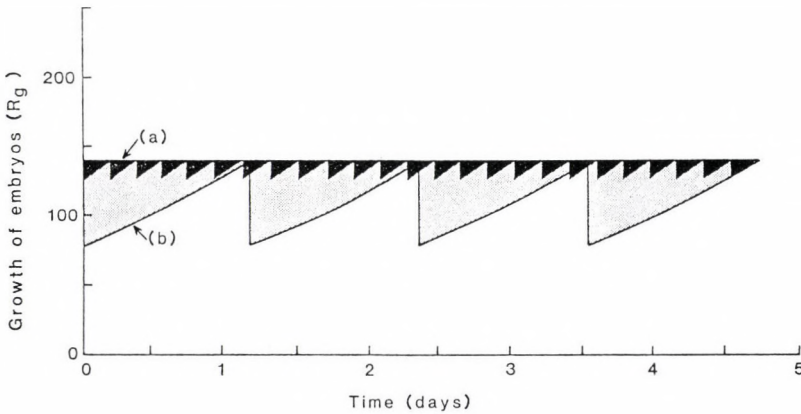
Fig. 4. The energy needed for the growth of embryos in time, Rg, when the offspring are produced (a) individually; n = 1, and (b) in clutches; n = 5. The size of gonads, g, declines instantaneously by n (s_O + g_O), whenever a clutch of n embryos is born. Then it grows as dg/dt = Rg, until size g_A is reached, when a new clutch of n embryos is born. Hatched areas represent the energy wasted when the size of the gonads is less than maximum.

That the optimal s_A/g_A ratio may be similar for all aphids is revealed by the relationship between the dry weight of the gonads and total dry weight for 10 species of aphid (Fig 5). The size of the gonads, in apterae at least, appears to be physiologically limited as their size is directly proportional to adult weight (i.e. W^1) (c.f. Sibly & Calow, 1986, p119). Thus all the apterous aphids so far studied are apparently

subject to similar physiological and developmental constraints.
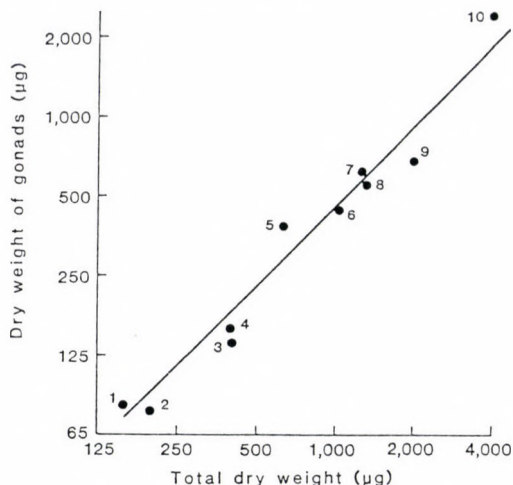
Fig. 5. The dry weight of the gonads in relation to the total dry
weight for the apterous morph of ten species of aphids:
1. Aphis fabae; 2. Sitobion avenae; 3. Amphorophora
tuberculata; 4. Metopolophium dirhodum; 5. Acyrtho-
siphon pisum; 6. Megoura viciae; 7. Macrosiphum
albifrons; 8. Uroleucon cirsii; 9. Tuberolachnus
salignus; 10. Stomaphis quercus.

The telescoping of generations was accompanied by very
extensive structural and physiological changes in the gonads. The
most striking differences between virginoparous and oviparous
aphids is that in the former the germaria are smaller, start
ovulating earlier and appear to play a smaller trophic role in
the early development of the oocytes. Vitello genesis and
chorionogenesis of one or occasionally two eggs per thick-
walled ovariole dominates the later development in oviparae,
whereas it is the embryogenesis of up to eight embryos per
thin-walled ovariole in virginoparae.

Parthenogenesis has enabled aphids to start developing
at ovulation, and more importantly inside immature, or even
embryonic mothers. Then given that there is a constraint on the
rate of growth (development) there are greater advantages in
terms of fitness in telescoping generations than in indulging in

a bang-bang reproductive strategy. A rough estimate of the order of increase in fitness measured in terms of the intrinsic rate of increase (r_m) can be obtained by comparing the rate of increase of aphids with that achieved by nine species of bisexual polyvoltine beetles of the family Ptinidae, which are approximately the same size as aphids (Andrewartha & Birch, 1954). Telescoping of generations gives aphids approximately a further 3-fold reproductive advantage (Fig. 1).

ALARY POLYMORPHISM : COST OF DISPERSAL

It is generally assumed that the lower rate of increase of alatae can be attributed to the cost in resources in developing and maintaining flight muscles (Dixon & Howard, 1986; Coffelt & Jones, 1989; Kieckhefer & Elliot, 1989). However, there is evidence to support the suggestion that hormonal changes necessary for the development of the flight apparatus reduce the rate of ovulation and embryogenesis.
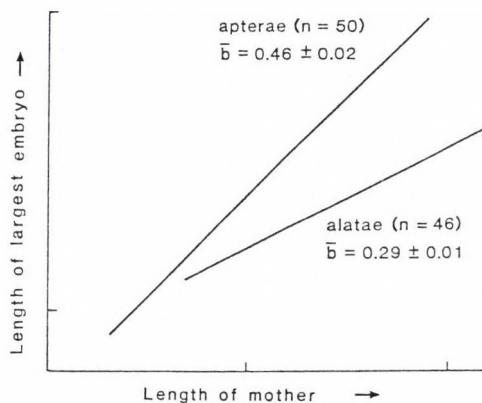
Fig. 6. The length of the largest embryo in the gonads of apterous and alate aphids in relation to the length of the parent aphid (After Tashev & Markova, 1983)

The switch to alate development in polymorphic species occurs early and affects not only an aphid's morphology but also its reproductive physiology (Fig. 6). Resources are diverted from developing the gonads to developing the flight apparatus. After dispersal there is a reallocation of resources enabling

alatae of polymorphic species to achieve reproductive rates
comparable to apterae (Newton & Dixon, 1990).   Nevertheless,
overall the production of alatae is costly both in terms of
extended development and a reduction in fecundity, which is
reflected in their lower intrinsic rate of increase.   Apterae
appear to have a 1.3-fold reproductive advantage over alatae
(Fig. 1).

In retaining functional wing muscles throughout adult
life, virginoparous Drepanosiphinae incur a continuing cost in
terms of reproduction - relatively small gonads and a low
reproductive rate.   The apparently low energy intake of
macropterous <u>Drepanosiphum dixoni</u> H.R.L. compared with
brachypterae and the observation that the mean relative growth
rate of alatae is lower than that of apterae of the same species
feeding on the same plant tissues argues very strongly for a
physiological constraint on the utilization of energy by alatae.
This constraint is associated with the development and
maintenance of the flight apparatus, which possibly requires a
lower level of juvenile hormone than is necessary for maximum
growth of the gonads (Dixon, 1990a).

Evolution of alary polymorphism

As in all species of aphids at least one morph is apterous
it appears they have all evolved a genetic control mechanism for
apterousness.   Thus, in view of the cost of alateness the
complete absence of apterous virginoparae in many species of
Drepanosiphinae is at first puzzling.   Roff (1984) has claimed
that alateness is of selective advantage to insects living in
highly unstable environments where continuous dispersal is
imperative for survival and Waloff (1983) that it is
advantageous in those species of aphids that exploit markedly
three-dimensional habitats like trees.

Among the Drepanosiphinae there are a few species, like <u>D.</u>
<u>dixoni</u> and <u>Myzocallis myricae</u> (Kalt.), which have a brachyp-
terous morph and could be seen as in the first stage in the
evolution of apterousness.   The niches occupied by both these

species are relatively uncommon as they prefer to infest plants
growing in special conditions and the aphids themselves are
uncommon. The best strategy in such circumstances would be to
exploit patches and only leave them when intraspecific
competition becomes intense, i.e., to switch between apterous-
ness and alateness. However, if a species is very common, then
intraspecific competition and natural enemy inflicted mortality
could become a regular and important feature of their lives. In
these circumstances to retain alateness in all asexual genera-
tions would give them an advantage as they would be better able
to avoid competition and natural enemies. The commoness of an
aphid may be determined by the abundance of its host plant, as
when a host plant is abundant and widely distributed its aphid
incurs lower costs in moving between host plants (Dixon, 1990b;
Dixon & Kindlmann, 1990). Many of the Drepanosiphinae live
on abundant and widely distributed species of trees.

In certain circumstances the possession of wings could be
a severe handicap. Such a situation would be the confined space
of a gall. In addition, once a resource such as a gall is
induced, it is advantageous to exploit it before moving else-
where, which is the observed pattern: one or more apterous
generations followed by a winged generation.

CONCLUSION

It is likely that parthenogenesis in the Aphidoidea
evolved because it conferred a considerable advantage in the
colonization and exploitation of the ephemeral and largely
unexploited habitats occupied by these insects. A partheno-
genetic individual can both initiate a colony and, because of
its high rate of increase, rapidly exploit a temporary resource.

Further increase in asexual reproductive potential was
achieved by overcoming developmental and physiological
constraints. The developmental constraint was overcome by the
evolution of the telescoping of generations and the physio-
logical constraint by the evolution of apterousness. It is

likely that the development of parthenogenesis gave aphids a 2-fold, the telescoping of generations a 3-fold and apterousness a further 1.3-fold reproductive advantage, or overall a staggering 7.8-fold reproductive advantage over comparable sized bisexual egg-laying insects.

Although apterousness offers a significant way of increasing the reproductive potential, not all aphids have evolved alary polymorphism in the asexual generations. For those species of aphids that are frequently abundant, intraspecific competition and natural enemy inflicted mortality are possible regular and important features of their lives. In these circumstances, to retain alateness would put them at an advantage as they would be better able to avoid competition and natural enemies. On the other hand, uncommoness and/or galling could have favoured the evolution of alary polymorphism in virginoparae.

ACKNOWLEDGEMENTS

REFERENCES

Andrewartha, H.G. & Birch, L.C. (1954): The distribution and abundance of animals. University of Chicago Press, 782 pp.

Brough, C.N. & Dixon, A.F.G. (1989a): Follicular sheath (ovarian sheath) structure in virginoparae of the vetch aphid, *Megoura viciae* Bucton. (Homoptera : Aphididae). Int. J. Insect Morphol. & Entomol. **18**.

Brough, C.N. & Dixon, A.F.G. (1989b): Reproductive investment and the inter-ovariole differences in embryo development and size in virginoparae of the vetch aphid, Megoura viciae Buckton. Entomol. exp. appl., **52**.

Brough, C.N., Dixon, A.F.G. & Kindlmann, P. (1990): Pattern of growth of somatic and gonadal tissues in parthenogenetic vetch aphids, *Megoura viciae* Buckton.

Clarke, W.C. (1973): The ecological implications of parthenogenesis. In: A.D. Lowe (Editor) <u>Perspectives in Aphid Biology</u>. Ent. Society of New Zealand Bull. No. 2 pp 103-113.

Coffelt, M.A. & Jones, J.A. (1989): Bionomics of *Hyadaphis tataricae* (Homoptera : Aphididae). Environ. Ent., **18**. 46-50.

Cohen, D. (1971): Maximising final yield when growth is limited by time or by limiting resources. J. Theor. Biol., **33**. 299-307.

Cuellar, O. (1977:) Animal parthenogenesis. Science, **197**. 837-843.

Dixon, A.F.G. (1987): Evolution and adaptive significance of cyclical parthenogenesis in aphids. In: A.K. Minks & P. Harrewijn (Editors) <u>Aphids Their Biology, Natural Enemies and Control 2A</u>. Elsevier, Amsterdam. pp 289-297.

Dixon, A.F.G. (1990a): Physiological constraint imposed by alateness on the rate of pathenogenetic reproduction in aphids. Adv. Invert. Reprod., **5**.

Dixon, A.F.G. (1990b): Population dynamics and abundance of deciduous tree-dwelling aphids. [In] <u>Population Dynamics of Forest Insects</u>. Eds. N. Kidd, S. Leather & A. Watt, Intercept.

Dixon, A.F.G. & Howard, M.T. (1986): Dispersal in aphids, a problem in resource allocation. In: Danthanarayana, W. (Editor) <u>Insect Flight : Dispersal and Migration</u>. Springer, Berlin. pp 145-151.

Dixon, A.F.G. & Kindlmann, P. (1990): Role of plant abundance in determining the abundance of herbivorous insects.

Eastop, V.F. (1978): Diversity of Sternorrhyncha within major climatic zones. In: L.A. Mound & N. Waloff (Editors), <u>Diversity of Insect Faunas</u>. Symp. Roy. Ent. Soc. Lond,. **9**, 71-78.

Jaenike, J. & Selander, R.K. (1979): Evolution and ecology of parthenogenesis in earthworms. Amer. Zool., **19**. 729-737.

Kieckhefer, R.W. & Elliot, N.C. (1989): Effect of fluctuating temperatures on development of immature Russian wheat aphid (Homoptera : Aphididae) and demographic statistics. J. Econ. Ent., **82**. 119-122.

Kindlmann, P. & Dixon, A.F.G. (1989): Developmental constraints in the evolution of reproductive strategies : telescoping of generations in parthenogenetic aphids. Funct. Ecol., (In press)

King, D. & Roughgarden, J. (1982): Multiple switches between regulation and reproductive growth in annual plants. Theor. Pop. Biol., **21**. 194-204.

Maynard-Smith, J. (1984): The ecology of sex. In: J.R. Krebs & N.B. Davies (Editors) Behavioural Ecology : An Evolutionary Approach. Blackwell, Oxford. pp 201-221.

Newton, C.A. & Dixon, A.F.G. (1990): Embryonic growth rate and birth weight of the offspring of apterous and alate aphids : a cost of dispersal. Entomol. exp. appl.

Parker, N.J.B. (1976): Biology and bionomics in Scotland, of *Anthocoris gallarumulmi* De G. and its two principal prey species *Eriosoma ulmi* (L.) and *Eriosoma patchae* Borner & Blunck, and their inter-relationships. PhD Thesis, University of Glasgow. 516 pp.

Roff, D.A. (1984): The cost of being able to fly : a study of wing poymorphism in two species of crickets. Oceologia (Berl.), **63**. 30-37.

Sibly, R.M. & Calow, P. (1986): Physiological Ecology of Animals. An evolutionary approach. Blackwells Scientific Publications, Oxford.
179 pp.

Tashev, D. & Markover, E. (1983): Morphofunctional basis of aphid fecundity (Aphidina, viviopara). V. Growth of the biggest embryo. Ann. Univ. Sofia 'Kliment Ohridski' Fac. Biol. (Zool.), **72/73**. 23-38.

Taylor, R.A.J. & Taylor, L.R. (1979): A behavioural model for the evolution of spatial dynamics. In: R.M. Anderson, B.D. Turner, & L.R. Taylor (Editors), Population Dynamics. Blackwell, Oxford. pp 1-27.

Templeton, A.R. (1982): The process of parthenogenesis. In: H. Dingle & P. Hegman (Editors), Evolution and Genetics of Life Histories. Springer, Hamburg. pp 75-101.

Uyenoyama, M.K. (1984): On the evolution of parthenogenesis : a genetic representation of the "cost of meiosis". Evolution, **38**. 87-102.

Waloff, N. (1983): Absence of wing polymorphism in the arboreal, phytophagous species of some taxa of temperate Hemiptera : an hypothesis. Ecol. Ent., **8**. 228-232.

Walters, K.F.A., Dixon, A.F.G. & Eagles, G. (1984): Non feeding by adult gynoparae of *Rhopalosiphum padi* and its bearing on the limiting resource in the production of sexual females in host alternating aphids. Entomol. exp. appl., **36**. 9-12.

White, M.J.D. (1973): _Animal Cytology and Evolution_. 3rd ed.
   Cambridge Univ. Press, Cambridge.

Ziolko, M. & Kozlowski, J.(1983): Evolution of body size : an
   optimisation model. Math. Biosci., **64,** 127-143.

BIENNIAL GALLS OF THE APHID ASTEGOPTERYX STYRACI

ON A TEMPERATE DECIDUOUS TREE, STYRAX OBASSIA

Shigeyuki Aoki and Utako Kurosu,

Laboratory of Biology, College of General Education, Rissho
University, Magechi 1700, Kumagaya, 360-01 Japan, and Laboratory
of Applied Entomology, Faculty of Agriculture, Tokyo Noko
University, Fuchu, Tokyo, 183 Japan

ABSTRACT

The cerataphidine Astegopteryx styraci Matsumura forms large,
coral-like galls on a temperate deciduous tree, Styrax obassia,
and produces many 2nd-instar soldiers there. It was found that
its galls are biennial. The fundatrix appears in May and causes
a small, closed gall on a shoot (twig-to-be) of the storax. The
gall grows a little before the onset of winter and may have an
ostiole or two, but no alates are produced. Apterae, larvae and
soldiers overwinter within the gall. The overwintered gall be-
gins growing again in April. The gall reaches its full size in
summer, and alate sexuparae are produced from August of the
second year onward.

INTRODUCTION

Most insect galls are annual. Although galls on evergreen
trees caused by a mite (Eriophyes pini on Pinus silvestris and P.
montana: Mani 1964, Darlington 1968) or by a subtropical aphid

(Ceratoglyphina bambusae on Styrax suberifolia: Kurosu & Aoki   in
prep.)   last for more than one year, it would seem unlikely   that
galls   on   a   temperate deciduous tree, whose   growth   ceases   in
winter, last and grow for more than one year.   Here, we report an
exceptional   case   of the aphid Astegopteryx   styraci   Matsumura,
which   causes biennial galls on a temperate deciduous   tree,   the
big-leaf storax Styrax obassia.

The monoecious, cerataphidine aphid Astegopteryx styraci forms
irregular, coral-like galls on Styrax obassia in Japan (see   Fig.
1 in Aoki & Kurosu 1989).   A mature gall on a lignified, 2nd-year
twig reaches up to 9.5 cm in diameter and sometimes contains more
than 15,000 aphids.   The species produces many 2nd-instar sterile
soldiers, which not only defend their gall but also keep it clean
by using their heads to push out cast-off skins, dead aphids   and
honey globules through the ostioles (Aoki & Kurosu 1989).

Since   the base of a mature gall of A. styraci is on an   over-
wintered,   lignified twig, we first erroneously thought that   the
aphid   transforms   a   winter bud into the gall in   early   spring.
However, just after bud burst of S. obassia, we found some   galls
which   already   had   ostioles and contained a   number   of   aphids
including apterous adults but no living fundatrix.   This   finding
led   us   to suspect that these galls might have been   formed   the
previous year; and in May, 1986, we eventually found a   fundatrix
of   A. styraci forming its incipient gall on a shoot of S.   obas-
sia.   How   the gall of this species is formed and   developed   is
described in this paper.

MATERIALS AND METHODS

Incipient galls of A. styraci were collected from 5 trees of S. obassia at the Shômaru Pass (36°N, ca. 600 m alt.), Honshu, Japan, between 1986 and 1989. Since the gall density was not very high, only a small number of galls needed for the study were collected. Most of them were located at considerable heights, so they were cut off with scissors attached to a bamboo pole. Some galls found at observable heights were marked and their development was followed. Galls collected were submerged in 80% alcohol immediately and later were dissected under a dissecting microscope. Before the dissection, the height and diameter of each gall were measured, and whether it had ostioles or not was recorded. The aphids in each gall were counted; and, when necessary, mounted and examined under a differential interference microscope to identify the morphs in the galls.

THE HOST TREE STYRAX OBASSIA

The big-leaf storax Styrax obassia is a deciduous tree. Its winter buds sprout in mid April and its leaves fall off by December at the Shômaru Pass. Its buds (except terminal ones on developing shoots) are intrapetiolar: i.e., when they are formed, they are completely hidden in the bases of petioles (Shidei & Saito 1978). So it seems difficult for A. styraci to utilize newly-formed buds of S. obassia for gall formation as Ceratovacuna nekoashi transforms exposed ones of Styrax japonica into galls (Kurosu & Aoki in press).

GALL FORMATION PROCESS

The number and date of collection, the size and the number of inhabitants for 23 successful 0-year-old galls are summarized in Table 1. The following description of the gall-formation process is mainly based on information about these galls.

1. Gall initiation

We found 2 yet unclosed incipient galls (nos. 86251 & 86010) each containing a 1st-instar fundatrix on May 9 and 23, 1986. The galls were formed on young shoots. Gall 86010 was collected immediately, while gall 86251 was marked for further observation. The latter was found completely closed on May 23, and collected on September 20 (see Table 1). Another incipient but already closed gall with a 1st-instar fundatrix was found on May 9 (no. 86007).

The shape of these unclosed incipient galls shows that, when the 1st-instar fundatrix settles on a shoot (twig-to-be), the surrounding parts grow and soon cover the fundatrix completely. The surface of this incipient swelling is densely covered with whitish pubescence, and this part later becomes the "navel" of the gall (see Fig. 1).

2. Growth of galls in the first year

The fundatrix becomes adult and begins larviposition from July (Galls 88035, 88037a & 88037b). She may not survive to autumn because living fundatrices were not found in galls collected after August (Table 1). The gall grows slightly as the fundatrix produces her progeny (Table 1). In the autumn, some galls (e.g.

Table 1   Size, the presence or absence of ostioles, and the
number of inhabitants for 0-year-old galls of A. styraci.

Gall #	Date of collection	Open or closed?	Diameter x height (mm)	Fundatrix	No. of other aphids
86007	May 9	closed	?	1st instar	0
86010	May 23	unclosed	2.0 x ?	1st instar	0
88035	Jul 2	closed	6.0 x 5.0	adult	2
88037a	Jul 2	closed	5.0 x 3.0	adult	1
88037b	Jul 2	closed	5.5 x 4.0	adult	2
88040	Jul 14	closed	4.5 x 3.5	adult	3
88041	Jul 14	closed	4.5 x 5.0	adult	6
88042a	Jul 14	closed	6.0 x 5.0	adult	4
88042b	Jul 14	closed	7.0 x 4.5	adult	7
88046	Aug 4	closed	5.0 x 4.5	unfound	6
88047	Aug 4	closed	6.0 x 4.0	unfound	10
88061a	Sep 10	open	8.0 x 4.5	unfound	68*
88061b	Sep 10	open	10.0 x 5.0	unfound	106*
86251	Sep 20	closed	4.0 x 5.0	unfound	30
88081	Oct 22	open	5.5 x 3.5	unfound	35
88082	Oct 22	open	5.5 x 4.0	unfound	37
89006	Mar 3	open	7.5 x 6.0	unfound	75
87006	Mar 30	closed	5.5 x 6.0	dead	107
89011	Apr 3	open	7.0 x 4.0	unfound	37
89014	Apr 3	closed	4.0 x 5.0	unfound	42
89017	Apr 10	open	7.5 x 6.5	unfound	145
89023	Apr 17	open	12.5 x 7.0	unfound	182
89026	Apr 28	open	22.0 x 13.0	unfound	346

First 2 figures of the gall number indicate the year of
collection.
* Twelve soldiers appeared from these neighboring 2 galls
at the time of collection, and it is not clear which gall
they belonged to.

88061a, 88061b) open, while others (e.g. 86251) remain closed.
An ostiole or two appear on some galls. However, no alates are
produced; no alatoid (wingpadded) larvae were found in 1st-year
galls.   Second-instar soldiers are also produced in autumn, but
they are smaller than those produced in mature, 2nd-year galls
(they will be treated in a separate paper).   When the aphids in a
1st-year gall stop growing and reproducing is not clear.   Galls
88081 and 88082 collected on October 22 contained some aphids
that had the next instar cuticle developing inside, suggesting
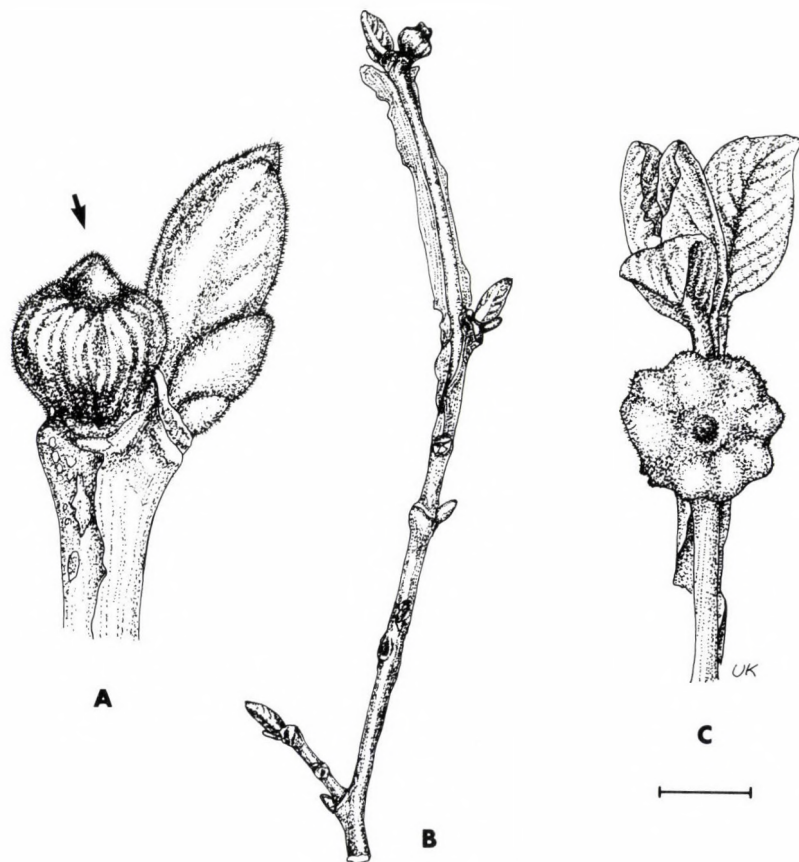
Fig. 1. Immature galls of <u>Astegopteryx</u> <u>styraci</u>. A, B: an overwintering gall (no. 87006 on March 30); arrow indicates the "navel." C: an overwintered, expanding gall (no. 89023 on April 17). Scale: 2.5 mm for A, 15 mm for B and 7.5 mm for C.

that the colonies were still growing.

3. Overwintering galls

First-year galls overwinter. They become brownish green and are covered with pubescence, so that they look like winter buds (Fig. 1A, B). The 2 galls collected in March (nos. 89006 &

87006) contained apterous adults, larvae of various instars and
soldiers, but no alatoid larvae or alates. No aphid that had the
next instar cuticle developing inside was found among them.
Therefore, aphids of various stages can hibernate in this
species. On March 3, 1989, we found a hibernating gall (no.
89001) with an ostiole and marked it with string for further
observation. When we were marking the gall, an aphid emerged
sluggishly through the ostiole. This aphid was collected and was
found to be 1st instar.

4. Growth of overwintered galls

In the following spring, the overwintered gall begins to grow
again. One of 2 galls collected on April 3 (no. 89011) contained
an aphid that had the next instar cuticle developing inside, and
a gall collected on April 10 (no. 89017) contained several such
aphids; the aphids began growing and reproducing again. At the
time when leaves of S. obassia unfold, the lateral parts around
the "navel" expand as in Fig. 1C; these newly expanded parts are
of a fresh green color. As the gall grows further, it becomes
irregular in shape and looks like coral, and a number of ostioles
appear at the tips of projections. By the mid summer the color
of the gall becomes yellow. Alate sexuparae appear from August
on, and fly to leaves of S. obassia where sexuales are produced
(Aoki & Kurosu 1989).

The marked, overwintered gall 89001 increased in size as fol-
lows: its diameter in mm was 6, 7, 9, 12, 21, 52, 59 and 79 on
March 3, April 3, 10, 17, 28, May 15, 17 and June 26,

respectively.

DISCUSSION

Thus, Astegopteryx styraci is biennial. It produces sexuales once in 2 years. From a 7-year (1983 - 1989) study at the Shômaru Pass, we had the impression that 2nd-year galls of A. styraci were apparently more common in odd years than in even years; we were able to find only a few 2nd-year galls in 1984, 1986 and 1988. The reason for this is now clear. However, it is premature to conclude that no gene flow occurs between odd- and even-year generations, because it remains to be investigated whether all the eggs deposited in autumn hatch in May of the following year; their diapause might last for more than one year for some eggs. Instances of such prolonged diapause are reviewed by Tauber et al. (1986).

It is also interesting to know how this biennial life cycle evolved. Our hypothesis is as follows: 1) The ancestor of A. styraci was annual, and at the end of each season it used to produce alates from its annual gall. 2) Some aphids remained in the gall without becoming alates and overwintered, and they pro-duced their progeny in the second year. At this transitional stage, alates were produced in the autumn of both the first and second years. Then, 3) the production of alates in the first year ceased. Although this hypothesis is admittedly speculative, we hope that it will stimulate the search for those relatives of A. styraci whose life cycles are indicative of its ancestor's life cycle.

In connection with this hypothesis, it may be worth noting

here   that we found 6 living aphids (2 apterous adults,   4   non-

alatoid larvae including a 1st-instar larva) in a large old   gall

on April 3, 1989. The gall had undoubtedly been initiated in

May, 1987; it was almost lignified and only a small area of its

basal interior remained greenish, to which the 6 aphids were at-

tached.   Such hibernation may have happened in galls of the sup-

posed annual ancestor of A. styraci.

REFERENCES

Aoki, S. & Kurosu, U., (1989) Soldiers of Astegopteryx styraci
    (Homoptera, Aphidoidea) clean their gall. Jpn. J. Ent. 57:
    407-416.

Darlington, A., (1968) The Pocket Encyclopaedia of Plant Galls in
    Colour. Blandford Press, London. 191 pp.

Kurosu, U. & Aoki, S., (in press) Formation of a "cat's-paw" gall
    by the aphid Ceratovacuna nekoashi (Homoptera). Jpn. J. Ent.

Mani, M. S., (1964) Ecology of Plant Galls. Dr. W. Junk, Publ.,
    The Hague. 434 pp.

Shidei, T. & Saito, S., (1978) [Illustrations of Deciduous
    Broadleaf Trees in Japan.] Kyôritsu Shuppan, Tokyo. 375 pp.
    (In Japanese.)

Tauber, M. J., Tauber, C. A. & Masaki, S., (1986) Seasonal
    Adaptations of Insects. Oxford Univ. Press, Oxford. 411 pp.

NOTES ON THE BIOLOGY AND ECOLOGY OF *DIPHYLLAPHIS MORDVILKOI* (AIZENBERG),

THE OAK WOOLLY APHID, IN CENTRAL ITALY

A. Binazzi and P.F. Roversi,

Instituto Sperimentale per la Zoologia Agraria Ministero

Agricoltura e Foreste, Via Lanciola 12/A, Cascine del Riccio,

50125 Florence, Italy

ABSTRACT

Diphyllaphis mordvilkoi (Aizenberg), the oak woolly aphid (OWA),

was first found in central Italy (Tuscany) in 1985. It was collected

from *Quercus pubescens* and *Q. cerris*. OWA is an holocyclic autoecious

species whose morphs are wingless and live on the lower surfaces of

leaves of oaks. In Tuscany, the overwintering eggs are laid beginning

the middle of November and hatch in early summer. The fundatrix

generations appear in the first half of July and are succeeded by 4-6

generations of parthenogenetic viviparous females. In midsummer, the

OWA colonies become smaller, and individuals can survive in diapause.

Sexuales appear in the middle of November, and eggs are laid until the

beginning of December. OWA colonies cause a yellowing and reddening of

infested oak leaves.

INTRODUCTION

All morphs of *Diphyllaphis mordvilkoi* (Aizenberg), the oak woolly

aphid (OWA), cover their bodies with copious white, waxy secretions that

appear to be woolly. OWA was discovered in 1932 in Caucasus at Ashe

near the eastern coast of the Black Sea. Later, it was found in Spain,
Turkey, and Sicily. In central Italy, it was first found in 1985 in
Tuscany. In 1988 it was found in Liguria in northern Italy. In these
regions, OWA was collected from *Quercus pubescens* and *Q. cerris*. OWA is
an holocyclic autoecious species whose morphs are wingless and live on
the lower surfaces of leaves of oaks.

BIOLOGY AND ECOLOGY

In Tuscany, the overwintering eggs are laid in the middle of
November and hatch in early summer so that they are the longest occuring
stage during the year. The fundatrix generation develops from the
fertilized, overwintered eggs after the time of bud burst of the oaks.
In recent years, generally at the end of July, numerous colonies of OWA
have been observed near Florence in a selected oak stand either on
leaves of seedlings or on leaves of coppice shoots and sometimes on
young plants and saplings. The crowded, showy colonies of OWA normally
live on the lower surfaces of leaves in cooler, protected areas, often
near the soil and sheltered from direct sunlight. When colonies occur
in leaves exposed to sunshine, they live protected inside caterpillar-
rolled leaves or in otherwise deformed leaves. By the end of July, OWA
colonies cause a yellowing and reddening of the infested leaves which
become noticeable even at a distance. In August, the colonies become
smaller and are usually found on small seedlings in the more sheltered
areas near the soil. In midsummer, several individuals were observed in
diapause and were more or less concealed under a dense waxy-thread
network in crevices of the bark on the trunk on the shady side of trees
near the ground. In September, OWA colonies were observed again on
either the young plants or the seedlings. From the beginning of

October to the middle of November, a few OWA colonies were found mainly on still green leaves of small seedlings near the soil. The sequence of 4-6 parthenogenetic generations of fundatrigeniae ends around the middle of November when sexuales, males and oviparous females, appear. After fertilization, the oviparous females lay their eggs from the end of the same month until the middle of December. The life cycle of the OWA is summarized in Fig. 1. The overwintering eggs are laid singly more or less concealed either in the same feeding sites of the oviparous females, i.e., the lower surfaces of leaves near the edge and veins, or in crevices of the bark of young plants and saplings where the oviparous females had previously aestivated. The eggs, orange-yellowish first, then blackish, are covered by bright-white, short and mostly bent, waxy sticks untidily arranged over their surface. The eggs are about 0.45 mm long and their width is about half that length. Scanning electron micrographs of the waxy sticks found on the eggs show that the latter have rhomboid cross-sections and are provided lengthwise with several
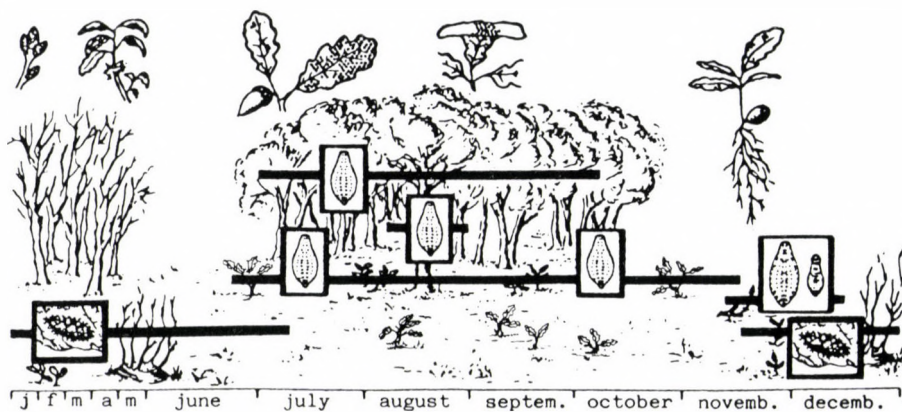
Fig. 1. Life cycle of *Diphyllaphis mordvilkoi*, the oak woolly aphid.

canaliculi inside and with numerous slightly marked grooves outside. This waxy covering of the eggs probably aims at giving them during a long period (since the beginning of winter until the beginning of the following summer) an adequate protection as regards mainly the degree of relative humidity and temperature.

CONCLUSION

OWA is an uncommon species in the natural oak stands of several south-European countries and Pontus. Nevertheless, when present, its colonies are very showy also at a distance because of their white woolly wax covering as well as the yellowing and reddening of the infested oak leaves. OWA colonies, moreover, prefer very cool feeding sites, associated probably with the environmental mesophilous requirements of their host plants, or however, with not high degree of continentality. If the OWA is able to spread over other suitable territories, it will become a new pest in oak stands, mainly to young plants and seedlings.

REFERENCES

Aizenberg, E. (1932): A new species of Aphididae of Caucasus (*Stegophylla mordvilkoi* sp.n.). Bull. Stat. Biol. Bolchevo, **5-6**. 75-80.

Barbagallo, S. & Stroyan, H.L.G. (1982): Biological, ecological and taxonomic notes on the aphid fauna of Sicily. Frustula Entomologica, N.S., 3(16). 1-182.

Binazzi, A. & Roversi, P.F. (1988): Il *Diphyllaphis mordvilkoi* (Aizenberg) in Toscana (Homoptera Aphidoidea Callaphididae). Redia, **81**(1). 201-211.

RESISTANCE OF ENDOPHYTE-INFECTED PLANTS OF TALL FESCUE AND PERENNIAL RYEGRASS TO DIURAPHIS NOXIA (MORDVILKO)

S.L. Clement[1], K.S. Pike[2], W.J. Kaiser[1] and A.D. Wilson[1]

[1]Agricultural Research Service, U.S. Department of Agriculture, Washington State University, Pullman, Washington 99164-6402, and [2]Department of Entomology, Washington State University, Prosser, Washington 99350, U.S.A.

ABSTRACT

Fewer aphids of Diuraphis noxia were found on tall fescue and perennial ryegrass plants harboring systemic fungal endophytes than on endophyte-free plants in laboratory tests. These results indicate that enhanced resistance in some perennial grasses to D. noxia is associated with the presence of endophytic fungi.

INTRODUCTION

Fungal endophytes occur intercellularly in the leaf and stem tissues of grasses and sedges (Diehl, 1950). Some endophytes (tribe Balansiae, family Clavicipitaceae) protect grasses from grazing cattle and sheep by producing poisonous chemicals. Moreover, recent work has shown that interactions between some grasses and their insect herbivores are mediated by endophytic fungi (Clay, 1988). Among aphid species, Rhopalosiphum padi

---

This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use by the U.S. Department of Agriculture.

(L.) and Schizaphis graminum (Rondani) (Homoptera:Aphididae) have been shown to be adversely affected by the principal tall fescue (Festuca arundinaceae Schreb.) endophyte, Acremonium coenophialum Morgan-Jones and Gams (Johnson et al., 1985; Latch et al., 1985).

A new and very serious threat to wheat and barley in the United States is the Russian wheat aphid, Diuraphis noxia (Mordvilko) (Homoptera: Aphididae), or 'barley aphid' as it is called in some parts of the world (Stoetzel, 1987). This laboratory study was undertaken to investigate whether or not endophyte-infected plants of tall fescue and perennial ryegrass (Lolium perenne L.) are resistant to D. noxia. In carrying out this study, we also provide new information on the role played by endo-phytes in protecting grasses against insect attack.

MATERIALS AND METHODS

Aphids used in tests (conducted October 1988-June 1989) were from colonies established from aphids collected in a commercial barley field near Prosser, Washington (Prosser colony), and in a Hordeum spp. germplasm nursery, Pullman, Washington (Pullman colony), in the summer of 1988. Each laboratory colony was maintained on barley ('Steptoe') and all tests were conducted in environmental chambers maintained at 22 $\pm$ 1°C with a photoperiod of 14:10 (L:D).

Seed of perennial ryegrass and tall fescue was obtained from R.E. Welty (Agricultural Research Service, U.S. Department of Agriculture, Oregon State University, Corvallis, Oregon, U.S.A.) and Jacklin Seed Co. (Post Falls, Idaho, U.S.A.). Assessments of endophyte presence in seed and leaf sheaths of individual plants were made microscopically using methods described by Welty et al. (1986a,b). Plants used in tests were

examined for endophytes when they were 7-9 weeks old.

Tests 1-4.   Aphids were exposed to tall fescue ('Arid') or
perennial ryegrass ('Repell') seedlings grown from endophyte-infected
and endophyte-free seed (Table 1).   For each test, alternating rows of
seedlings from two seed lots (seedlings grown from infected and non-
infected seed) of tall fescue or perennial ryegrass were established in
a greenhouse flat (25 X 33.8 cm) filled with a standard soil mix to 7 cm.
Ten rows of 10 seedlings or eight rows of 16 seedlings were established
with uniform spacing.   When seedlings were 12-14 days old (4-10 cm tall),
barley leaves heavily infested with aphids were placed between rows to
allow aphids to crawl to seedlings.   The Prosser colony supplied aphids for
tests 2 & 3, and the Pullman colony was the aphid source for tests 1 & 4.
Soil in each experimental flat was water saturated at the start of each
test.   Live aphids on the seedlings were counted after 4 (tests 2 & 3)
or 5 (tests 1 & 4) days.

Tests 5-7.   Plants for tests 5 and 6 were grown in white plastic
Supercells (Ray Leech Conetainers, Canby, Oregon, U.S.A.) (3.8 X 20.6
cm) placed in holding racks positioned over trays filled with water.
Test plants were randomly arranged in holding racks.   Clear plastic tubes
(3.6 X 30 cm) fitting tightly into the cells were used to confine the
aphids.   When the plants were 8 (test 5) and 2 (test 6) wks old, 15 late-
instar to adult apterous aphids were transferred with a camel's hair brush
to the base of each plant.   There were eight plants of each treatment group
(infected or noninfected plants of perennial ryegrass ['Repell']) and 10
plants of each treatment group (infected or noninfected plants of tall
fescue ['Forager']) in tests 5 and 6, respectively.   Plants for test 7
were grown individually in 15 cm pots in a greenhouse (15-29.4° C; natural

photoperiod). Six endophyte-infected and six noninfected plants of perennial ryegrass ('Repell') were 14 wks old when they were infested by placing three aphid-infested barley leaves on each plant. Plants were placed in contact with each other so aphids could move freely between plants. The number of live aphids on each plant was recorded 6 days after infestation in tests 5-7.

Data from tests 1-4 were analyzed with a Chi-square test and data from tests 5-7 were evaluated using one-way ANOVA.

RESULTS

Aphid numbers were significantly greater (P=0.001) on tall fescue and perennial ryegrass seedlings grown from endophyte-free seed than from endophyte-infected seed in tests 1-4 (Table 1). Seed infection percentages were less than 100% for the infected treatment group of each grass species; therefore, some aphid counts undoubtedly were taken from noninfected plants or escapes in these infected treatment groups. In test 5, the number of aphids found on noninfected plants of 'Repell' perennial ryegrass was 1.38 ± 0.71 ($\bar{x} \pm$ SEM). By contrast, no aphids were found on endophyte-infected plants. In test 6, noninfected and infected plants of 'Forager' tall fescue averaged 58.30 ± 11.68 and 0.50 ± 0.31 aphids/plant, respectively (F=208.89; d.f.=1,18; P=0.001). In test 7, the mean number of aphids found on noninfected and infected plants of 'Repell' perennial ryegrass was 20.50 ± 4.21 and 2.83 ± 0.48, respectively (F=17.39; d.f.=1,10; P=0.001).

DISCUSSION AND CONCLUSION

The results indicate that endophyte-free plants of tall fescue and

Table 1

Numbers of D. noxia on groups of endophyte-infected and noninfected plants
4-5 days after infestation

Test no.	Source of aphids	Grass species	Treatment groups (% infected seed)[a]	Number of aphids[b]
1	Pullman, WA	Tall Fescue	Infected (48) Noninfected (0)	169* 447
2	Prosser, WA	Tall Fescue	Infected (48) Noninfected (0)	527* 1,057
3	Prosser, WA	Tall Fescue	Infected (48) Noninfected (0)	667* 1,171
4	Pullman, WA	Perennial Ryegrass	Infected (48) Noninfected (0)	99* 153

[a] Values based on 150 seeds per lot.
[b] For comparisons among treatment groups, we pooled the counts for the replicates (rows).
* Values significantly different (P=0.001) based on Chi-square test.

perennial ryegrass are more suitable host plants for D. noxia than are
endophyte-infected plants. Moreover, these results provide evidence
that some perennial grasses may be naturally resistant to D. noxia and
that a group of naturally occurring fungi could be of great potential
in controlling this pest. Whether this enhanced resistance in endophyte-
infected plants is a result of the presence of a feeding deterrent or a
toxic factor has not been determined.

REFERENCES

Clay, K. (1988): Fungal endophytes of grasses: a defensive mutualism
  between plants and fungi. Ecology, 69. 10-16.

Diehl, W.W. (1950): <u>Balansia</u> and the Balansiae in America. Agric. Monogr.,
  4, U.S.D.A., Washington, D.C.

Johnson, M.C., Dahlman, D.L., Siegel, M.R., Bush, L.P., Latch, C.M.,
  Potter, D.A. & Varney, D.R. (1985): Insect feeding deterrents in
  endophyte-infected tall fescue. Appl. Environ. Microbiol., 49. 568-571.

Latch, G.C.M., Christensen, M.J. & Gaynor, D.L. (1985): Aphid detection
  of endophyte infection in tall fescue. N.Z.J. Agric. Res., 28. 129-132.

Stoetzel, M.B. (1987): Information and identification of <u>Diuraphis noxia</u>
  (Homoptera:Aphididae) and other aphid species colonizing leaves of wheat
  and barley in the United States. J. Econ. Entomol., 80. 696-704.

Welty, R.E., Azevedo, M.D. & Cook, K.L. (1986a): Detecting viable <u>Acremonium</u>
  endophytes in leaf sheaths and meristems of tall fescue and perennial
  ryegrass. Plant Dis., 70. 431-435.

Welty, R.E., Milbrath, G.M., Faulkenberry, D., Azevedo, M.D., Meek, L. &
  Hall, K. (1986b): Endophyte detection in tall fescue seed by staining
  and ELISA. Seed Sci. Technol., 14. 105-116.

THE ROOT-FEEDING GENERATIONS OF GALL-MAKING APHIDS OF THE GENERA *PACHYPAPPA* KOCH, *PACHYPAPPELLA* BAKER, AND *GOOTIELLA* TULLGREN (HOM. APHIDOIDEA. PEMPHIGIDAE)

Roy Danielsson,

Dept. of Systematic Zoology, Helgonav.3, S-223 62 Lund, Sweden.

ABSTRACT

The present knowledge of heteroecy among species belonging to the genera *Pachypappa* Koch, *Pachypappella* Baker and *Gootiella* Tullgren is presented. By making transfer tests with alate migrants from galls on the primary host to presumed secondary host plants, the life cycles of most species occurring in Sweden have been confirmed. All species but one have conifers as secondary host, the roots of which are colonized by the apterous alienicolae. North American material of "*Rhizomaria piceae*" have been studied and separated into two species which are tentatively linked to the two species *Pachypappa rosettei* (Maxson) and *Pachypappa sacculi* (Gillette). A key is presented for separation of known apterous alienicolae of these genera.

INTRODUCTION

The life cycles of many aphid species within the family Pemphigidae are still insufficiently studied. Often, only the gall generations on the primary host plant are known.

The exule generations of many species belonging to the tribe Prociphilini are known to live on roots of conifers. Smith (1969) clarified the life cycles of many North American species of the genus *Prociphilus*, but

the exule generations of species belonging to the genera *Pachypappa*, *Pachypappella* and *Gootiella* are less well known.

Hartig (1857) described the new genus and species, *Rhizomaria piceae*, from roots of spruce, and this name has since been used for the exule generations of many different species of the above mentioned genera. The name *piceae* Hartig has subsequently been placed in various genera, i.e. in *Pemphigus* by Tullgren (1909) and Baker (1920), in *Prociphilus* by Börner & Blunck (1916) and Börner (1930) and in *Pachypappella* by Theobald (1929).

Börner (1931) reported the successful transfer of *Pachypappa vesicalis* Koch to roots of *Picea excelsa*, and the occurrence of this species on spruce roots have subsequently been reported from Czechoslovakia by Prihoda (1965) and Hochmut (1966). Börner (1952) also mentioned *Asiphum tremulae* (L.) as having *Picea excelsa* as secondary host, based on transfer tests made in 1948.

Hottes (1960) reported *Rhizomaria piceae* from roots of *Picea pungens* in North America, and Zak (1965) reported it with some reservation also from *Pseudotsuga menziesii*. Smith (1969) gave a detailed description of apterous viviparae, first instar larvae and sexuparae of *R. piceae* from *Pseudotsuga* and *Picea* in North America but did not make any attempt to connect these root aphids with any described species of Pemphiginae.

Stroyan (1975) gave a detailed description of the viviparous morphs of *Pachypappa tremulae* (L.), a detailed review of the literature on spruce root aphids as well as a thorough examination of Börner's preserved slide material of this group of aphids. He also placed the genus *Asiphum* Koch as a subjective synonym of *Pachypappa* Koch and this opinion was followed by Smith & Parron (1978).

MATERIAL AND METHODS

Four species of *Pachypappa* Koch have been found in Sweden, viz. *tremulae* (L.), *populi* (L.), *vesicalis* Koch, and *warschavensis* (Nasonov). The two species *Pachypappella lactea* (Tullgren) and *Gootiella tremulae* Tullgren were described from Sweden.

Transfer tests with alate migrants of these species from galls on the primary hosts to the presumed secondary hosts have been performed, and the life cycles of most species occurring in Sweden have now been confirmed. All species but one have conifers as secondary host, the roots of which are colonized by the apterous summer generations.

The author has also collected material of the three *Pachypappa* species occurring in North America but no transfer tests to secondary hosts have been made. Available slide material of North American root aphids from *Picea* and *Pseudotsuga* has been studied, and an attempt has been made to connect these root aphids to the gall generations using morphological criteria.

RESULTS

Detailed morphological descriptions of the species discussed here will be published elsewhere (Danielsson in press).A short review of the present knowledge of the biology for each species is given below and a provisional key for separation of known apterous alienicolae is presented.

Pachypappa tremulae (L., 1761)

This species is heteroecious between *Populus tremula* as primary host and *Picea abies* as secondary host This heteroecy was reported by Börner (1952) and later confirmed by Stroyan (1975) This is the most common species in Sweden and it seems to have a wide distribution in the Palearctic region. I

have seen material from China, and after having studied the type material
of *Pachypappa shirobamba* Aoki from Japan, I regard this species to be
conspecific with *P. tremulae* (L.).

Anholocyclic hibernation is common and this species is often reported as
a pest on cultivated seedlings of spruce in nurseries in Sweden.

Pachypappa populi (L., 1758)

This species is also heteroecious between *Populus tremula* and *Picea
abies*. This was confirmed by transfer tests made by me in 1976 and repeated
in 1979. Galls with alate migrants were placed in cages with potted *P. abies
v. nidiformis* (a cultivated variety sold by garden centers in Sweden).
Large, flocculent colonies developed on the roots during summer and alate
sexuparae appeared at the beginning of September.

Anholocyclic hibernation occurs, and I have found colonies of this
species in early spring on fine spruce roots growing among mosses near the
surface of the ground in spruce forests in southern Sweden.

Pachypappa vesicalis Koch, 1856

The heteroecy of this species between *Populus alba* and *Picea abies* (=
P.excelsa) was reported by Börner (1931) and slide material in Börner's
collection from transfer tests made by him in 1948 (Stroyan, 1975) confirms
that statement. In 1978 I made a transfer test of this species to *Picea
abies v. nidiformis*, the roots of which was successfully colonized.
Apterous adults and larvae were collected from the roots in September and
October the same year but no alate sexuparae were obtained before the
colonies died out.

A series of alate sexuparae caught in traps at the end of September
1974 in southern Sweden probably belongs to this species

Pachypappa warschavensis (Nasonov, 1894)

This species produce leaf nest galls on twigs of *Populus alba*. I have found it at two localities in southern Sweden and several transfer tests have been made to various species of *Picea*, *Juniperus* and *Pinus* but no infestations of the roots were observed.

At one of the localities for this species I found dense colonies of a small root aphid, but the identity of the roots could not be established with certainty. Only herbaceous trees and shrubs were growing nearby. The most probable identity of the roots was either *Salix caprea* or *Rubus idaeus*, but no transfer tests have confirmed this hypothesis.

Pachypappa rosettei (Maxson, 1934)

This North American species has been regarded as conspecific with the European species *Pachypappa tremulae* (L.) (Eastop & Hille Ris Lambers, 1976; Smith & Parron, 1978). It produces a leaf nest gall on *Populus tremuloides*, similar to the ones found on *P. tremula* and *P. alba* caused by *Pachypappa tremulae* and *P.warschavensis* respectively. There are however morphological differ-ences between the species in all the morphs studied and I therefore regard the North American form as a distinct species.

Slide material of apterous "*Rhizomaria piceae* " from North America, which I have seen, seems to consist of two different species. One of these forms is characterized by very short and thin hairs on first tarsal joints, which is also typical for the apterous alienicolae of the two species making similar galls in Europe. I have seen material of this form from roots of *Pseudotsuga menziesii*, *Picea glauca* and *P. mariana*, and I tentatively regard this form as the alienicolae of *P. rosettei*.

Pachypappa sacculi (Gillette, 1914)

This North American species makes a bag-like pseudogall of a leaf on *Populus tremuloides*. Similar galls are made by the European species *Pachypappa populi* (L.) and *P. vesicalis* Koch on *Populus tremula* and *P. alba* respectively.

The second North American form of "*Rhizomaria piceae* " I have found is characterized by thicker hairs on first tarsal joints, which is also typical for the alienicolae of the two related European species mentioned above. I have seen material of this form from *Picea pungens* and *P. mariana* and I tentatively regard this form as the alienicolae of *P. sacculi* .

Pachypappella lactea Tullgren (1909)

This species makes a cone-shaped leaf gall on *Populus tremula*. The gall, as well as adjacent leaves on the twig, have a bright orange colour. Certain years the aspens suffer from heavy attacks by this species, and infested trees can be spotted far away by their orange coloured leaves. Some years, however, hardly any galls can be found on the aspens.

A positive transfer test to *Picea abies v. nidiformis* was made in 1976. A lot of apterae and juveniles were obtained in September the same year but no sexuparae developed during the autumn. Hibernating apterous specimens were collected on the plant in May the following year. Anholocyclic hibernation seems to be very common in this species, and I have often found colonies on spruce roots in southern Sweden from March to May.

Gootiella tremulae Tullgren, 1925

The primary host of this species is *Populus tremula* and the fundatrix makes a large bag-like yellowish gall of a single leaf, usually situated rather high up in older aspens. Successful transfer tests to *Juniperus*

communis were made in 1978. In nurseries I have found heavy infestations of this species on roots of *J. horizontalis v. glauca* and a few specimens also on *J. chinensis*. The alienicolae lives hidden in small, round cocoons made of wax threads, and only one aphid is found in each cocoon. Anholocyclic hibernation seems to be common and some apterae have also been found in April in nests of the ant *Lasius flavus* together with root aphids of other genera. Some hibernating apterae differed considerably from normal apterae in having longer hairs on abdomen and legs.

DISCUSSION

The heteroecy of some other species within these genera is still unknown. *Pachypappa marsupialis* Koch, 1856 seems to be a rare species making bag-like leaf galls on *Populus nigra*. The subspecies *lambersi* Aoki, 1976, which lives on *Populus maximowiczii* and *P. laurifolia* in East Asia, seems to make a somewhat different gall (Aoki, 1976) and have dimorphic first instar larvae produced by the fundatrix (Aoki, 1979). *Pachypappa pseudobyrsa* (Walsh, 1863) lives on *Populus deltoides* in North America. The fundatrix causes a small blister-like swelling of the midvein near the center of the leaf and her progeny lives on the lower surface of the leaf. Smith (1974) suspected that this might be a monophagous species, but there is no evidence that this is the case.

Gootiella alba Shaposhnikov, 1952 is probably a monophagous species living in cone-shaped leaves on *Populus alba*. Only apterous specimens have been found which contains embryos of an exule type normally found in alate migrants and apterous alienicolae. The possible affinity of this species to *Alponeura juniperi* Juchnevitch is discussed elsewhere (Danielsson in press.)

Another possibly monophagous species of this group, living on *Populus trichocarpa* and *P. balsamifera* in North America (Danielsson in press), is only known as apterous specimens too. There is also an undescribed, probably monophagous species living in leaf nest galls on *Populus euphraticus* in the Middle East (Danielsson in prep.), which besides alate migrants, also have a second apterous generation on the primary host.

CONCLUSION

Key to apterous alienicolae of the genera *Pachypappa*, *Pachypappella*, and *Gootiella*.

(The following abbreviations are used: HT1=first hind tarsal segment. HT2=second hind tarsal segment. FT1=first fore tarsal segment. PT=processus terminalis)

1. Two hairs on HT1 very small or with long, pointed apices, much smaller or thinner than the apical spine-like hairs on hind tibia 2

—   Hairs on HT1 thicker, sometimes spine-like, with short or blunt apices 6

2. Tarsal segments distinctly separated from each other; FT1 with 2-3 hairs 3

—   Tarsal segments not distinctly separated from each other; FT1 with 2 hairs 4

3. Hairs on HT1 and apical dorsal hairs on HT2 small, 0.004-0.008 mm long with short apices; FT1 usually with 2 hairs, if third middle hair present, it is longer than the lateral hairs. On *Pseudotsuga menziesii*, *Picea glauca*, and.*P. mariana* . ...? .*Pachypappa rosettei* (Maxson)

— Hairs on HT1 and apical dorsal hairs on HT2 longer, 0.010-0.015 mm long, with long pointed apices; FT1 almost always with 3 hairs, the middle hair shorter than the lateral hairs. On *Picea abies* ....*Pachypappa tremulae* (L.)

4. Hairs on HT1 and apical dorsal hairs on HT2 with long pointed apices, 0.015-0.020 mm long; wax-gland cells with a large dark central field; hind femur very thick, less than 3x as long as broad. On roots of *Juniperus communis* and *J. horizontalis* ....*Gootiella tremulae* Tullgren

— Hairs on HT1 and apical dorsal hairs on HT2 short, 0.004-0.008 mm long; hind femur more than 3x as long as broad 5

5. PT very short and inconspicuous, only about 0.008 mm long; apical dorsal hairs on HT2 spinelike, larger than the hairs on HT1; wax-gland cells with a small dark central area. On roots of *Salix* or *Rubus* ? ....? *Pachypappa warschavensis* (Nasonov)

— PT longer, at least 0.015 mm long; hairs on HT1 stouter, usually larger than the dorsal apical hairs on HT2 6

6. PT 0.015-0.020 mm long; legs short; hind femur less than 4x as long as broad; tarsal segments not distinctly separated; HT2 less than 0.10 mm long and with dorsal apical hairs short and spinelike. On *Picea abies* .. ..*Pachypappella lactea* (Tullgren)

— PT and legs longer; hind femur more than 4x as long as broad 7

7. Antennae usually 6 segmented, with a long finger-like PT which is 0.034-0.050 mm long; FT1 with 2 hairs; hairs on first tarsal joints spine like, about the size of the apical spines on tibiae; hind tibiae

along outer side with 2-5 spinelike hairs with short, blunt apices. On
Picea abies ....*Pachypappa populi* (L.)

— Antennae usually 5 segmented, PT less than 0.035 mm long and hairs on
first tarsal joints distinctly smaller than the apical spines on
tibiae; larger hairs on outer side of hind tibia with long, pointed
apices. ....8.

8. Hair on abdominal wax glands more than 0.025 mm long; glandular cells
each with a pigmented zone inside the pale outer ring. On *Picea abies*....
....*Pachypappa vesicalis* Koch

— Hair on abdominal wax glands less than 0.025 mm long; glandular cells
each without a distinct pigmented zone inside the pale outer ring. On
Picea pungens and *P. mariana*. ....? *Pachypappa sacculi* (Gillette)

REFERENCES

Aoki,S.,(1976). On two species of Pachypappa (Homoptera, Aphido-idea) found
    in East Asia. -Kontyu 44:255-262.

Aoki,S.,(1979). Dimorphic first instar larvae produced by the fundatrix of
    Pachypappa marsupialis (Homoptera:Aphidoidea). -Kontyu 47:390-398.

Baker,A.C.,(1920). Generic classification of the hemipterous family Aphididae. -U.S.Dept.Agr.Bull.826:1-93.

Börner,C. & Blunck,E.,(1916). Beiträge zur Kenntnis der wandernden Blatt- läuse Deutschlands. -Mitt.Kaiserl.Biol.Anst.Land -Forstwirtsch. 16:25- 42.

Börner,C.,(1930). Beiträge zu einem neuen System der Blattläuse. -Arch. klass.u.phyl.Ent.1:115-180.

Börner,C.,(1931). Mitteilungen über Blattläuse.-Anz.Schädlingsk. 7:42-43.

Börner,C.,(1952). Europae centralis Aphides. -Mitt.thüring.bot.Ges.,Bei- heft 3:488 pp.

Danielsson,R. (in press). The life cycle of Gootiella tremulae Tullgren, 1925 with descriptions of all viviparous morphs and a redescription of Gootiella alba Shaposhnikov, 1952. (Homop-tera: Aphidoidea:Pemphigidae). -Ent.scand.

Danielsson,R. (in press). Clydesmithia canadensis, a new genus and species of Pemphigidae living on Populus in North America (Homoptera: Aphidoidea). -Ent.scand.

Eatop,V.F. & Hille Ris Lamber,D.(1976). Survey of the World's aphids. - Junk, the Hague.573 pp.

Hartig,T.,(1857). (Brief über Wurzelläuse an Fichten). -Verhandl .d.Hils.- Solling-Forstvereins 1856 (1857):52-57.

Hochmut,R.,(1966). Korenové msice ve skolkách (Aphids on roots in plantations).-Lesnická Práce 45 (11):510-511.

Hottes,F.C.,(1960). Rhizomaria piceae Hartig new to America.-Pan- Pac.Entomol.36:199-202.

Prihoda,A.,(1965). Msice na korenech smrku. (Aphids on roots of spruce). - Lesnická Práce 44 (6):271-272.

Smith,C.F.,(1969). Pemphiginae associated with the roots of Conifers in North America (Homoptera:Aphididae). -Annls.Ent. Soc.Amer. 62:1128-1152.

Smith,C.F.,(1974). Keys to and descriptions of the genera of Pemphigini in North America (Homoptera:Aphididae:Pemphiginae) .-North Carolina Agr. Exp.Sta.Techn.Bull.226:i-vi, 1-61.

Smith, C.F.and Parron,C.S.,(1978). An annotated list of Aphididae (Homoptera) of North America. -North Carolina Agr. Exp. Sta.Techn. Bull. 255:i-viii, 1-428.

Stroyan,H.L.G.,(1975). The life cycle and generic position of Aphis tremulae L.,1761 (Aphidoidea:Pemphiginae), with a description of the viviparous morphs and a discussion of spruce root aphids in the British Isles. -Biol.J.Linn.Soc. 7:45-72.

Theobald,F.V.,(1929). The Plant Lice or Aphididae of Great Britain Vol. III.:1-364.

Tullgren,A.,(1909). Aphidologische Studien. -Ark.Zool.5(14):1-190.

Zak,B.,(1965), Aphids feeding on Mycorrhizae of Douglas-Fir. -Forest Sci. 11: 410-411.

HOST PLANT SHIFT, HOST RACE FORMATION AND SPECIATION IN CRYPTOMYZUS (HOMOPTERA, APHIDIDAE)

J. Adriaan Guldemond

Department of Entomology, Agricultural University Wageningen, P.O.
Box 8301, 6700 EH Wageningen, The Netherlands

ABSTRACT

The species complexes Cryptomyzus galeopsidis and C. alboapicalis were examined in a biosystematic study in order to unravel their (taxonomic) relationships and to assess the impact of host preference, suitability and host-alternation on reproductive isolation of closely related taxa. Its consequences for speciation are discussed.

INTRODUCTION

Evolution in aphids has been the subject of several publications since the work of Mordvilko at the beginning of this century (e.g. Mordvilko, 1934). Special attention has been focussed on the achievements of Hille Ris Lambers (1950, 1980), Heie (1967), Shaposhnikov (1984) and Müller (1985). Nevertheless, an experimental approach to the process of speciation has as yet hardly been developed. Shaposhnikov (1984) succeeded in the creation of a new aphid form by severe selection of a population on a previously unused host plant. Müller studied host plant suitability and the possibility of hybridization between closely related forms (Müller, 1976, 1980, 1982).

It is generally acknowledged that the host plant not only plays an important role in the life of aphids, but also in speciation (e.g. Shaposhnikov, 1984). Due to the strict binding of most (99%) aphids to one or a few closely related plant species (Eastop, 1973), a shift to a new host can be a decisive step in the formation of a reproductively isolated population and finally a new

species (Futuyma & Peterson, 1985). In this context the host preference of the presexual morphs (gynoparae and sexuparae) which produce sexuals and of males is important, because sexual reproduction occurs on hosts selected by these morphs. Also, the loss of host-alternation and the consequent restriction to a previously selected secondary host may have led to speciation in many aphids (Hille Ris Lambers, 1950).

The aphid species Cryptomyzus galeopsidis (Kaltenbach) and C. alboapicalis (Theobald) provide a suitable complex for the study of speciation, because it includes seven closely related taxa, which either alternate between the primary host Ribes and various labiateous herbs, or which remain on a secondary or even a primary host (Hille Ris Lambers, 1953; Guldemond, 1987; Fig. 1). Morphological and biochemical evidence argues for a monophyletic origin of these taxa (Börner, 1930; Guldemond & Eggers-Schumacher, 1989).

In this biosystematic study the role of host preference, reproductive performance and host-alternation is considered in the process of speciation in Cryptomyzus. A complete taxonomic and nomenclatorial evaluation will be provided in another publication (Guldemond, in prep.).

MATERIALS AND METHODS

The host plant relationships of the seven taxa of C. galeopsidis and C. alboapicalis are described in Fig. 1 and further data are to be found in Hille Ris Lambers (1953) and Guldemond (1987). Allozyme variation was measured by starch gel electrophoresis and is described in Guldemond & Eggers-Schumacher (1989). Twelve enzymes were examined and yielded 15 presumed loci. Host preference was measured by assessing the distribution of aphids, 24 h after releasing them on two different plants in a choice experiment. The reproductive performance was established by counting the number of offspring produced by a group of females after seven days on a selected plant. The terminology follows Thompson (1988a) and further details are in Guldemond (in press).

Cryptomyzus galeopsidis   Cryptomyzus alboapicalis
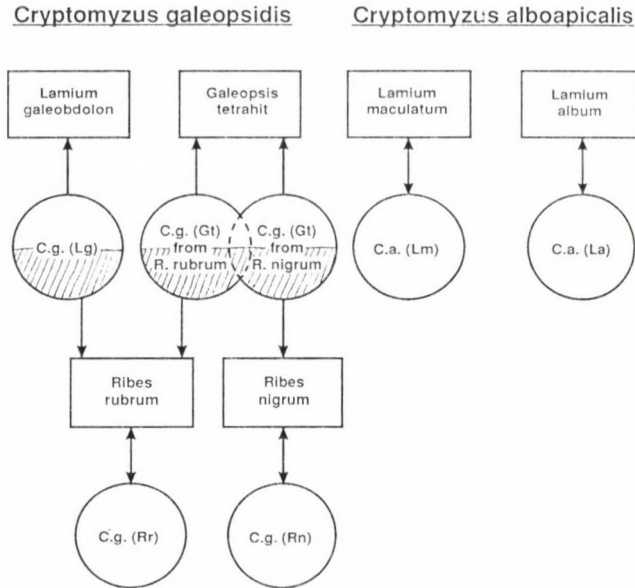
Fig. 1. Life cycle and host plants of Cryptomyzus species studied. Abbreviations of host in parentheses after taxon name

RESULTS

Table 1 shows the results, for the seven taxa of C. galeopsidis and C. alboapicalis, on the life cycle, host plant preference, reproductive performance and allozyme data. The two monoecious forms of C. alboapicalis appear to be different species on the basis of host preference, suitability, allozyme data and the wingless condition of males in the form from L. album versus winged males in the form from L. maculatum. C. alboapicalis from L. album is morphologically different from the other taxa in having a larger number of hairs on the abdominal tergites. The form from L. maculatum resembles morphologically C. galeopsidis, but can be separated by a linear discriminant function (Guldemond, in prep.).

C. galeopsidis consists of several forms, and the one that

Table 1. Taxa of C. alboapicalis and C. galeopsidis with characteristic host plants in parentheses, life cycle, host plants and allozymes. + indicates preference, - no preference, o indiffe e; () indicates occasional weak reproductive performance. Letters of allozymes follow Guldemond & Eggers-Schumacher (1989)

Taxon	Life cycle	Prim. host.	Sec. host	Preference exules	Preference /pre/sexuals	Reproductive performance	males	Allozymes Hk-1	Sdh	Gpdh	Pgi
C.albo /La/	monoecious	L. album		La+ Lm-	La+ Lm-	La	wingless	B	C	E	B
C.albo /Lm/	monoecious	L. maculatum		La- Lm+	La- Lm+	Lm /La/	winged	A	A	C	B
C. gal /Lg/	heteroecious	R. rubrum	L. galeobdolom	Lg+ Gt-	Rr+o Rn-o	Lg /Gt/;Rr	winged	A	C	C	BDG
C. gal /Rr/	monoecious	R. rubrum		Rr+ Gt-		Rr	winged	A	C	C	BEG
C. gal /Rr/Gt/	heteroecious	R. rubrum	Galeopsis	Lg- Gt+	Rr+o- Rn-o+	Gt; Rr Rn	winged	A	C	C	BEG
C. gal /Rn/	monoecious	R. nigrum		Rn+ Gt-		Rn	winged	A	C	C	BEG
C. gal /Rn/Gt/	heteroecious	R. nigrum	Galeopsis	Lg- Gt+	Rr- Rn+	Gt; Rn	winged	A	C	C	BEG

alternates to L. galeobdolon should be considered as a separate
 species, not only because its secondary host is not shared by any
other Cryptomyzus species but also because it has a unique allozyme
 of phosphoglucoisomerase (PGI). Furthermore, hybridization with
the C. galeopsidis form, which alternates between R. rubrum and
Galeopsis, gave F1 generations that showed a decreased reproductive
performance on the secondary hosts of both parents. The F2 and a
backcross even died out on the primary host (Guldemond, in prep.).
The mechanism of reproductive isolation between these species on
the shared primary host R. rubrum is unknown and will be subjected
to further research.

The host-alternating forms of C. galeopsidis on R. rubrum and R.
nigrum can be descibed as host races (Guldemond, in press). The
gynoparae and males of both forms are differentiated by their
preference for their primary host plants and by the survival of the
oviparae on those plants. Nevertheless, there is an intermediate
group from R. rubrum which selects R. nigrum and whose oviparae
mature on this host. This indicates that a certain degree of
hybridization remains possible between both forms. Genetic
separation between the non-alternating forms on R. rubrum and R.
nigrum was demonstrated by different allele frequencies of PGI
(Guldemond & Eggers-Schumacher, 1989). Moreover, the forms are
unable to reproduce on each others hosts (Guldemond, 1987).

Alternating and non-alternating forms, occurring on the same
primary host, hybridized without any restriction in the laboratory
and their offspring developed normally. It is likely that those
forms also interbreed freely in the field, despite the earlier
appearance of sexuals of the non-alternating form (Hille Ris
Lambers, 1953), because there is a long period during which sexuals
of both forms are present. Summarizing, there is good evidence for
a partial separation between forms from R. rubrum and R. nigrum,
but there are no grounds for separating alternating and non-alter-
nating forms which occur on the same host.

Hybridization experiments with alternating and non-alternating
forms from Ribes rubrum showed that host-alternation is probably

determined by only one gene(complex). An inbreeding experiment has
shown the existance of a homozygous non-alternating clone: all
offspring (n=30) appeared non-alternating. A cross of this clone
with a presumed heterozygous host-alternating clone, yielded 8
alternating and 5 non-alternating clones. Despite the low numbers,
this result is consistent with a one gene regulation, and host-
alternation being the dominant character over non-alternation
(Guldemond, in prep.).

DISCUSSION

When speciation of insects involves a shift to a new host plant,
Futuyma & Peterson (1985) consider that a change in host plant
preference is usually the first step, followed by adaptation of
reproductive performance. Data from my study indicate that host
preference is an important factor in establishing reproductive
isolation between the closely related forms of C. galeopsidis on R.
rubrum and R. nigrum. However, host preference does not constitute
an absolute barrier to gene flow, because the landing of a male on
a "wrong" host, followed by insemination of the oviparae of another
form cannot be excluded (Guldemond, in press). More information is
required about the genetic basis of host preference in aphids in
order to estimate the probability of such a change in preference.
It is known that the oviposition preference of a swallowtail
butterfly was regulated by only a few genes (Thompson, 1988b). If
this condition is widespread then the initial colonization of a new
host could occur quite often.

When reproductively adapted to the new host, gene flow is
prevented, because oviparae are not able to mature on the "wrong"
host any more. In a model study, Rausher (1984) demonstrated that
under certain conditions the changes in preference and performance
do not necessarily have to take place simultaneously, which may
facilitate host race formation and subsequent speciation.

The loss of host-alternation may be another mode of speciation
in aphids. If a female, which is heterozygous for the character of
host-alternation, arrives on a new host plant and produces oviparae

and males, segregation leads to a non-alternating form. There is
probably little or no gene flow with the original population and
speciation might just be a question of time (Guldemond, in prep.).
Hille Ris Lambers (1950) gives several examples of genera with
host-alternating species and so-called secondary monoecious species
living exclusively on a secondary host. Although speciation in
aphids has kept most of its secrets, our knowledge of the
underlying mechanisms is gradually increasing.

ACKNOWLEDGMENTS

I like to thank Peter de Vrijer and Michael Latcham for improv-
ing the text.

REFERENCES

Börner, C., (1930) Beiträge zu einem neuen System der Blattläusen.
    Arch. f. Klassifikat. u. Phylogen. Ent., I, 115-194.

Eastop, V.F., (1973) Deductions from the present day host plants of
    aphids and related insects. In: Insect/plant relationships. (ed.
    by H.F. van Emden), pp. 157-178. Symp. Roy. Ent. Soc. London 6,
    London.

Futuyma, D.J. & Peterson, S.C., (1985) Genetic variation in the use
    of resources by insects. Ann. Rev. Ent. 30, 217-238.

Guldemond, J.A., (1987) Biosystematics of the Cryptomyzus complex.
    Preliminary results on host plant acceptance, electrophoretic
    data and sexual isolation. In: Population structure, genetics
    and taxonomy of aphids and thysanoptera. (ed. by J. Holman, J.
    Pelikán, A.F.G. Dixon and L. Weismann), pp. 96-99. SPB Academic
    Publishing, The Hague.

Guldemond, J.A., (1990) Choice of host plant as factor in reproduc-
    tive isolation of the aphid genus Cryptomyzus (Homoptera,
    Aphididae). Ecol. Entomol., in press.

Guldemond, J.A. & Eggers-Schumacher H.A., (1989) Biosystematics of
    the aphid genus Cryptomyzus (Homoptera, Aphididae): an
    electrophoretic analysis. Z. zool. Syst. Evolut.-forsch. 27, 14-
    25.

Heie, O.E., (1967) Studies on fossil aphids (Homoptera: Aphido-
    idea). Spolia Zool. Mus. Haun. 26, 1-274.

Hille Ris Lambers, D., (1950) Host plants and aphid classifica-
    tion. Proc. 8th Int. Congr. Entomol., Stockholm, 141-144.

Hille Ris Lambers, D. (1953) Contribution to a monograph of the
    Aphididae of Europe. Temminckia 9, 82-114.

Hille Ris Lambers, D., (1980) Aphids as botanists? Sym. Bot. Upsal.
    12, 114-119.

Mordvilko, A. (1934) On the evolution of aphids. Archiv. f. Natur-
    geschichte, N.F. 3, 1-60.

Müller, F.P., (1976) Host and non-host in subspecies of Aulacorthum
    solani (Kaltenbach) and intraspecific hybridizations (Homoptera:
    Aphididae). Symp. Biol. Hung. 16, 187-190.

Müller, F.P., (1980) Wirtzpflanzen, Generationsfolge und reproduc-
    tive Isolation intraspecifiker Formen von Acyrthosiphum pisum.
    Entomol. exp. appl. 28, 145-157.

Müller, F.P., (1982) Das Problem Aphis fabae. J. appl. Ent. 94,
    432-446.

Müller, F.P., (1985) Genetic and evolutionary aspects of host
    choice in phytophagous insects, especially aphids. Biol.
    Zentralbl. 104, 225-237.

Rausher, M.D., (1984) The evolution of habitat preference in
    subdivided populations. Evolution, 38, 596-608.
Shaposhnikov, G.Ch., (1984) Aphids and a step toward a universal
    species concept. Evolut. Theor. 7, 1-39.

Thompson, J.N., (1988a) Evolutionary ecology of the relationship

    between oviposition preference and performance of offspring in
    phytophagous insects. Entomol. exp. appl. 47, 3-14.

Thompson, J.N., (1988b) Evolutionary genetics of oviposition
    preference in swallowtail butterflies. Evolution 42, 1223-1234.

MORPHOLOGICAL DIFFERENTIATION OF THE FUNDATRICES AND FUNDATRIGENIAE IN SOME MONOECIOUS APHID SPECIES

Jaroslav Holman

Institute of Entomology, South Bohemian Biological Centre,
Czechoslovak Academy of Sciences, České Budějovice,
Czechoslovakia.

ABSTRACT

The size and morphology as well as the postnatal growth in parthenogenetic females of the 1st and 2nd generation (fundatrices and fundatrigeniae) of Symydobius oblongus (v. Heyden) and Schizolachnus pineti (Fabricius) were studied. In both species the new born fundatrigeniae had longer appendages than the new born fundatrices, whereas the body length and head width was slightly larger in the latter morph. The difference in the average lengths corresponds to approximately a one-instar delay in the development of the hind femora, hind tibiae and the basal segment (future segments III-V) of the flagellum, and a nearly two-instar delay in the growth of the VIth antennal segment in the fundatrices.

In fundatrices of S. Oblongus the postnatal growth rates of the appendages was distinctly higher than in the fundatrigeniae so that the difference in the length of the legs and antennae at birth was to a large extent compensated for. The highest growth rates were recorded for antennal segment III, which in the fundatrices of Symydobius was on average longer and made up a larger proportion of the flagellum than in the fundatrigeniae.

In the two morphs of S. pineti studied the trends in the postnatal growth of the appendages were similar. The morphological differentiation of fundatrices and subsequent generations early in their embryonic development is a common feature of aphids. There exist differences in the extent to

which the size of the appendages at birth in fundatrigeniae and,
presumably, the subsequent generations is advanced. Differen-
tial postnatal growth of the appendages results in the adult
fundatrices and fundatrigeniae of Euceraphis and Symydobius
being little differentiated, which is correlated with the part
the fundatrices play in the dispersal of the population early in
the season.

INTRODUCTION

In most aphid species the fundatrices differ from the
subsequent generation in having shorter appendages and often in
the proportional lengths of their antennal segments. These
differences arise early in the course of embryogenesis and to
various degrees are modified postnatally (Holman 1987; Holman,
Raha 1989). The newborn fundatrices and fundatrigeniae of
Euceraphis betulae (Koch) differ greatly both in the relative
lengths of their appendages and the segmentation of their
antennae. As a result of different trends in postnatal growth
the adults of the two morphs are difficult to separate on
external morphology. The nymphal morphology of the two
generations correlates with their behaviour in the field: the
fundatrices are relatively sessile on buds and later in folded
young leaves, the fundatrigeniae are active on mature leaves.
However, the adult fundatrices of Euceraphis actively search for
favourable feeding sites and in this respect do not differ from
the subsequent generation (Holman, Raha 1989). In view of this
the development of Symydobius oblongus (v. Heyden) and
Schizolachnus pineti (Fabricius) was studied as in these species
the nymphal and adult fundatrices and fundatrigeniae have
similar feeding sites.

MATERIAL AND METHODS

Samples of Symydobius oblongus and Schizolachnus pineti were
collected from April 1988 to June 1989 from the same group of
trees (Betula pendula Roth and Pinus silvestris L. respectively)
near Český Krumlov, South Bohemia. The specimens for the morph-

ometric studies were preserved in 96% alcohol, cleared and
mounted on microscope slides. The head width (HW) and the
lengths of the body and the main parts of the appendages
(antennal flagellum - FL, antennal segments III-V, hind femur -
HFM and hind tibiae - HTB) of 33-54 specimens of each instar of
the 1st (fundatrices) and 2nd (fundatrigeniae) generations were
measured.
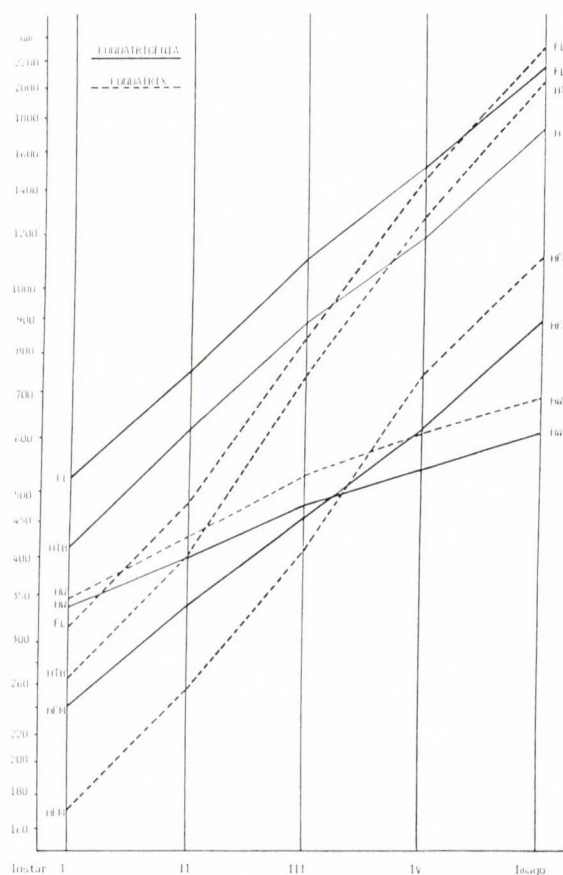
Fig. 1. Symydobius oblongus, fundatrix and fundatrigenia: post-
natal growth in the width of the head and lengths of the
flagellum, hind femur and hind tibia.
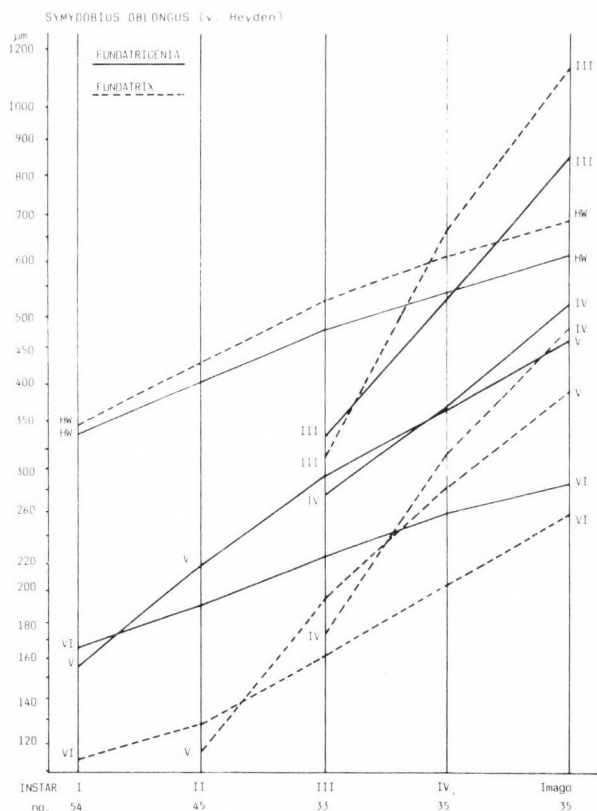
Fig.2. Symydobius oblongus, fundatrix and fundatrigenia: Average postnatal growth in the width of the head and lengths of the antennal segments III-V1.

RESULTS

The main results presented in Figs. 1 - 2 and Table 1 can be summarized as follows:

1)   The average size and width of the head of newborn fundatrices and fundatrigeniae of the two species studied is essentially equal.

2)   The newborn fundatrices differ from those of fundatrigeniae in having shorter appendages. The average lengths of hind tibiae, hind femora and antennal segments III-V of newborn

fundatrigeniae and that of 2nd instar fundatrices are similar.
The first instar fundatrigeniae and third instar fundatrices are
similar in the average length of the ultimate antennal segment.
3)   In the fundatrices of _Symydobius oblongus_ the postnatal
growth rates of the appendages is distinctly higher than in the
fundatrigeniae. As a result the differences in both absolute
and relative length of the legs and the antennal flagellum that
exist at birth in these two morphs are compensated for as the
two morphs grow to maturity.
4)   In both species the 1st instar larvae of the two morphs have
a two-segmented antennal flagellum (future segments III-V and
segment VI). In a few newborn fundatrigeniae segment V could be
measured but usually it is not fully formed until after the
first moult. In both species the antennae are fully formed
after the 2nd moult.
5)   The length of the newly formed antennal segment III in 3rd
instar fundatrices of _S.oblongus_ is nearly equal (on average
about 0.9) to that of 3rd instar fundatrigeniae but it grows
faster than that of the fundatrigeniae and of any of the other
structures measured in this species. As a result, in adult
fundatrices of _S. oblongus_, antennal segment III is on average
longer and makes up a distinctly larger proportion of the
flagellum than in fundatrigeniae (0.502 ± 0.009 and 0.400 ± 0.012,
respectively).
6)   In the fundatrices and fundatrigeniae of _Schizolachnus_
pineti the postnatal growth rates of the body and the appendages
are similar so the differences between the adults of the two
morphs of this species are more pronounced than in _S. oblongus_.

DISCUSSION

     The differences between newborn fundatrices and fundatri-
geniae most probably arise as a result of different timing
(heterochrony) of the formation of respective primordia in the
course of embryonic development (Holman, 1987). In _Symydobius_
and _Schizolachnus_ the difference in the average length of the
legs and antennal flagellum suggests an approximately one-instar

advance in development in the fundatrigeniae. A similar situa-
tion has been reported for Euceraphis betulae (Koch) (Holman,
Raha 1989), whereas in Acyrthosiphon pisum (Harris) the longer
appendages of the fundatrigeniae correspond to a developmental
advance of two instars (Holman, 1987).

Table 1   Average postnatal growth (adult/neonate) of the body
and the appendages.

Aphid species	Symydobius oblongus (v. Heyden)		Schizolachnus pineti (Fabricius)	
Morph	Fundatrix	Fundatrigenia	Fundatrix	Fundatrigenia
Body	3.43	2.57	2.20	2.23
Head width	1.97	1.82	1.47	1.32
Flagellum	6.91	4.09	2.83	2.75
Antennal segment III[+]	3.66	2.57	1.80	1.79
Hind tibia	7.14	4.22	3.91	3.67
Hind femur	6.12	3.67	4.24	3.88

[+]Adult/IIIrd instar

The accelerated postnatal growth of the appendages in the
fundatrices of S. oblongus resembles that in Euceraphis. In the
latter species the resulting morphological similarity of the
adult fundatrices and fundatrigeniae correlates with their
similar, active way of life. The same seems to be true also for
Symydobius in which the fundatrices are both apterous and alate
and are involved in the dispersal of the population rather early
in the season when the growth of birch terminates, the leaves
become mature and the nutritive value of the phloem sap
deteriorates.

On the other hand, both the 1st and 2nd generation
Schizolachnus live on mature, last year's needles of pine. The
fundatrices are sessile and the dispersal of the population
takes place later in the season. The conditions of nutrition
presumably are not essentially different for the fundatrices and

fundatrigeniae.

That newborn fundatrices have shorter appendages in comparison with newborn fundatrigeniae and the parthenogentic females of subsequent generations, possibly also occurs in other aphid species because the adult fundatrices show these morphological differences. It seems to be a plesiomorphic and hence conservative feature that results from the differences in the development of the morphs involved (after sexual reproduction, in an egg, with embryonic diapause in fundatrices; parthenogenetically, without diapause inside the mother in fudatrigeniae and subsequent generations).

In the species so far studied the differences in the appendages of newborn fundatrices and fundatrigeniae corresponds to a developmental advance of either one or two instars in fundatrigeniae. The differential postnatal growth results in adaptive, fine tuning of the body proportions in the adults. In *Euceraphis* and, to a lesser degree, in *Symydobius* this results in a secondary postnatal morphological convergence of the fundatrices and fundatrigeniae. This is correlated with the role the fundatrices of these species play in the dispersal of the population early in the season when birch ceases growing.

REFERENCES

Holman, J. 1987. Heterochrony as one possible mechanism of morph differentiation in aphids. In: Population structure, genetics and taxonomy of aphids and Thysanoptera. Holman, J. et. al. (eds) SPB Academic Publishing, The Hague, pp 190-203.

Holman, J., Raha, S.K. 1989. Generation-specific reproductive and growth tactics in the birch aphid, *Euceraphis betulae* (Koch). In: Regulation of insect reproduction IV. Tonner, M. et al. (eds) Academia Publishing House of the Czechoslovak Academy of Sciences, Praha, pp. 413-429.

WHY IS APHID FLIGHT DENSITY DEPENDENT?

N.A.C. Kidd
School of Pure and Applied Biology,
University of Wales, Cardiff, U.K.

ABSTRACT

This paper explores one possible reason why aphid
populations commonly produce migrant alatae in a density
dependent fashion, namely, that it may be the best strategy
for maximising the number of migrants produced during the life
of the colony. Evidence in support of this hypothesis was
obtained using a simulation model of a generalized aphid
population. On short-lived plants, the best density-dependent
strategy produced about 50% more dispersants than the best
density-independent one, with no greater net cost to the
resident population. On longer-lived plants, such as trees,
the advantage of density-dependence is removed where stable
environmental conditions prevail, but returns when
environmental variations induce fluctuations in aphid
numbers.

INTRODUCTION

During spring and summer adult aphids generally appear in
two parthenogenetically reproducing forms, winged alatae and
wingless apterae. Apterous adults are usually produced when
the number of aphids in a colony is low, while alatae are
characteristic of densely populated colonies.

How far can this relationship between population density
and alate production be taken as evidence for density-
dependent dispersal in aphids?   The situation is complicated
by the fact that not all alatae fly, some remaining on the
plant to reproduce (Kidd & Cleaver, 1984). In Aphis fabae
Scop., however, where this phenomenon has been explored in
detail, the 'urge' of alatae to both disperse from the plant
and migrate also appears to be density-dependent (Kidd &
Cleaver, 1984; 1986).

Why then should flight dispersal in aphids be density-
dependent? It is tempting to argue that as apterae tend to be
larger and more fecund than alatae, their production when
colony numbers are low (after initial colonisation) would be
advantageous in ensuring the success of the colony through
rapid population growth. Delaying the appearance of alatae
would maximise the production of apterae at the start of
colony development, thus maximizing population growth rates.
However, it has been shown, in Aphis fabae at least, that the
instrinsic rate of increase of alatae is just as high as that
of apterae (Dixon & Wratten, 1971), so this argument lacks
support.

The alternative view which is explored in this paper, is
formulated on the basis that two alternative dispersal
strategies are possible in aphid populations. (The terms
'population' and 'clone' are here used synonymously to
simplify the argument.) Dispersants (=winged alatae) can be
produced in a density-dependent fashion, as outlined above, or
in a density-independent way, either as a constant or random
proportion of the adult population. The questions to answer
then become:

   a) Is there a selective advantage in having a density-
   dependent strategy as opposed to a density-independent
   one?
   b) How is aphid fitness affected by the strategy adopted?

In approaching an answer to those questions, an important point to note is that aphid populations are all dependent on ephemeral resources, namely, their host plants. Even trees have a limited lifespan, so that ultimately extinction of local aphid colonies is inevitable. I would argue, therefore, that fitness in aphids can only really be measured accurately in terms of the number of dispersants from the plant produced by the doomed clonal line. Other measures of fitness which have previously been used, e.g. individual fecundity or egg production at the end of the season, are inappropriate in the present context, as they are only confined to a restricted period during the clonal 'life -cycle' on the plant.

Thus, adaptations in aphids can be viewed as mechanisms for getting the maximum number of dispersing units off the plant, while it is in a suitable condition for colonisation. Flight, as the key means of dispersal, is likely to be a central focus for selection. The theory to be tested, therefore, is that populations will maximise the number of dispersing units (alatae) by optimizing their rate of dispersal and that this is best achieved by a density-dependent strategy. In practical terms, this yields the falsifiable hypothesis that a colony will produce a greater number of alatae during its lifetime by a density dependent mode of production than a density independent one. In this paper I present results obtained from a computer simulation model, constructed to test this hypothesis.

METHODS

The simulation model used here was based on the variable life-table approach used frequently to analyse the population dynamics of aphid species (Gilbert et al., 1976). The current model was based on that constructed for the large pine aphid, Cinara pinea (Mordv.), the details of which are described elsewhere (Kidd, 1985, 1989). In its present form, the model assumes a nymphal development time of 20 days, an adult lifespan of 20 days, and a per capita maximum reproductive

output of 2 offspring/day. High population densities produced negative feedback effects on nymphal growth, adult size and hence reproduction. All adults are parthenogenetic females, the proportion of apterae/alatae determined by an alate production function, which determines the morph of each adult at the final moult (see Figure 1). Where emigration and low reproduction resulted in a decline in the population to low numbers, a delay in reproductive recovery was incorporated to simulate a decline in the nutritive quality of the plant to the aphids.

Figure 1. Theoretical aphid dynamics with examples of density dependent (D D) and density independent (D I) emigration functions.
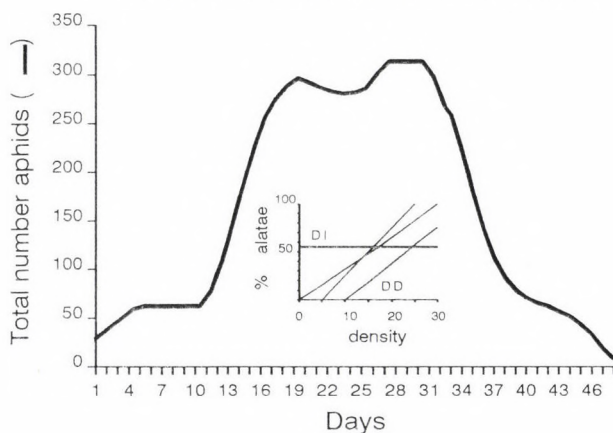
RESULTS

An example of the population patterns produced by the model is given in Figure 1, together with examples of the density-dependent and density-independent flight emigration functions used. For the density dependent strategy, simple linear functions were used throughout, with a threshold density for the onset of alate production. Iteration was carried out using different parameter values in order to find the optimum solutions for both strategies.

Table 1 shows the optimum solutions for a population completing its cycle on the plant in 40 days, i.e. equivalent to a relatively short-lived plant species. The results are expressed in terms of the total number of adult aphids produced during the colony's life on the plant, and the number and percentage of those which were dispersants (alatae). Here, the density-dependent strategy produced, not only a greater total number of adult aphids, but also 53% more dispersants than the density-independent strategy.

Table 1   The production of dispersants over 40 days by aphid populations using optimal density dependent or density independent strategies

	optimal strategy	
	density dependent	density independent
Number of aphids produced	648	556
Number of dispersants	454	297
% dispersants	70	53

On a longer-lived plant, over 120 days, the differences between the two strategies were eroded. This occurred because both populations stabilized at an equlibrium density after about 50 days, each then producing a constant daily proportion of dispersing adults. However, the introduction of a density-disturbing factor restored the advantage to the density dependent strategy. A 98% mortality was applied to each age group every 40 days, simulating the effects of, for example, heavy rainfall. In this case, 1254 dispersants were produced by the density dependent strategy as opposed to 840

by the density independent strategy, an increase of 49%. In both cases the populations tended to stabilize around 300 aphids per plant.

DISCUSSION

An important point which emerges from these results is that the density dependent strategy can produce a greater number of dispersants with no net loss in resident population numbers on long-lived plants. This is likely to be important when considering how selection might operate on mixed-clonal populations occupying long-lived habitats such as trees. Consider, for example, two populations M and N of an aphid species initially occupying two separate habitats A and B respectively. Each population differs in the number of emigrants (E_M and E_N) it can produce and the number of residents left in a given time interval t. Of those dispersing from each population, a constant and equal proportion (0.1) immigrate into both habitats during interval t. Thus, the two habitats have the potential to contain both M and N individuals. Each population is capable of doubling during interval t, but as the carrying capacity in each habitat is set at 100, the numbers of M and N are corrected in proportion to their relative abundances.

This situation can be modelled analytically using the following equations. Thus, for each habitat :

$$N_{t+1} = \frac{(N_t - E_N) + (0.1 * E_N) * 200}{N+M} \quad \dots\dots\dots\dots (1)$$

$$M_{t+1} = \frac{(M_t - E_M) + (0.1 * E_M) * 200}{M+N} \quad \dots\dots\dots\dots (2)$$

Where both populations are similar in every respect they come to occupy both habitats in equal measure. However, where population N produces emigrants with no net loss to the population number (i.e. $N_t - E_N = N_t$ in equation (1)), as occur with the density dependent strategy, it gradually occupies both habitats to the exclusion of population M (Figure 2). This simple illustration indicates the powerful selective advantage that the density-dependent emigration strategy may have, even amongst aphid populations on long-lived hosts.

Figure 2. Selection between density dependent (DD) and density independent (DI) strategies on perennial hosts.
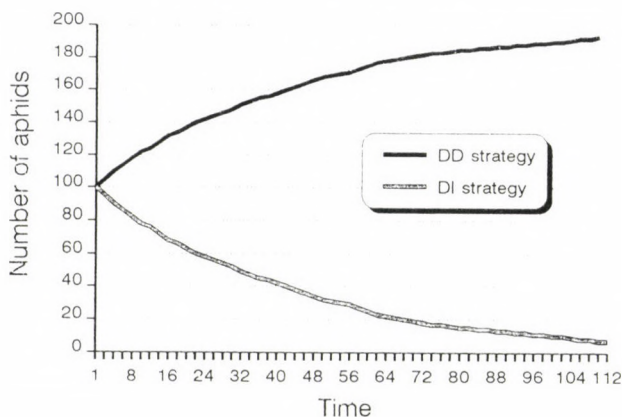
LITERATURE

Dixon & Wratten (1971) Laboratory studies on aggregation, size and fecundity in the black bean aphid, Aphis fabae Scop. Bull. ent. Res. 61, 97-111.

Gilbert, N., Gutierrez, A.P., Frazer, B.D. and Jones, R.E (1976) Ecological Relationships. Freeman, Reading.

Kidd, N.A.C. (1985) The role of the host plant in the population dynamics of the large pine aphid, Cinara pinea. Oikos, 44, 114-122

Kidd, N.A.C. (1989) The large pine aphid on Scots pine in
        Britain.   In 'Dynamics of Forest Insect Populations'
        (ed. A.A. Berryman) Plenum, New York, pp. 111-128.

Kidd, N.A.C. and Cleaver, A.M. (1984) The relationship
        between pre-flight reproduction and migratory urge
        in alatae of Aphis fabae Scopoli
        (Hemiptera:Aphididae). Bull. ent. Res, 74, 517-527.

Kidd, N.A.C. and Cleaver, A.M. (1986) The control of
        migratory urge in Aphis fabae Scopoli
        (Hemipera:Aphididae). Bull. ent. Res., 76, 77-87.

TRANSFORMATION OF THE GALLS OF ASTEGOPTERYX BAMBUCIFOLIAE BY ANOTHER APHID, CERATOGLYPHINA BAMBUSAE

Utako Kurosu and Shigeyuki Aoki,

Laboratory of Applied Entomology, Faculty of Agriculture, Tokyo Noko University, Fuchu, Tokyo, 183 Japan, and Laboratory of Biology, College of General Education, Rissho University, Magechi 1700, Kumagaya, 360-01 Japan

ABSTRACT

Astegopteryx bambucifoliae (Takahashi) and Ceratoglyphina bambusae van der Goot form galls on Styrax suberifolia in Taiwan. In 1987 and 1988, 4 galls showing mixed characters of the 2 species' galls were found at Sun Moon Lake. They contained living aphids of both species or only of C. bambusae. A close examination of their structure and inhabitants revealed that these galls were initially formed by A. bambucifoliae and later invaded and transformed by C. bambusae.

INTRODUCTION

Astegopteryx bambucifoliae (Takahashi) (= A. sasakii Takahashi) and Ceratoglyphina bambusae van der Goot (= Astegopteryx styracicola Takahashi) are cerataphidine aphids that migrate between Styrax suberifolia (their primary host) and bamboos (their secondary hosts) in Taiwan (Aoki & Kurosu 1989). Both form galls on S. suberifolia and produce 2nd-instar soldiers there (Aoki et

al. 1977, Aoki & Kurosu unpubl.). The mature galls of the 2 species are very different in appearance. The gall of A. bambucifoliae has a number of thin subgalls (see Fig. 1 in Takahashi 1939) and is yellow or light brown. It is formed on a developing shoot (twig-to-be) of the host plant (Kurosu & Aoki unpubl.). The gall of C. bambusae, on the other hand, has only a small number of subgalls (1 to 5). The "head" of each subgall consists of many ramified thin projections (see Fig. 1 in Aoki et al. 1977). These projections first grow from the inner wall, and then expand outwards through the original opening slit, making the entire subgall look like a cauliflower. The surface is coated with wax and brightly white (see Fig. 1 in Aoki 1979a). It is still unclear whether the fundatrix of C. bambusae utilizes a developing shoot (as in A. bambucifoliae) or an axillary bud (as in Ceratovacuna nekoashi; Kurosu & Aoki in press), or both, for gall formation. The galls at times occur on thick branches or stems, so the fundatrices might also attack latent buds.

In 1987 and 1988 we found 4 galls that showed a curious set of characters; they had a number of subgalls like normal galls of A. bambucifoliae, but also had ramified projections like those of C. bambusae. These galls contained living aphids of both species or only of C. bambusae. Below we show that these "chimeral" galls were first formed by A. bambucifoliae and later invaded and transformed by C. bambusae. Akimoto (1988) and Setzer (1980) have shown that aphids of the genera Eriosoma and Pemphigus intrude into galls of congeners, but transformation of another species' galls has hitherto been unknown among aphids.

MATERIALS AND METHODS

The 4 galls (nos. 87076, 87094, 87095 & 88012) were collected at Sun Moon Lake, Nanto Hsien, Taiwan. They were immediately submerged in 80% alcohol, and later dissected and the number of aphids counted. The aphids were boiled in KOH solution, stained with acid fuchsin, and mounted in balsam for microscopic observation. All the aphids in galls 87076 and 87095 were mounted and examined. We divided the whole aphids in each of galls 87094 and 88012 into 4 roughly equal parts in a petri dish after stirring. A part of gall 87094 contained 217 aphids, and a part of gall 88012 213 aphids. All the aphids of these samples were mounted and examined.

Mounted specimens of both species could be classified as one of the following 7 morphs: alate adult, 4th-instar alatoid larva, 3rd-instar alatoid larva, apterous adult, nonwingpadded 2nd to 4th instar larvae, 1st instar larva and (2nd instar) soldier. We failed to discriminate between alates-to-be and apterae-to-be in the 2nd instar. It was easy to discriminate under a differential interference microscope between the 2 species for each morph. Except for 1st instar larvae, all the gall inhabitants had 1 sensory peg or 2 in addition to a pair of long pointed setae on the 1st segment of each mid tarsus; the number was always 1 for A. bambucifoliae and 2 for C. bambusae. Moreover, the number of apical setae on each antenna was 6 for A. bambucifoliae (but 5 in the 1st instar) and 5 for C. bambusae. In the 1st instar, discrimination between the species was easy because A. bambucifoliae almost always had 3 pairs of spine-like setae on the

frons, while C. bambusae had 2 pairs of such setae. This charac-
ter was also useful for the discrimination of the later stages
except the alate morph. We also examined whether mounted aphids
had the next instar cuticle developing inside.

RESULTS

1. Gall 87076

On November 3, 1987, we found an unusual gall of Astegopteryx
bambucifoliae on a small tree of Styrax suberifolia (tree D) at
Sun Moon Lake (Fig. lA). On tree D, there were 3 well-developed
galls of Ceratoglyphina bambusae and a few others of A. bam-
bucifoliae. This gall (no. 87076) had 17 subgalls and needle-
like projections at the base, and was on a slender twig (ca. 2.5
mm in diameter). These are typical characters of A. bam-
bucifoliae galls. However, the surface of this gall was unusu-
ally waxy, and subgalls were somewhat thick; the thickest subgall
was 5 mm in width. Having dissected this gall, we found well-
developed coral-like projections occurring from the walls of sub-
galls (Fig. lB - D). Many apparent soldiers were walking on the
gall surface. When the gall was touched, one of them climbed on-
to a finger and bit the skin with its stylets. Microscopic exam-
ination confirmed that it was a soldier of C. bambusae. Others
were no doubt also soldiers of this species. A total of 1203
aphids was found in the gall; 52 (4.3%) were A. bambucifoliae,
and the rest C. bambusae (Table 1). Alatoid larvae of both spe-
cies were included.
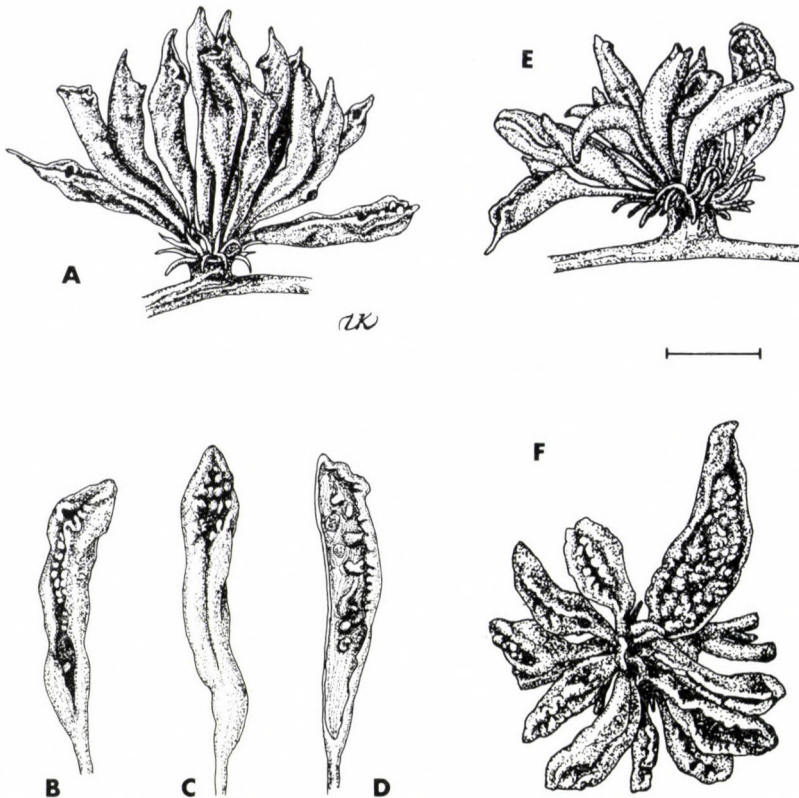
Fig. 1. "Chimeral" galls: A, gall 87076; B, a subgall of gall
87076; C, another subgall of gall 87076; D, its longitudinal
section; E, gall 87095; F, gall 88012. Scale: 10 mm for A &
E and 7.5 mm for B, C, D & F.

2. Galls 87094 and 87095

Galls 87094 and 87095 were found on another tree at Sun Moon
Lake on October 28, 1987. When we collected these galls, we
thought that they were normal galls of A. bambucifoliae. Later,
we noticed some soldiers of C. bambusae at the bottoms of vials
in which the galls were preserved. Both galls were on slender
twigs (ca. 1.5 mm for gall 87094 and 2.0 mm for gall 87095 in

Table 1   Composition of inhabitants for 4 galls of Astegopteryx bambucifoliae which were invaded by Ceratoglyphina bambusae.

Gall #	No. of aphids*							
	Alate adult	Alatoid L4	L3	Apterous adult	L2-4**	L1	Soldier	Total
87076 (colony size = 1203)								
C.b.	0	4(0)	26(0)	168	177(36)	360(131)	416(0)	1151
A.b.	1	21(8)	9(4)	2	10(2)	5(1)	4(0)	52
87095 (colony size = 153)								
C.b.	0	0	0	28	49(16)	47(20)	29(0)	153
A.b.	0	0	0	0	0	0	0	0
87094 (colony size = 986)								
C.b.	0	0	0	42	77(11)	75(22)	22(0)	216
A.b.	0	0	0	1	0	0	0	1
88012 (colony size = 768)								
C.b.	0	2(0)	0	53	32(2)	63(18)	63(0)	213
A.b.	0	0	0	0	0	0	0	0

Abbreviations. C.b.: Ceratoglyphina bambusae; A.b.: Astegopteryx bambucifoliae; L1, L2, L3 & L4: 1st, 2nd, 3rd & 4th instar larvae, respectively.
* No. of those aphids that had the next instar cuticle developing inside in parentheses.
** Nonwingpadded larvae.

diameter) and had a number of needle-like projections at their bases as in normal galls of A. bambucifoliae (Fig. 1E).

Gall 87094 had 14 subgalls; one of them had developed ramified projections inside, 6 had very short projections, and the remaining 7 had no such projections. Almost all the aphids in this gall were C. bambusae with only a few A. bambucifoliae (Table 1).

Gall 87095 had 15 subgalls. One subgall had well-developed projections inside. Most aphids were among the projections in this subgall. The other subgalls had no such projections. There were no living aphids of A. bambucifoliae in this gall, but a

dead and deformed lst-instar exule of A. bambucifoliae was found, which had probably erroneously been deposited by an alate.

Neither alates nor alatoid larvae of C. bambusae were found in these 2 galls (Table 1).

3. Gall 88012

Gall 88012 (Fig. lF) was collected on a tree (tree KL) at Sun Moon Lake on February 29, 1988. At first glance we mistook this for an ill-developed gall initiated by C. bambusae, because one of its subgalls was wholly coated with wax and looked remarkably white. Also, this subgall was thick (8 mm in diameter) and many coral-like projections were exposed just like an immature or ill-developed subgall of C. bambusae. Many aphids of C. bambusae were in and on the surface of this subgall. However, this gall was on a slender twig (ca. 2.5 mm in diameter), and consisted of 10 subgalls and a few short needle-like projections. These characters show that the gall was originally formed by A. bambucifoliae. Although all the living aphids (including alatoid larvae) in the gall were C. bambusae (Table 1), we were able to find a dead 4th-instar alatoid aphid of A. bambucifoliae among carcasses in a withered subgall.

4. Soldiers' sterility

We examined a total of 530 mounted specimens of C. bambusae soldiers under a microscope. None of them had the next instar cuticle developing inside (Table 1). This is the first case where all the soldiers in a gall were examined in this respect.

DISCUSSION

There is no doubt that galls 87094 and 87095 had originally been formed by A. bambucifoliae despite the fact that few (in gall 87094) or no (in gall 87095) living aphids of A. bambucifoliae were found. We think that the same is true of galls 87076 and 88012, and not that they were initiated by C. bambusae, for the following reasons. 1) There were too many subgalls for them to be normal galls of C. bambusae. 2) Needle-like projections remained at the bases of the 2 galls. Such projections soon fall off the gall of C. bambusae (Kurosu & Aoki unpubl.). 3) The primary slit of each subgall of these 2 galls nearly reached the base (see Fig. 1A, B, C & F), while that of a normal gall of C. bambusae does not. 4) The 2 galls were on slender twigs and contained alatoid larvae. A 0-year-old gall of C. bambusae may occur on such a slender twig, but produces no alates. Thus, we conclude that the 4 galls with mixed characters of the 2 species' galls were initially formed by A. bambucifoliae and later invaded and transformed by C. bambusae. On trees D and KL, from which galls 87076 and 88012 were collected, we found 3 and a number of normal galls of C. bambusae, respectively. Unfortunately, we did not record which tree galls 87094 and 87095 were collected from, but it is likely to have had galls of C. bambusae since all the trees we examined at Sun Moon Lake harbored some galls of this species at that time. The distance between gall 87076 and the nearest gall of C. bambusae was 65 cm.

Gall invasion is no doubt advantageous to C. bambusae; galls 87076 and 88012 contained alatoid larvae, showing that the invaders actually or almost succeeded in producing alate migrants

that fly to bamboos, in addition to the presumed production of a-
lates in their maternal galls. When and how aphids of C. bam-
busae invade galls of A. bambucifoliae remain to be investigated.
It is reasonable to suppose that it is apterae and/or immatures
that invade galls. Takahashi (1930; cited by Aoki et al. 1977)
observed that apterous adults and immatures of C. bambusae
crawled out of their gall and walked around on twigs, though we
have not yet seen such behavior except in soldiers (cf. Aoki
1979a). It is also interesting to know whether soldiers of A.
bambucifoliae and C. bambusae fight each other. Lastly, we sug-
gest the occurrence of aphid migration between conspecific galls
of C. bambusae. If the invasion of galls of A. bambucifoliae is
advantageous to C. bambusae, invasion of other conspecific galls
will also be advantageous to individual clones of C. bambusae
(cf. Aoki 1979b, 1982, Hamilton & May 1977).

REFERENCES

Akimoto, S., (1988) Competition and niche relationships among
    Eriosoma aphids occurring on the Japanese elm. Oecologia
    75: 44-53.

Aoki, S., (1979a) Further observations on Astegopteryx
    styracicola (Homoptera: Pemphigidae), an aphid species with
    soldiers biting man. Kontyû 47: 99-104.

Aoki, S., (1979b) Dimorphic first instar larvae produced by the
    fundatrix of Pachypappa marsupialis (Homoptera: Aphidoidea).

Kontyû 47: 390-398.

Aoki, S., (1982) Soldiers and altruistic dispersal in aphids. In
    Breed, M. D., Michener, C. D. & Evans, H. E. (eds.), The
    Biology of Social Insects, pp. 154-158. Westview Press,
    Boulder.

Aoki, S. & Kurosu, U., (1989) Host alternation of two Taiwanese
    cerataphidines (Homoptera, Aphidoidea). Akitu n.s. (107): 1-11.

Aoki, S., Yamane, Sk. & Kiuchi, M., (1977) On the biters of
    Astegopteryx styracicola (Homoptera, Aphidoidea). Kontyû
    45: 563-570.

Hamilton, W. D. & May, R. M., (1977) Dispersal in stable
    habitats. Nature 269: 578-581.

Kurosu, U. & Aoki, S., (in press) Formation of a "cat's-paw" gall
    by the aphid Ceratovacuna nekoashi (Homoptera). Jpn. J. Ent.

Setzer, R. W., (1980) Intergall migration in the aphid genus
    Pemphigus. Ann. Entomol. Soc. Amer. 73: 327-331.

Takahashi, R., (1930) An aphid species with the habit of biting
    man. Trans. Nat. Hist. Soc. Formosa 20: 43-44 (in
    Japanese).

Takahashi, R., (1939) A new aphid producing galls in Formosa.
    Zool. Mag. 51: 425-427 (in Japanese with English summary).

THE INDUCTION OF PERFORMANCE CHANGES IN APHIDS

Aulay   Mackenzie

School of Biological Sciences,
University of East Anglia,
Norwich, U.K.

ABSTRACT

Induction of a change in lifetime fecundity was observed in *Aphis fabae* and *Myzus persicae* when each was offered a novel diet. General evidence for the ubiquity of this effect is considered. A simple discrete generation mathematical model is used to analyse the effect of this on optimal host choice. The cost of the inductive period is found to diminish with time if the novel host is of poorer quality than that to which the herbivore is already acclimatised, but rises to a constant if the novel host is of equivalent quality.

INTRODUCTION

An individual polyphagous herbivore in search of food has essentially two criteria on which to choose its' next host, i) the quality of available plants and ii) the local abundance of any species. Higher quality hosts (those conferring a higher fitness) will be preferred to lower quality hosts; for example, Müller (1958) showed that *Aphis fabae* was ten times as likely to accept a susceptible *Vicia faba* variety as a resistant one. However, even a poor host may be accepted if the herbivore finds nothing else. Jermy (1987) has reviewed the induction of preference changes and shown that many polyphagous species will accept a previously rejected plant after continued exposure. This behaviour may be interpreted purely in the context of bet-hedging, but is any other criterion at work? Various

authors have indicated that herbivores across the animal kingdom may acquire physiological adaptations to a specific diet. Does this occur in aphids, and what is the consequence of this to the decision-making process?

Firstly, let us consider some existing evidence for diet-induced performance changes in herbivores. Bank voles (*Clethrionomys glareolus*) have been shown to increase assimilation efficiency and decrease throughput times after exposure to a particular diet (Partridge & Green,1985). Karowe (1989) measured relative growth rate in fifth instar larvae of *Colias philodice* (Lepidoptera) on one of three diets as a function of the plant species consumed in earlier instars.In each case forced host-switching resulted in reduced larval growth largely attributable to a reduced capacity to convert digested food into larval tissue (Figure 1a).

Figure 1a.

Performance of *Colias philodice* larvae.
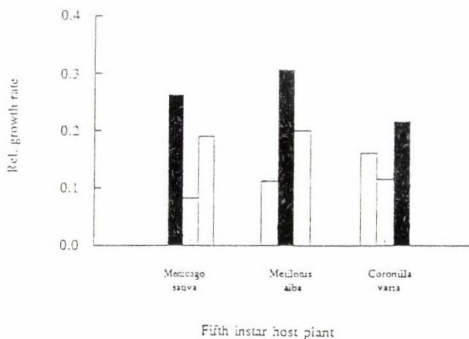
Figure 1b.

Growth rates of *Deroceras reticulatum.*
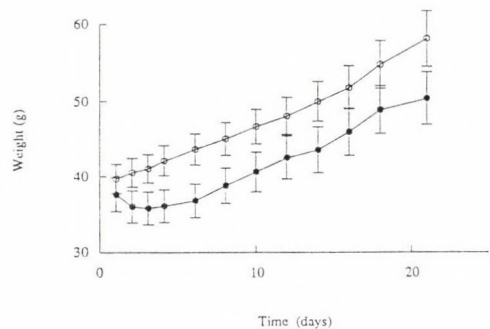
Solid bars represent individuals which spent first four instars on that host.. Symbols : solid = HP, open =BH. Error bars above and throughout are standard errors.

Mackenzie (1987) recorded a weight gain in two populations of the mollusc *Deroceras reticulatum* on a diet of *Trifolium repens*. One population (HP) had not been exposed to *T. repens* in the field, and this population initially performed poorly on this diet and then gained weight at an equivalent rate to the preadapted population BH (Figure 1b). This effect was not due to initial differential feeding rates.

The above examples both refer to physiological changes within a generation. In a study of adaptation of populations of the thrips *Aterothrips secticornis* to individual host plants (Karban,1989), a change across generations is apparent (P<0.0001 paired t-test) (Figure 2a. Data recalculated from Karban (1989)). Micha (1989) looked for this affect in the aphid *Myzus persicae* and showed a gradual but non-significant increase in r_m over four generations on *Rumex obtusifolius* (Figure 2b).

Figure 2a. Change in rate of increase   Figure 2b.Change in r_m
in *Myzus persicae* over four   in *Aterothrips secticornis*
generations.
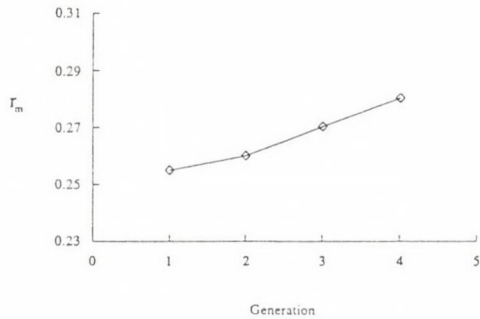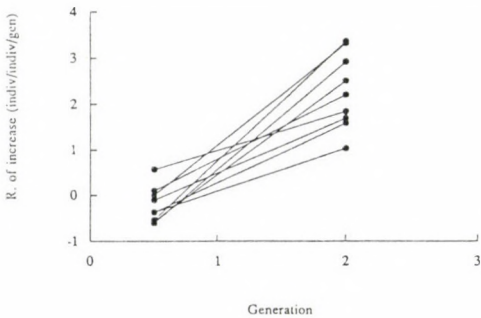
The physiological mechanism of performance induction is likely to differ in detail between organisms and diets, but whether detoxification processes are involved (Ahmad,1982) or nutritional differences (Ishaaya & Swirski,1976), the changes observed are consistent with changes in enzyme levels and activities.

MATERIAL AND METHODS

Fecundity and survival of individual aphids was recorded in two experiments,in both of which aphids were introduced to a new diet. The previous diet, on which the clone had been maintained for at least 4 generations, was used as a control.

1) *Aphis fabae* on *Tropaeolum majus* (new host) and *Vicia faba* (control);

2) *Myzus persicae* on low (50%) amino acid level artificial diet (new diet) and. artificial diet (Kunkel,1977) (control).

All treatments were conducted at 20°C and 16L:8D day length with irradiance at 200 ± 50 μmol m-2 sec-1. Aphids were confined to plants by the use of clipcages, those on artificial diets by perspex cylinders (Kunkel,1977). Aphid density was controlled within each cage by nymph removal every 48 hours. Plants and artificial diets were replaced regularly. Only one genotype of each aphid species was used.

Measurement of each generation continued for 20 days of adult life. To test for the effect of changes in acceptance directly upon performance, in the second experiment the feeding status of all individuals was recorded over a 10 minute interval at each fecundity assessment.

RESULTS

The cumulative fecundities of each treatment for each generation are shown in Figure 3 a) and b).A significant change in the total fecundity after 20 days of adult life was observed between the first and second generations on the novel diet in both experiments.

Figure 3.

a) The change in cumulative fecundity of *Aphis fabae* over three generations on *Tropaeolum majus*.

b) The change in cumulative fecundity of *Myzus persicae* over two generations on reduced (50%) amino acid artificial diet.
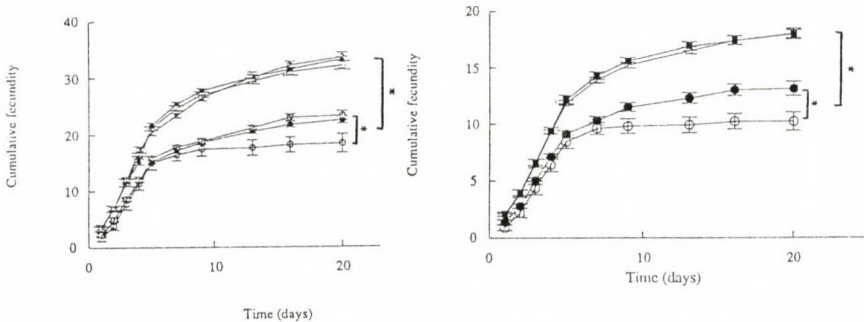
Symbols: squares = control diet , circles = experimental diet, open symbols = 1st generation, closed symbols = 2nd generation, shaded symbols= 3rd generation. Significance at day 20 is as indicated (Mann-Whitney U test).

The feeding status of 1st generation *Myzus persicae* individuals on the experimental diet is shown in Figure 4. No diet rejection was observed by the control animals, nor by either group in the 2nd generation.

Figure 4. Change in acceptance of a novel diet in *Myzus persicae*.
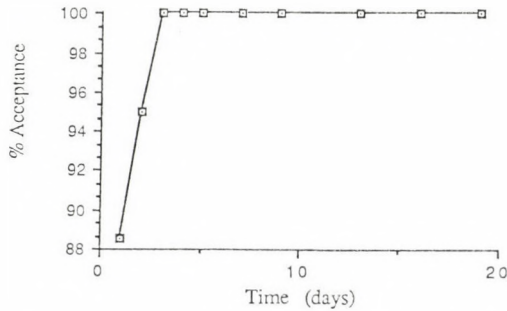
DISCUSSION

The above evidence strongly supports the hypothesis that physiological acclimation to a novel diet does occur in aphids. The initial difference in diet acceptance shown in Figure 4 is not large enough to create the significant difference in fecundity observed.

What affect should we predict physiological acclimation to have on aphid behaviour ? As fecundity is initially lower than its final value, one would expect that a novel host on which induction of performance occurs (an "inductive host") is chosen less readily than if there were no inductive lag. We can address this with the use of a simple model. Considering the simplified case of discrete generations, an inductive host is preferable to that which the aphid is acclimatised to if

$$\frac{P_x}{P_a} > \frac{F^n}{\prod_{i=1}^{n} (F - C_i - D)}$$

where

P_a =   probability of eventually finding host A to which aphid
is acclimatised

P_x =   probability of eventually finding any inductive host

F =   lifetime fecundity on host A

C_i =   pre-acclimation fecundity deficit in generation i on
novel host

n =   number of generations

D =   difference in lifetime fecundity on host A and inductive
host, after acclimation

Thus, if the chance of an aphid finding the host to which it is
acclimatised (P_a) is low relative to P_x, it should accept any potential
host, even if the eventual fecundity on that host is low . If   D=0 then
$F^n/\Pi(F-C-D)$ will tend to a constant after C=0 (when the inductive period is
over) as the number of generations (n) before another host-shift occurs
increases. However, if D>0 (the inductive host is of poorer quality) then
$F^n/\Pi(F-C-D)$ will decrease exponentially with increasing n, by F-D/F per
generation after C=0. Similarly, the cost of the inductive period, given by
the difference between the 'preference index' $F^n/\Pi(F-C-D)$ with ΣC = 0 and
ΣC > 0 for a given non-negative D will fall. The effect of induction in
these two alternative situations, with D = 0 and D > 0 are illustrated by
two example scenarios in Figure 5. Clearly, in this case, the number of
generations before a comparison in fitness is made is critical. The
carrying capacity of the host, the graininess of the environment (i.e.
the degree to which host species are aggregated) and the type of life cycle
of the aphid (whether autoecious or heteroecious) are key factors in
determining when a host-shift will occur,and hence will affect the optimal
host choice decision.

Figure 5. The effect of the cost of the inductive lag on the preference index, $F^n/\Pi(F-C-D)$.
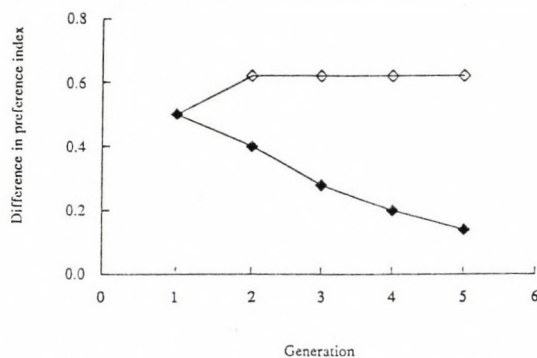
Symbols : open :   D = 0,   closed D=3.   Example data set   F=10, ($C_{i=1}$=5, $C_{i=2}$=2.5, $C_{i=3}$ = 0)

CONCLUSION

Aphids may experience a change in performance after exploiting a new host species. This performance change will affect the optimal host choice decision in a way that depends on the difference, after induction, between lifetime fecundity accrued by the aphid on the new host and that accrued on the previous host plant species. The number of generations the aphid can expect on the new host will also affect the decision.

LITERATURE

Ahmad, S. (1982) Roles of mixed-function oxidases in insect herbivory. In Proc. 5th Int. Symp. Insect-Plant Relationships. Eds Visser, J.H. and Minks, A.K. Pudoc, Wageningen.

Ishaaya, I. & Swirski, E. (1976) Trehalase, invertase, and amylase activities in the black scale, *Saissetia oleae* and their relation to host adaptability. J. Insect Physiol. 22:1025-1029.

Karban, R. (1989)   Fine-scale adaptation of herbivorous thrips to individual host plants. Nature 340,60-61.

Karowe, D.N. (1989) Facultative monophagy as a consequence of prior feeding experience: behavioural and physiological specialization in *Colias philodice* larvae. Oecologia 78,106-111.

Kunkel, H. (1977) Membrane feeding systems in aphid research.in Aphids as Virus Vectors Eds Harris,K.F. & Maramorosch,K. Academic Press, NY.

Mackenzie, A. (1987) An investigation into the effect of monomorphic diets of cyanogenic and acyanogenic *Trifolium repens* on the weight gain of different populations of the grey field slug, *Deroceras reticulatum*. BSc (Hons) Thesis, University of Edinburgh.

Micha, S.G. (1989) A study of the phenomenon "induction" in the green peach aphid (*Myzus persicae*) on broad-leaved dock (*Rumex obtusifolius*) as an unsuitable host plant. BSc (Hons) project. University of East Anglia.

Müller, H.J. (1958) The behaviour of *Aphis fabae* in selecting its host plants,especially different varieties of *Vicia faba* .Ent. exp. appl. 1,66-72.

Partridge, L. & Green, P. (1985) Intraspecific feeding specializations and population dynamics. In Behavioural Ecology Ecological Consequences of Adaptive Behaviour Eds Sibly, R.M. and Smith, R.H. Blackwell,Oxford.

CONJECTURAL EVOLUTION OF APHIDS ON PTERIDOPHYTA

Fritz Paul Müller

Phyto-Entomologie, Sektion Biology,
Wilhelm Pieck-Universität, DDR-2500 Rostock

ABSTRACT

Among the Pteridophyta ferns and horse-tails are colonised
by aphids. The species in question belong to modern genera, and
their host specificity cannot be the consequence of coevolution.
Most probably the speciation happened not earlier than the end
of the Miocene when ancestoral Macrosiphoninae shifted from
Angiospermae to Pteridophytina and Sphenophytina. Pteridophyta
inhabiting aphids examined by the author are sciophilous and
hygrophilous. This pecularity reflects the habitat requirements
of the host colonized by these aphids.

INTRODUCTION

Material for this paper was furnished by collecting trips in
the low- lands of the Rostock district and the subalpine
mountains of Saxony.

MATERIALS AND METHODS

Aphids were collected as for taxonomic purposes. Moreover,
some species were conveyed alive to Rostock and there reared on
their natural host plant in a field insectary. This allowed
aphids to be transferred to normally growing potted plants for
ascertaining the spectrum of potential hosts and other
autecological pecularities.

RESULTS

All finds were made in humid and very shaded sites.   I found
Utamphorophora alpicola H.R.L. on Dryopterus carthusiana and
Asplenium trichomanes in Saxony and Austria.   In the field
insectary the aphids inclusive of the fundatrix developed best
on Cystopteris fragilis and also on Asplenium ruta muraria and
A. septentrionale.   However, the latter three ferns grow on
sunny dry walls and rocks, and I never found U. alpicola on them
in nature.   Consequently both the nature of the habitat and the
presence of a suitable plant are important for the survival of
this aphid.

In very similar biotopes I found Sitobion dryopteridis
(Holman) on Athyrium filix-femina and Gymnocarpium robertianum.
Nevertheless the aphids inclusive of the fundatrix developed and
propagated best on Cystopteris fragilis on which I have never
found this aphid in the field.   S. dryopteridis was observed in
two colour varieties, a yellowish green and a bright green,
which have similar host preferences (F.P. Muller, 1987).
Amphorophora ampullata Buckton is so demanding of a suitable
environment that it is difficult to maintain permanent cultures
in an insectary.   I found A. ampullata on the underside of the
leaves of Athyrium filix-femina, particularly when the
fern-fronds projected over brooklets in forests.

Preference for a distinct habitat involves close linkage
with the choice of the mate.   Differential host choice implies
bringing together of the sexuales, and according to Jermy (1976)
it is logical to suppose that in many cases mutational changes
in feeding behaviour resulted in sufficient isolation for
sympatric speciation, and the choice of a plant species often
means also the choice of a well-defined combination of biotic
and abiotic factors.   Both behavioural and ecological
characteristics are inherent in organisms and limit gene flow by
intrinsic barriers.   They are premating isolating mechanisms.
The origin of fern aphids and most probably those living on
Equisetum represent examples of the two-allele speciation
recently discussed by Diehl and Bush (1989).

It is interesting that fern and horse-tail inhabiting aphids
belong to modern genera. Apparently the colonisation of
Pteridophyta was not a result of co-evolution. Probably the
differentiation of Aphididae sensu Börner (1952) began not
earlier than in the middle Tertiary when the Angiospermae
existed in higher diversity than in the present flora.
According to Hille Ris Lambers (1950) Rosaceae played a
mediating role in the evolution and host acceptance of aphids.
Factually, the genera Amphorophora and Macrosiphum, inclusive of
Sitobion, are Rosaceae inhabiting species. The same is true for
Utamphorophora according to the review of Remaudière (1983).

   With the exception of Amphorophora ampullata, which occurs
in North America as well as in Japan and Europe, and the
world-wide distributed Idiopterus nephrelepidis, the North
American fern aphids differ from the European ones. This
appears explicable historicozoogeographically. Up to the
Oligocene North America and Eurasia were joined allowing
far-reaching dispersal of the then existing aphid genera. By
the end of the Miocene the Nearctic fauna became isolated from
that of Eurasia, and the shift to ferns happened independently
in the two continents. Thus Utamphorophora produced fern
inhabitants only in Eurasia (Miyazaki 1968).

   I have never found on outdoor ferns and horse-tails aphids
other than the above mentioned species. Yet, I have observed
vigorous colonies of Aulacorthum solani on Adiantum sp. during
winter in a greenhouse at Rostock. Obviously Spermatophyta are
not colonised by fern aphids in the natural environment.
However, Iglisch (1968) succeeded in transfering Idiopterus
nephrelepidis from Adiantum to some Angiospermae. Such
exceptional feeding of Aulacorthum solani and Idiopterus
nephrelepidis on unusual plants can be interpreted as xenophagia
in the sense of Hering (1955). Xenophagia is possible because
many non-host plants can supply the nutritional requirements of
a phytophagous insect (Jermy, 1984). Host plant specificity is
basically a behavioural phenomenon because aphids distinguish
between hosts and non-hosts mainly by means of the chemical

information received by their receptors when probing after
alighting. Probing evokes either an arrestant or deterrent
response with differential intensity. When collectors think
they have found a new host plant for a given aphid, then they
should determine whether euphagia or xenophagia is involved.

REFERENCES

Borner, C. (1952): Europae centralis Aphides. Mitt. Thür. Bot.
    Ges. Beiheft 3, Weimar. 448 pp.

Diel, S.R. & Bush, G.L. (1989): The role of habitat preference
    in Adaptation and Speciation. In: Speciation and its
    Consequences, ed by D. Otte and J. Endler. Sinauer Assoc. 28
    pp.

Hering, E. (1955): Die Nahrungswahl phytophager Insekten. Verh.
    Deutsch. Ges. ang. Ent. **13**. 29-38.

Hille Ris Lambers, D. (1950): Host plants and aphid
    classification. Proc. Int. Cong. Entom., Stockholm **8**.
    141-144.

Iglisch, I. (1968): Uber die Bewertung von Pflanzen als
    Nahrungsquelle für polyphage Blattlausarten
    (Homoptera:Aphididae). Z. angew. Zool., **55**. 489-492.

Jermy, T. (1976): Insect-host-plant relationship, co-evolution
    or sequential evolution? Symp. Biol. Hung. **16**. 109-113,
    Budapest.

Jermy, T. (1984): On the evolution of insect/host plant systems.
    Verh. X. Int. Symp. uber Entomofaunistik Mitteleuropas 1983.
    13-17.

Miyazaki, M. (1968): A revision of fern aphids of Japan with
    descriptions of three new species. Ins. Matsumurana,
    Sapporo. **31**(3). 13-24.

Müller, F.P. (1987): Faunistisch-ökologische Untersuchungen über
    Aphiden im westlichen Erzgebirge und Vogtland. Faun. Abh.
    Mus. Tierk. Dresden **14**, Nr. 105-129.

Remaudière, G. (1983): Pucerons nouveaux et peu connus du
    Mexique, 5e note. Ann. Soc. Ento. France **19**(2). 227-233.

OVERLOOKED MEMBERS OF THE BLACK BEAN AND BEET
APHID COMPLEX

Fritz Paul Müller

Phyto-Entomologie, Sektion Biologie,
Wilhelm Pieck-Universitat, DDR-2500 Rostock.

ABSTRACT

The three most common black aphids of the group under
consideration are Aphis fabae Scopoli, A.cirsiiacanthoidis
Scopoli, and A. solanella Theobald. They host alternate to
Euonymus europaea. Aphis mordwilkoi Börner and Janisch, which
host alternates to Virburnum opulus, and the autoecious A.
philadelphi Börner and Janisch are uncommon. Aphis euonymi
Fabricius is autoecious on Euonymus and differs from the other
forms of the complex in that the mothers of the oviparous
females are apterous. The four forms living on Euonymus
europaea are subspecies. Aphis armata Hausmann is the 7th aphid
in this group. It is autoecious on Digitalis and classified as
a sibling species.

INTRODUCTION

Faunistic investigators often record only "Aphis fabae" and
are unaware that one of at least seven biologically different
forms may be involved. Recognition of a form depends on testing
many populations taken from colonized plants and on observations
on the yearly life-cycle.

MATERIAL AND METHODS

Black aphids were taken from different plants and subjected
to our test method (F.P. Muller, 1982). Transfer trials and

host choice experiments were made in a field insectary using potted plants that had been treated with a non-residual insecticide. Particular care had to be exercised in maintaining stock cultures in order to avoid contamination. Observations on hibernation and the results of hybridization experiments are included.

RESULTS

The exules of the four heteroecious members have a broad host spectrum. The three aphids that host alternate to Euonymus europaea may be distinguished by a biological test because each of them has its particular marking host, which is Vicia faba for fabae sensu stricto, Cirsium arvense for cirsiiacanthoidis Scop., and Solanum nigrum for solanella Theob.

However, we have not identified a marking host for mordwilkoi Börn. and Janisch, the primary host of which is Viburnum opulus. Janisch (1926) supposed Arctium lappa was the typical host of mordwilkoi. But our tests and transfer experiments have demonstrated that burdock is also colonized by fabae s.str. and cirsiiacanthoidis. The marking hosts of the three first-named aphids are rejected by mordwilkoi. Suitable hosts for mordwilkoi, in addition to Arctium lappa, are Tropaeolum majus and Rheum rhabarbarum, however, garden nasturtium may be colonized also by fabae s.str., and rhubarb is an important host moreover of solanella. Aphis barbarae Robinson, 1980, found in Canada possesses a host spectrum similar to mordwilkoi, but it seems not to be identical with the latter because it is reported by Lamb (1980) from Cirsium arvense, which is rejected by mordwilkoi. Mordwilkoi is very common at Naumburg where Börner made his observations on aphids. It occurs rarely in the district of Rostock, and Iglisch (1968) could not find it in Berlin. Its scarcity may be the reason why this aphid has been overlooked since 1926.

Euonymus europaea is colonized not only by the three host alternating aphids mentioned above but also by the autoecious A.euonymi F. (= A. cognatella Jones). The four Euonymus

inhabiting aphids produce viable hybrids. Aphis euonymi is
distinguished from the other three aphids on spindle by having
apterous gynoparae and by its brown colour. The former
character is inherited dominantly. Thus in the F_1 the oviparous
females were exclusively the daughters of apterae. The colour
of the F_1 lineages was dark brown, i.e. intermediate. In the F_2
there were 41 black, 88 dark brown and 44 brown, an appropriate
Mendelian pattern. The black lineages behaved in their host
choice like fabae s.str., whereas the brown ones proved to be
restricted to Euonymus europaea. Thus colour is coupled with
host choice.

The autoecious A. philadelphi Borner and Janisch has also
been overlooked since 1926. I have found it regularly at
Naumburg but never at Rostock. It has not been found in Berlin
(H.J. Muller, 1951) or Quedlinburg (County of Halle). All in
all it may be denoted a rare aphid. Its host, Philadelphus
coronarius, is everywhere heavily infested by black aphids of
the fabae group. Predominantly such aphids belong to cirsiia-
canthoidis, but mordwilkoi may colonize on mock orange too. If
fundatrices are found on Philadelphus coronarius then
philadelphi is present.

Aphis armata Hausmann is autoecious on Digitalis. The
oviparous females can be the offspring of apterae or alatae. In
its morphology it resembles cirsiiacanthoidis which, however,
does not settle on Digitalis purpurea. On the other hand,
Digitalis purpurea is an excellent host for fabae s.str. and
solanella. The latter aphid may be recognised by its shorter
hairs and by the higher number of marginal tubercles on the 2nd
to 5th abdominal segments. However, the morphological
conformity with fabae s.str. is rather complete. Black aphids
living at Naumburg and in Thuringia on Digitalis purpurea
readily accepted Vicia faba and consequently proved to be fabae
s.str. Identification of A. armata solely on the basis of its
occurrence on foxglove is inadmissible. Aphis armata has hardly
attracted any attention even though Jacob (1945) and Borner
(1952) recognised it as a real species. Because of their

morphological similarity and their host relations, records of A. armata and A. fabae from Digitalis purpurea must be regarded with some caution.

CONCLUSIONS

Three of the seven members of the fabae group, i.e. mordwilkoi, philadelphi and armata, have been usually overlooked. This is because of their rarity and the fact that many plants are suitable hosts for two or even more of these aphids. The most common forms, that is, fabae s.str., cirsiiacanthoidis, solanella and euonymi, whose sexuales occur on Euonymus europaea at the same time, may produce viable hybrids in an insectary. They should be treated as subspecies. This rank is also pertinent to mordwilkoi and to philadelphi because a race of fabae s.str. also uses Viburnum opulus as its primary host thus allowing the sexuales to meet those of mordwilkoi, and the gynoparae of cirsiiacanthoidis accept Philadelphus coronarius as well as Euonymus europaea. As shown by the hybridization between euonymi and fabae s.str. genetic recombination ensures the maintenance of each form. The monophagy of A. armata implies a strict premating isolation machanism, and on the basis of this A. armata is classified as a sibling species of A. fabae sensu latiore.

ACKNOWLEDGEMENT

REFERENCES

Börner, C., (1952): Europae centralis Aphides. Mitt. Thur. Botan. Ges., Weimar, Beiheft **3**. 484 pp.

Börner, C. und Janisch, R., (1922): Zur Lebensgeschichte und Bekampfung der "Schwarzen Blattlause". Nachrble. Deutsch. Pflanzenschutzdienst Berlin-Dahlem **8**. 1-3

Iglisch, I. (1968): Über die Entstehung der Rassen der Schwarzen
    Blattläuse (Aphis fabae Scop. und verwandte Arten), über ihre
    phytopathologische Bedeutung und über die Aussichten für
    erfolgversprechende Bekämpfungsmaßnahmen (Homoptera:
    Aphididae). Z.ang. Zool., Berlin **52**(2). 153-160.

Jacob, F.H. (1945): Note on classification of British species of
    "black aphides" (Hemiptera, Aphididae). Proc. R. Ent. Soc.
    London (B) **14**. pts 7-8, 102-110.

Janisch, R., (1926): Lebensweise und Systematik der "Schwarzen
    Blattläuse". Arb. Biol. Reichsanst. f. Land-u.
    Forstwirtschaft Berlin-Dahlem **14**(3). 291-364.

Lamb, R.J. (1980): The rise and decline of a local population of
    the aphid Aphis barbarae (Homoptera: Aphididae). Canad. Ent.,
    Ottawa **112**. 1285-1289.

Müller, F.P. (1982): Das Problem Aphis fabae. Z. ang. Zool.,
    Hamburg und Berlin **94**. 432-446.

Müller, F.P. (1988): Revision of Börner's black 'Naumburg' Aphis
    species (Homotera: Aphididae). Entomol.Gener., Stuttgart
    13(3/4). 263-268.

Müller, H.J. (1951): Über die Bedeutung der Winterwirte für die
    Bekämpfung der Schwarzen Bohnenblattlaus (Doralis fabae
    Scop.). Nachrble. Deutsch. Pflanzenschutzdienst N.F., Berlin
    5. 111-115.

Robinson, A.G. (1980): A new species of Aphis L. (Homoptera:
    Aphididae) from nasturtium. Canad. Ent. **112**. 123-125.

SPRING MIGRATION OF THE CARAWAY ROOT APHID,
Pemphigus passeki BÖRNER (HOMOPTERA: APHIDOIDEA)

Jacomijn D. Prinsen
Research Institute for Plant Protection
P.O. Box 9060, 6700 GW Wageningen, The Netherlands.

ABSTRACT

Pemphigus passeki Börner, the caraway root aphid, often
causes severe damage in caraway (Carum carvi) in the first
year of this two-year crop. It host alternates between the
primary hosts Populus nigra and P. italica and the secondary
host caraway. Migration from poplar to caraway takes place
from mid-June to mid-August. From year to year the number of
aphids collected range from a few aphids per season to several
dozen per week per yellow trap. In 1987 gall density on
poplars in a caraway area was low, at most one per 20 leaves,
and four yellow traps in commercial caraway fields captured a
total of only 16 specimens of P. passeki. Yet these fields
were succesfully colonized. Since two of these fields were
situated three kilometers from the nearest trees, P. passeki
seems a highly efficient colonizer.

The production of alatae is induced by daylength, a
decrease in temperature is not necessary. Part of the
population does not develop wings and hibernates in the soil.
Severe winters can be survived on caraway roots. Alatae
originating from caraway are sexuparae and contain embryos
without functional mouthparts. One possible virgino-sexupara
has been found, therefore the possibility of migration between
secondary hosts cannot be excluded.

INTRODUCTION

Pemphigus passeki Börner can cause considerable damage to
caraway (Carum carvi) in the first year of this two-year crop.
In some years a quarter of the acreage has to be ploughed in
because of massive infestation. Symptoms, e.g. retarded
growth, discolouration of leaves, often followed by death of
the plants, become manifest in autumn. So far chemical control
has been unsuccesful.

The biology of Pemphigus species, predominantly of P.
bursarius, has been studied by Dunn (1959a), Lampel (1961), De
Brouwer (1962), Dolgova (1970), Herfs (1973), Alleyne and
Morrison (1977), Goszcsyński and Cichocka (1978) and others.
P. passeki is mentioned by Börner (1952) who described apterae
and alatae from caraway, by Lampel (1961) who stated
implicitly that its gall is similar to that made by P.
populinigrae, by Hille Ris Lambers and De Hey-Wiltenburg
(1966) who developed a rearing technique on caraway roots, and
by Blackman and Eastop (1984) who mention only the forms on
caraway.

To find ways to control damage by P. passeki, research has
been started on its identity and biology. This paper
concentrates on spring migration. Data concerning aphid
morphology and identification of galls are used here when
relevant but will be published in detail elsewhere.

METHODS AND MATERIALS

In the Oldambt, a Dutch caraway area, a survey of winter
hosts (Populus nigra and P. italica) was made in an area with
about 6 km diameter. Groups of trees were mapped, and
information on number, size and health of the trees was
recorded. For 24 trees, leaves on shoots within reach were
counted and classified as with/without midrib galls, in all
others only the total number of galls was recorded. With the
aid of binoculars a rough estimate was made of gall numbers in
the higher parts of the tree. A previous pilot study (Prinsen,

unpublished) had revealed that P. passeki makes a midrib gall, so other gall types could be omitted. A total of 215 midrib galls were collected for transfer tests.

In the same area, four yellow water traps monitored flights of P. passeki in four commercial caraway fields from June 26 to August 25, 1987. The traps measured 60 x 40 x 6 cm, were painted yellow with Sikkens Rubbol AZ nr. D826, contained water with a few drops of detergent, and were emptied twice a week.

To confirm immigration a root sample of about 10 caraway plants and surrounding soil was taken weekly from each field from June 30 to August 11. Samples weighed between two and four kg. If a first, non-destructive inspection did not reveal aphids, the clump was gently bedded in potting soil and left in an insect cage for three weeks for further development of the aphids, after which it was subjected to a final inspection.

A permanent culture of P. passeki was maintained in a greenhouse under long-day conditions (L16:D8) with additional lighting, and at a temperature of 10°C at night and 20°C during the day.

In spring, some root samples were taken from caraway sown in the previous year to assess overwintering on the secondary host. Alatae were collected from field and laboratory populations on caraway to assess the possible existence of a form which migrates between secondary hosts.

Meteorological data of weather station Eelde were taken from the Monthly Weather Report (KNMI, 1987).

RESULTS

The survey of winter hosts yielded a total of over 350 trees at 40 locations (Fig. 1). The fungus disease Marssonina had infested most P. italica trees and caused symptoms ranging from some brown spots on leaves to severe die-back. Forty-five trees were dead and not sampled, as were 5 locations which

were inaccessible. The remaining 15 P. nigra and 281 P.
italica trees were sampled for midrib galls.

    Gall density in the lower part of the tree ranged from nil
to one midrib gall per 20 leaves. Total counts on low shoots
plus an estimate of midrib galls on higher branches resulted
in an arbitrary division of trees into groups with many (over
50) and with few (less than 50) galls. Galled leaves occurred
more frequently on shoots with many leaves, but gall density
per leaf had no relation to the number of leaves per shoot. No
differences in gall density were found between P. italica and
P. nigra. Galls contained alatae throughout the sampling
period (June 30 to August 4), though in August most galls were
empty. Of the 215 leaves with midrib galls collected for
transference tests, 190 were positively identified as caused
by P. passeki. Among them three twin galls were found (Fig.2).
Since some variation occurs, part of the remaining galls might
also be associated with this species.

    The yellow water traps captured only 16 Pemphigus
fundatrigeniae between 7 and 17 July (Table 1). These were
identified as P. passeki, though P. bursarius might be
included because of morphological resemblance. Other Pemphigus

TABLE 1   IMMIGRATION OF PEMPHIGUS PASSEKI IN FOUR CARAWAY
           FIELDS, 1987.

date	A	B	C	D
30-6	0 (-)	0 (-)	0 (-)	0 (-)
7-7	1 (-)	4 (-)	4 (-)	0 (-)
14-7	1 (-)	0 (+)	1 (+)	1 (+)
21-7	0 (-)	1 (+)	2 (+)	1 (+)
28-7	0 (-)	0 (-)	0 (-)	0 (-)
4-8	0 (+)	0 (-)	0 (+)	0 (-)
11-8	0 (+)	0 (-)	0 (+)	0 (+)

A,B,C,D   field code as in Fig. 1.
left columns   number of fundatrigeniae in yellow water traps
+/-   with/without Pemphigus on root sample.
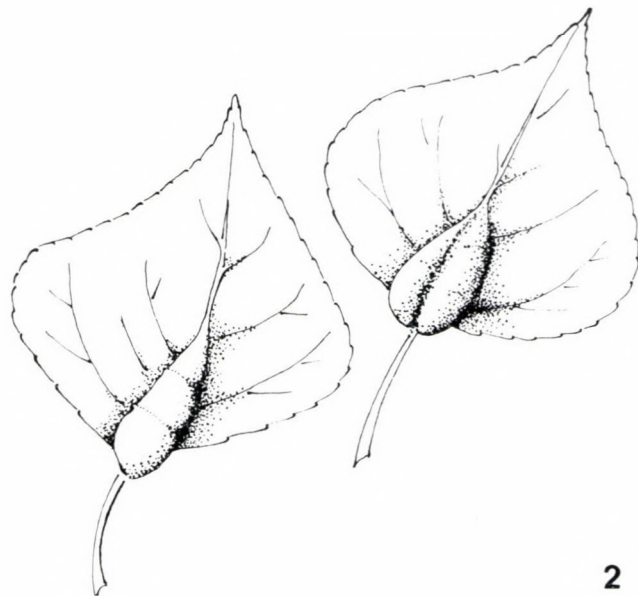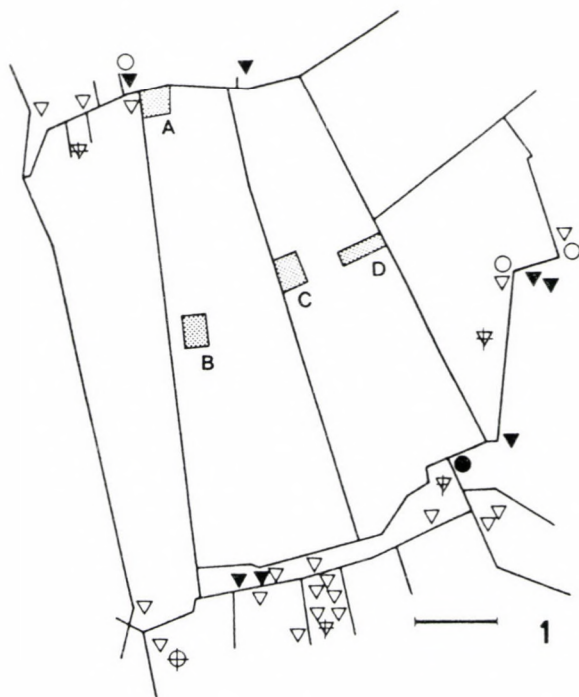
Fig. 1. Map of study area. Scale line = 1 km; ▭ caraway fields used in this study;
▽▼ Populus italica; ○● Populus nigra; ▽○ tree groups with < 50 galls,
▼● tree groups with > 50 galls by Pemphigus passeki; + Populus not sampled.
Fig. 2. Pemphigus passeki. Left: single gall, right: twin gall.

species have not been captured.

The first P. passeki aphids appeared on the root samples on July 14. From this date onwards half of the root samples were positive (Table 1). Spring samples of caraway roots taken in April 1987, after a severe winter, were positive.

The permanent greenhouse culture of P. passeki on caraway produced alatae in autumn and spring. A total of 142 alatae from this culture and from the field were mounted and screened for embryos with functional mouthparts. One out of 314 embryos possessed stylets. Its mother was a spring migrant from the greenhouse culture, had some morphological aberrations and contained three arostrate embryos too.

DISCUSSION

The highest gall density found in 1987, one midrib gall per 20 leaves, is low compared to densities found in previous years. Since a detailed survey of gall distribution in higher parts of the trees could not be made, the number of P. passeki galls may well be underestimated. Whether P. passeki has a preference for the higher parts of the tree, as does the related Thecabius lysimachiae (Heie 1980), or whether it is evenly distributed as are P. bursarius and P. spirothecae (Herfs, 1973), is not known. The occurrence of twin galls (Fig. 2) suggests seemingly peaceful cohabitation by two fundatrices sharing the same leaf, but since twin galls are each smaller than the maximum size of single galls, reproductive success may well be negatively affected (Whitham 1986).

The incidence of infestation on roots is high, when compared to the low number of fundatrigeniae in the traps (Table 1), especially because root samples were small, and taken before exules could have multiplied and spread over larger areas. Either a yellow water trap is a poor instrument to monitor Pemphigus flights, or P. passeki is a highly efficient colonizer. According to most authors, fundatrigeniae

deposit larvae on the foliage of secondary host plants, but P. phenax fundatrigeniae deposit their larvae on the soil in the vicinity of carrot plants (Goszczyński and Cichocka, 1978). Where host plant density is high, as is the case in arable crops, such behaviour will result in higher initial aphid incidence than deposition of all larvae on one plant. Whether P. passeki deposits its larvae on the soil has not yet been confirmed.

In this survey P. passeki succesfully colonized fields 3 km from the nearest aphid source (Fig. 1). It is unlikely that poplars have been overlooked in this vast stretch of treeless arable land between three villages. Wind velocity and direction during the period of migration were too variable to permit more detailed conclusions about the origin of migrants. Herfs (1973) claims that P. bursarius usually migrates less than 500 m, though distances of up to 4 km (McDaniel, 1958) have been recorded. Cichocka (pers. comm.) considers distances of more than 2 km irrelevant for colonization by P. phenax. This strongly contrasts with Elton's (1925) record of numerous Dilachnus (= Cinara) found alive at 1300 km from their hostplants.

A strong urge to give birth exists in fundatrigeniae of P. bursarius kept in small containers with a piece of lettuce leaf, where most larvae were produced within two hours after emergence from the gall (Dunn, 1959b). P. passeki fundatrigeniae deposited larvae even in containers without caraway. If such an urge exists also during flight, this will restrict the duration of flight and hence the distance covered by fundatrigeniae. Removal of trees is a possible strategy to reduce the number of aphids colonising caraway, but if substantial migration occurs over long distances such a measure becomes impractical.

The production of alatae in the greenhouse culture in autumn and spring was caused by insufficient intensity of the additional lighting, because temperature fluctuated only a few

centigrade degrees around the adjusted values. Since P.
passeki overwinters on roots in caraway fields and is able to
produce sexuparae in spring, spring migration to poplar is
expected. Such migration in Pemphigus can result in galls
later in the same spring (Bingham & Sokal, 1986) or in the
following year (Hille Ris Lambers and De Hey-Wiltenburg,
1967). Harvest of caraway takes place before autumn migration
starts, but if sexuparae migrate in spring before their
habitat is destroyed these will contribute to future
populations.

   In Pemphigus alate virginoparae from secondary hosts are
unknown except in the monoecious P. saliciradicis, which
produces both virginoparae and virgino-sexuparae, the latter
being a form with both rostrate and arostrate embryos (Aoki,
1975). Thecabius affinis, which some authors place in
Pemphigus, produces alate sexuparae in autumn and alate
virginoparae in spring, so the occurrence of both holocyclic
and anholocyclic migration in one species is not too
unexpected in this group. If the single virgino-sexupara found
in P. passeki is not an aberration but a form capable of
producing viable rostrate larvae, populations on caraway are a
potential source of immigrants in newly-sown fields.

CONCLUSIONS

   Pemphigus passeki is a host-alternating species with
Populus nigra and Populus italica as its primary host and
Carum carvi as its secondary host. It is able to overwinter on
its secondary host, and its fundatrigeniae are able to migrate
over distances of at least 3 km. Removal of primary hosts on a
small scale will not protect caraway from colonisation by
fundatrigeniae. The existence of virgino-sexuparae, and hence
of migration from caraway to caraway, cannot be excluded.

to use their fields for trapping and sampling, and other
inhabitants of the Oldambt who gave acces to their poplar
trees, this study would not have been possible. K.A. Smant
introduced me to caraway and caraway growers. With E. Cichocka
I spent some pleasant hours of stimulating discussion, and A.
Bednarek helped to translate a Polish text. The assistance of
K.J. Schutter, who did all the field work, is much
appreciated.

REFERENCES

Alleyne, E.H., & Morrison, F.O. (1977): The lettuce root
    aphid, Pemphigus bursarius (L.) (Homoptera: Aphidoidea) in
    Quebec, Canada. Ann. Entomol. Soc. Quebec 22: 171-180.

Aoki, S. (1975): Descriptions of the Japanese species of
    Pemphigus and its allied genera (Homoptera: Aphidoidea).
    Insecta Matsum. (NS) 5: 1-63.

Blackman, R., & Eastop, V.F. (1984). Aphids on the worlds
    crops. Wiley and Sons, Chichester etc, 466 pp.

Bingham, B., & Sokal, R.R. (1986): Host tree effects on the
    morphology of Pemphigus populitransversus (Homoptera:
    Aphididae). J. Kansas Ent. Soc. 59: 287-295.

Börner,C. (1952): Europae centralis Aphides. Die Blattläuse
    Mitteleuropas. Privately published, 488 pp.

Brouwer, W.M.T.J. de (1962): De wollige slawortelluis
    (Pemphigus bursarius L.) bij andijvie. Meded. Dir. Tuinb.
    25: 316-324.

Dolgova, L.P. (1970): The heteroecious life cicle of Pemphigus
    borealis Tullg. (Homoptera, Aphidoidea). Entomol. Rev. 49:
    17-23.

Dunn, J.A. (1959a): The biology of the lettuce root aphid.
    Ann. Appl. Biol. 47: 475-491.

Dunn, J.A. (1959b): The effect of temperature on reproduction
    by the alatae of Pemphigus bursarius (L.). Ann. Appl. Biol.
    47: 772-777.

Elton, C.S. (1925): The dispersal of insects to Spitsbergen.
    Trans. R. Ent. Soc. London: 289-299.

Goszczyński, W., & Cichocka, E. (1978): Mszyce żerujące na

częściach podziemnych marchwi. Zesz. Probl. Post. Nauk Roln.
    208: 45-65.

Heie, O.E. (1980). The Aphidoidea of Fennoscandia and Denmark,
    I. Fauna Ent. Scand. 9:   1-239.

Herfs, W. (1973): Untersuchungen zur Biologie der
    Salatwurzellaus Pemphigus bursarius (L.). Z. Aangew.
    Entomol. 74: 225-245.

Hille Ris Lambers, D., & Hey-Wiltenburg, N.H. de (1966):
    Onderzoek over Pemphigussoorten. Jaarverslag 1966,
    Instituut voor Plantenziektenkundig Onderzoek, Wageningen:
    50.

Hille Ris Lambers, D., & Hey-Wiltenburg, N.H. de (1967):
    Onderzoek over Pemphigussoorten. Jaarverslag 1967,
    Instituut voor Plantenziektenkundig Onderzoek, Wageningen:
    46.

KNMI (1987): Maandoverzicht van het weer in Nederland.

Lampel, G. (1961): Die morphologischen un ökologischen
    Grundlagen des Generationswechsels monözischer und
    heterözischer Pemphiginen der Schwarz- und Pyramidenpappel.
    Z. Angew. Entomol. 47: 334-375.

McDaniel, I.N. (1958): The lettuce root aphid in Maine. Maine
    Farm Res. 6(3): 5-8.

Whitham, T.G. (1986): Costs and benefits of territoriality:
    behavioral and reproductive release by competing aphids.
    Ecology 67: 139-147.

INTERACTIONS BETWEEN APHID POPULATIONS

AND THEIR ENDOPARASITES

G. Raddatz, J. Tomiuk and K. Wöhrmann

Institute of Biology, Department of Population Genetics,
University of Tübingen, Auf der Morgenstelle 28,
D-7400 Tübingen, FRG

ABSTRACT

Matrix equations were used to simulate interactions between
aphid and endoparasite populations. The results suggest that
the time of appearance of predators is of great importance
in determining whether they will effectively control aphid
populations. Additionally, the spectrum of host plants, their
physiological state and spatial distribution all affect aphid
populations. Thus, such randomly varying external conditions as
temperature and host plants, aphids are exposed to, affect the
fate of populations.

INTRODUCTION

Effective control requires a good knowledge of the external
and internal factors that influence pest populations. In a
theoretical approach, Nicholson & Bailey (1935) proposed a
system of difference equations to describe interactions between
animal populations. This model has been improved by many workers
(e.g. Hassell, 1971, 1975; Hassell & Waage, 1984; Holling, 1959).

Natural populations of the rose aphid, *Macrosiphum rosae*, show
large fluctuations in population size from year to year, and it
has been assumed, that interactions with competing species, e.g.
Macrosiphum euphorbiae, and their predators were responsible for
this (Tomiuk & Wöhrmann, 1982). The present simulation study was

carried out to test this hypothesis and investigate the
importance of different parameters within interacting
populations.

MODEL

Life history parameters (fertility and survival rates) were
estimated from rose aphid clones reared in the laboratory. Mean
lifetime was 24 days. This period was subdivided into 6 discrete
age classes, the first class corresponding to the first and
second instars, the second class to the third and fourth
instars, and the third to sixth classes describe different
adult stages. Assuming that the ecological niche occupied by
aphids is not resource limited, aphid population growth can be
simulated with matrix equations (e.g. Roughgarden, 1979). For
the purpose of studying the interactions between parasites and
aphids, the percentage of parasitized aphids was calculated by a
negative binomial distribution which describes 1) spatial
heterogeneity of the aphid population density or, in other
words, the aggregated distribution of parasitism; 2) the
population density of aphid and parasite populations;
3) handling time, sex ratio and attack rate; and 4) the
operation of interference between parasites. This functional
relation specified the number of parasitized aphids randomly
distributed among the different age classes. Parasitized
aphids became infertile four days after parasitization and,
in the four days before, their fertility rate was decreased by
a factor of two. There is no hyperparasitism and the larval
stage of the parasite lasts 8 days. Adult parasites live eight days
and in this period their searching activity remains constant.

Simulations were stopped when 1) one population became
extinct; 2) aphid populations reached 100,000 individuals;
or 3) after 300 iterations, which corresponds to 1200 days.
Mean values were estimated from the results of 120 runs.

RESULTS

Table 1 lists the various parameters considered to operate
on aphid and parasite populations, and indicates their influence
on the stability of aphid populations.

The initial population densities had no significant effect.
Indeed some populations became extinct, but parasitism randomly
operating on the various age classes ensured the survival of
other populations, so that after a relatively short time stable
interactions occurred throughout the population as a whole.

Table 1   Parameters operating on aphid and parasite populations
           that influence aphid population growth. Their effect on
           the stability of aphid populations is indicated.

aphid	endoparasite	effect
initial population density	initial population density	none
1st age class is (not) parasitized		number of aphids decreases when this age class is parasitized
last age class is (in)fertile		none
subdivision into colonies		survival rate of aphid population increases
competition between clones and species		clones colonizing plants late in the season are effectively controlled
	handling time	none
	sex ratio	none
	attack rate	none
	interference	correlated with aphid population density
	first individuals appear after aphids	aphid population density increases

Finally, competition between clones and species acting contemporaneously with predators is of great importance. When parasites and aphids appear at the same time at the beginning of the season, aphid populations are effectively controlled, and they are only able to reach a modest density peak at the end of the season (Fig. 1, A1, broken line). On the other hand, when the appearance of parasites is retarded, aphid populations increase rapidly and reach densities at least twice as large (Fig. 1, A2). This interaction can explain the low density of clones and species that appear late in the season, as they are immediately exposed to predator activity.

As expected, population subdivision increased the stability of the simulated population.

Handling time, attack rate and sex ratio of the parasite were not shown to be important; but interference between parasites was found to cause an increase in aphid population size.

Since the first age class represents about 60% of all individuals, population density increased markedly when this age class was excluded from exposure to parasitism. On the other hand, excluding the last age class, which makes up 6% of the total population, had little effect.

CONCLUSIONS

In the field, we observed that population densities of competing rose aphid species varied from year to year, and attributed these findings partly to the effect of predation (Tomiuk & Wöhrmann, 1982). Furthermore, Kareiva (1987) has shown that the subdivision of populations into colonies of varying sizes can significantly affect predation. The results of the present simulations suggest that endoparasites can act on aphid populations in such a way as to produce fluctuations (Fig. 1). However, endoparasites are only one of many regulatory factor influencing aphid populations: in addition, other environmental conditions determine directly or indirectly the fate of local
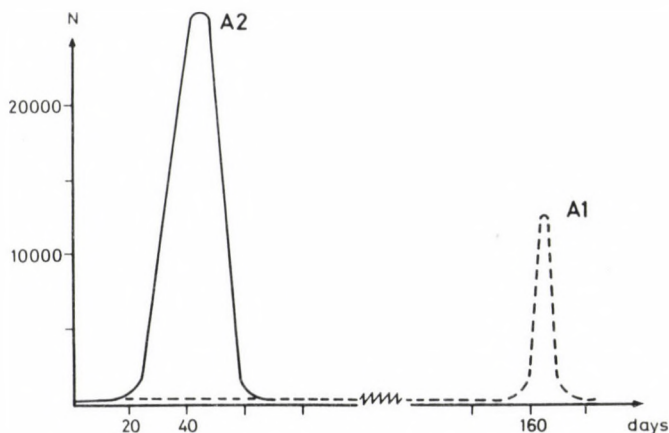
Fig. 1. Schematic graphs of aphid population growth. A1: No
        temporal difference in the initial population growth of
        aphids and parasites. A2: Growth of parasite population
        begins 32 days later than growth of aphid population.

aphid populations and their predators. The timing of egg-hatch
in spring, for example, depends on the temperature aphid and
parasite populations are exposed to (Campbell and Mackauer, 1975).
The spectrum of host plants, their physiological state and spatial
distribution additionally affect aphid populations. Such environ-
mental conditions obviously change from year to year and may
explain the variation in aphid population sizes observed from
year to year. Random variations in the temperature and host
plants, aphid populations are exposed to, seem to be of great
or even of crucial importance.

REFERENCES

Campbell, A. & Mackauer, M. (1975): The effect of parasitism by *Aphidius smithi* on reproduction and population growth of the pea aphid. Can. Ent., 107. 919-926.

Hassell, M.P. (1971): Mutual interference between searching insect parasites. J. Anim. Ecol., 40, 473-486.

Hassell, M.P. (1975): Density dependence in single species populations. J. Anim. Ecol., 44. 283-295.

Hassell, M.P. & Waage, J.K. (1984): Host-parasitoid population interactions. Ann. Rev. Entomol., 29. 89-114.

Holling, C.S. (1959): The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. Can. Ent., 91. 293-320.

Kareiva, P. (1987): Habitat fragmentation and the stability of predator-prey interactions. Nature, 326. 388-390.

Nicholson, A.J. & Bailey, V.A. (1935): The balance of animal populations. Part I. Proc. Zool. Soc. London. 551-598.

Roughgarden, J. (1979): *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan, New York.

Tomiuk, J. & Wöhrmann, K. (1982): Effect of temperature and humidity on natural populations of *Aphis pomi* DeGeer and *Macrosiphum rosae* (L.) (Hemiptera: Aphididae). Z. Pfl.krank., Pfl.path., Pfl.schutz, 89. 157-169.

NUMBERS, RICHNESS AND DIVERSITY OF APHIDS TRAPPED IN MOERICKE AND SUCTION
TRAPS IN LEÓN, SPAIN

V. Seco*, M. Hullé** and J.M.Nieto Nafría*

*Departamento de Biología Animal, Universidad de León, 24071, León, Spain.
**Laboratoire de Zoologie, I.N.R.A. Centre de Recherches de Rennes, B.P.
29, 35650 Le Rheu, France.

ABSTRACT

   Two kinds of traps were used: Moericke yellow water traps of 0.6 m. x
0.6 m. placed at different heights (0.0 m., 0.7 m. and 12.2 m.) and a
Rothamsted suction trap.

   The catches were carried made from 1980 to 1983 and 1986 to 1988, using
different traps.

   The richness and the diversity index of each trap are analyzed. Furthermore,
the seasonal analysis of the 0.7 m. Moericke trap catches are carried out.

INTRODUCTION

   Three Moericke traps at different heights and one Rothamsted suction trap
were placed at the "Escuela de Ingeniería Técnica Agrícola", University of
León, Spain (840 m., U.T.M.: 30TTN81).

   From 1980 to 1983, the Moericke traps were operated at ground level
(Moericke-1) and at 0.7 m. (Moericke-2). From 1986 to 1988 the Moericke traps
were operated at heights of 0.7 m. (Moericke-2) and 12.2 m. (Moericke-3). The
suction trap (Suction-4) began working in November, 1986; and for this reason,
only data for November and December 1986 and for the year 1987 and 1988 are
available for the suction trap.

   We tried to find out the composition of the aerial aphid fauna in León and
to analyze the number and diversity of aphids caught by each trap from year
to year and season to season.

MATERIAL AND METHODS

   The Moericke traps used are those described previously (Luis Calabuig et

al., 1983, Nieto *et al.*, 1987 and Seco *et al.*, 1988); and the suction trap
is of the Rothamsted type.

The land where the traps were placed contains herbeaous plants, bushes,
fruit and garden trees, vegetables plots, cereals and hop plantations.

The aphids caught were collected twice a week, or three time a week when
high temperatures could have evaporated the water in the traps and destroyed
the aphids. All the winged aphids were kept in 70% alcohol and were identified
using both stereo and compound microscopes and various keys.

RESULTS AND DISCUSSION

The number of aphids collected was higher in the Moericke-1 at ground level
than in Moericke-2. In 1980 and 1983, fewer aphids were collected in Moericke-1
than in Moericke-2. In 1981 and 1982, the reverse was true. On average, the
number of aphids collected in Moericke-3 was less than that collected in
Moericke traps 1 and 2. When Moericke-3 and Suction-4 are compared, more
aphids were collected in Suction-4 trap, and the difference is almost 5.5
times greater in 1988.

The number of taxa collected each year in the Moericke traps at different
heights is fairly constant with the exception of 1986 when 110 taxa were
collected in Moericke-2, and only 68 taxa were collected in Moericke-3.
However, if the catches of the Suction-4 and those of Moericke-2 and Moericke-3
are compared in 1987 and 1988, the number of taxa collected in Suction-4 is
higher.

According to our data (Figure 1) as the number of individuals collected in
a trap rises, so does the number of taxa with the exception of 1987, when few
aphids were collected but a greater number of taxa were identified.

The Williams or the Fisher diversity index has been calculated for each
trap and year. On the average, the highest index value corresponds to the
Suction-4, although traps 86.2, 82.1 and 82.2 show even higher index values
for their individual years. In 1982, a year in which the Suction-4 had not
yet been installed, the number of taxa collected was especially high.
Moericke-1 and Moericke-2 had similar diversity indices, with neither
maintaining dominance. Moericke-2 and Moericke-3 had similar diversity
indices, with the notable difference in 1986. From our data, it is not possible

		Moericke-1	Moericke-2	Moericke-3	Suction-4
		0.0 m.	0.7 m.	12.2 m.	12.2 m.
1980	Trap	80.1	80.2		
	N	2264	2356		
	R	51	56		
	D.I.	9.08	9.47		
1981	Trap	81.1	81.2		
	N	3861	3542		
	R	60	54		
	D.I.	10.08	9.03		
1982	Trap	82.1	82.2		
	N	7153	7059		
	R	91	92		
	D.I.	14.69	14.52		
1983	Trap	83.1	83.2		
	N	5059	6089		
	R	68	72		
	D.I.	11.11	11.47		
1986	Trap		86.2	86.3	86.4
	N		8271	3209	30*
	R		110	68	10*
	D.I.		17.72	12.01	5.37*
1987	Trap		87.2	87.3	87.4
	N		8749	5336	4915
	R		61	64	79
	D.I.		8.49	10.06	13.81
1988	Trap		88.2	88.3	88.4
	N		3321	1150	6269
	R		56	49	83
	D.I.		9.37	10.40	13.72

Figure 1. Number of individual aphids and taxa collected. N= Number of individuals; R= Richness of number or taxa; D.I.= Diversity Index. * Data only for November and December 1986.

		Moericke-1	Moericke-2	Moericke-3	Suction-4
		0.0 m.	0.7 m.	12.2 m.	12.2 m.
1980	Trap	80.1	80.2		
	W	0.00	0.00		
	S	7.52	8.49		
	SU	7.52	7.96		
	A	6.93	7.62		
1981	Trap	81.1	81.2		
	W	0.00	0.00		
	S	9.28	8.30		
	SU	6.93	7.27		
	A	8.49	7.96		
1982	Trap	82.1	82.2		
	W	2.44	0.00		
	S	14.16	13.77		
	SU	8.74	10.10		
	A	7.96	8.15		
1983	Trap	83.1	83.2		
	W	3.61	1.08		
	S	7.52	11.86		
	SU	7.52	8.64		
	A	9.91	8.42		
1986	Trap		86.2	86.3	
	W		0.00	0.00	
	S		14.45	10.06	
	SU		12.30	10.15	
	A		8.88	5.37	
1987	Trap		87.2	87.3	87.4
	W		1.66	2.44	0.00
	S		8.59	9.32	13.03
	SU		6.20	6.49	9.96
	A		4.79	6.74	7.32

1988	Trap	88.2	88.3	88.4
	W	0.00	0.00	0.00
	S	10.45	9.28	10.35
	SU	7.13	10.84	12.64
	A	7.52	7.03	10.93

Figure 2. Seasonal Diversity Index. W= Winter; S= Spring; SU= Summer; A= Autumn.
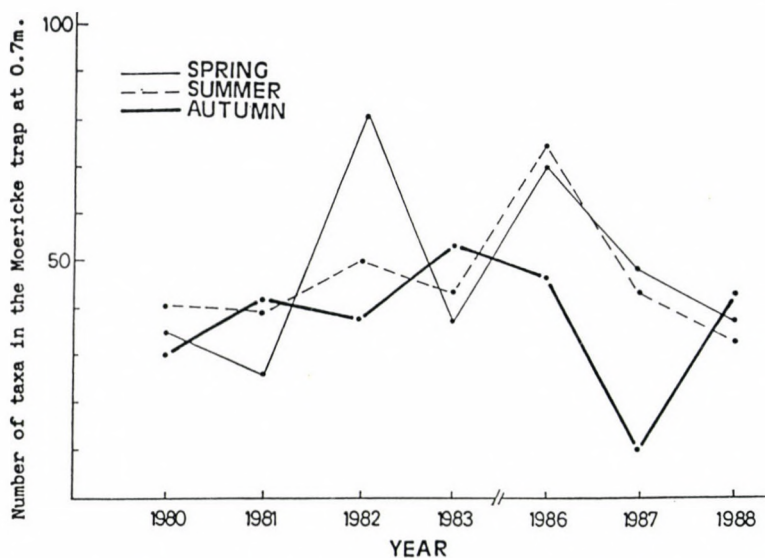
Figure 3. Chart of the number of taxa collected in Moericke-2 during all seven years of sampling.

to predict at what level the greater number of individuals and taxa will be collected.

The seasonal diversity indices (Figure 2) were calculated in order to give a more detailed analysis of the data and were obtained by dividing the number of aphids caught each year into the four corresponding time periods.

Just as in the suction traps and those of the Moericke in Brittany, France (Robert et al., 1987), the highest diversity index corresponds to spring (or spring-summer, as in 1980) and the lowest to autumn (except for trap 83.1 which shows higher seasonal diversity index in autumn). Traps 86.3, 88.3 and 88.4 show maximum diversity indices in summer, although the values are very close to those of spring.

Moericke-2 is the only trap for which data are available for all seven years of sampling. The numbers of taxa caught in spring, summer and autumn of each year are shown in Figure 3. Winter was not taken into account because the number were considered to low to be of significance.

There is a similarity between the number of taxa caught in spring and summer of each year, except for 1982 when there were high early spring temperatures and a very dry summer. A further analysis of the number of individuals caught in each taxon throughout 1982 indicates that a total of 33 taxa were collected in spring and not in summer; and this explains the high peak in the spring 1982.

Similar analysis of the results of the spring and summer of 1986 indicates that the drop in spring counts is due, perhaps, to the lack of spring rain and the early summer of 1986. Our data show that, of the 69 and 74 taxa caught in spring and summer, 25 were collected only in the spring and 29 were collected only in the summer. All taxa caught exclusively in spring or summer are generally rare.

Further comparison of the data reveals that, 36 of the 81 taxa collected in the spring of 1982 were not collected in the spring of 1986. Of the 69 taxa caught in the spring of 1986, 25 taxa had not been collected in the spring of 1982.

An analysis of the taxa collected in Moericke-2 in the autumn of 1987 and less obvious for those collected in 1980, reveals that the unusual decrease in the number of taxa collected was due to the absence of 17 taxa caught in abundance in the autumns of the other years. Several taxa collected in low numbers in the autumns of 1981, 1982, 1983, 1986 and 1988 were not collected in 1980 or 1987.

REFERENCES

Luis Calabuig, E., Mazé González, R. and Suáñez Fidalgo, A. (1983). Análisis

cuantitativo de la población de áfidos capturados en trampas de Moericke durante dos años. Act. I. Congr. Ib. Entom., León: 419-440.

Nieto, J.M., Mier, M.P., Mazé, R. and Suáñez, A. (1987). Courbes de vol de quelques espèces d'aphides d'intérêt agricole aux environs de León (Espagne). En Cavalloro, R. (Ed.): Aphid migration and forecasting "Euraphid" systems in European Community Countries: 37-47. Commission of the European Communities. Luxembourg.

Robert, Y, Turpeau, E. and Tanguy, S. (1987). Complementarité des pièges à succion et des pièges jaunes. En Cavalloro, R. (Ed.): Aphid migration and forecasting "Euraphid" systems in European Community Countries: 103-111. Commission of the European Communities. Luxembourg.

Seco M.V. and Nieto, J.M. (1988). Dinámica de la población aérea de pulgones en las cercanías de León en el trienio 1980-1982. Bol. San. Veg. Plagas, 14: 371-381.

INTERSPECIFIC AND INTRASPECIFIC DIFFERENCES IN ADAPTIVE TACTICS AND OTHER PECULARITIES OF TWO CLOSELY RELATED APHID SPECIES

G.Ch. Shaposhnikov

Zoological Institute of USSR Academy of Sciences,
Leningrad 199034, USSR.

ABSTRACT

Two closely related heteroecious species, _Dysaphis chaerophyllina_ Shap. and _D. brachycyclica_ Shap., differ in several respects and particularly in the way they exploit their primary and secondary hosts both between species and between populations from different parts of each species range. The origin of some forms is discussed.

INTRODUCTION

The evolution of aphids is determined by r-selection (r is rate of population growth) according to Beketov's (1860, p.220) law: "The more living creatures are exposed to annihilation the better they are provided with means of reproduction". Hence the life and evolution of aphids are based on an r-strategy. Aphids achieve exceedingly high rates of reproduction by synchronizing their life cycles with the seasonal cycles of their host plants, which enable the aphids to exploit their host plants when they are favourable (Shaposhnikov, 1959; Dixon, 1985). Aphids experience different conditions locally, which results in site-specific selection and adaptive alteration of life cycles (Moran and Whitham, 1988) and apparently still more considerable alterations within the whole species range. Therefore, since an r-strategy is regarded as a general feature of all aphids, the alteration of the life cycle of particular species or populations should be considered as adaptive.

MATERIALS AND METHODS

The material for this paper came from a study of the life cycles of Dysaphis chaerephyllina and D. brachycyclica. This involved observations made in many localities in the field as well as transfer experiments, when aphids were allowed to choose a suitable plant. The biological and morphologicial features of both species and their various morphs are also compared.

RESULTS

The two species have the same primary hosts, Malus orientalis and M. domestica, on which they induce D. devecta-like galls on the leaves. Their secondary hosts belong to the umbelliferous plant genus Chaerophyllum. The range of D. brachycyclica completely overlaps that of D. chaerophyllina.

Biological differences between species

The differences in the life cycles of the two species (Figs. 1-3), other biological pecularities and colouration are listed in Table 1.

Morphological differences between species

The species may be distinguished, using any morph, but best of all by males. The following empirical index identifies apterous exules:

$$\frac{2a + b + c + d}{e + 2}$$

where a- is the number of marginal tubercles on abdominal tergite VI, b - secondary hairs on ultimate rostral segment, c - hairs on tergite VIII, d - hairs on cauda, e - is the degree of sclerotization (see Stekolshchikov in these proceedings, Fig. 1). As the index is universal and applies to any locality one can estimate the extent of the morphological difference between sympatric populations of the two species from various parts of their ranges (Fig. 4).
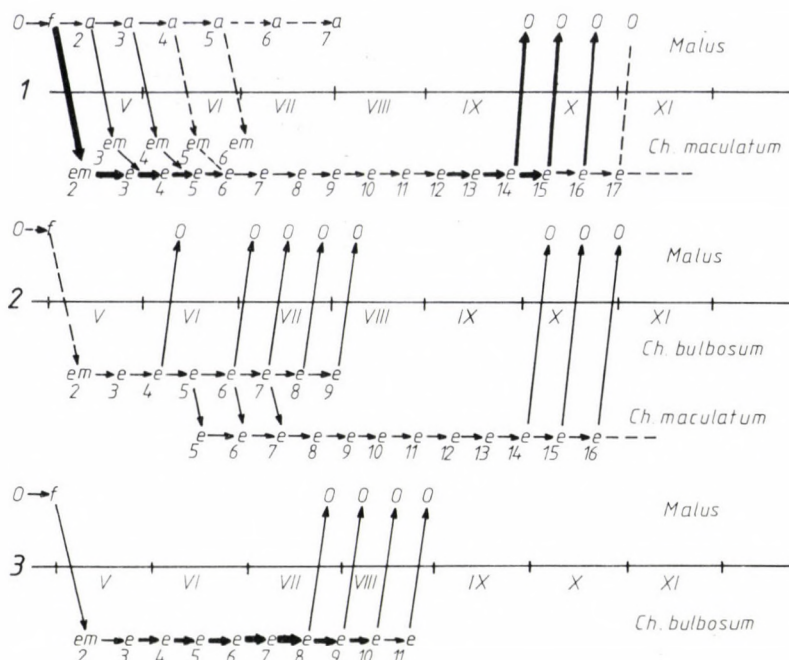
Figs.1-3. Life cycles of the aphids. 1-2. <u>Dysaphis
chaerophyllina</u> Shap.1. typical cycle, 2. three-host cycle
(clone); 3.<u>D. brachycyclica</u> Shap O. overwintered eggs; f,
em, e, thelytokous females; f, fundatrices; em, emigrants;
e, exules; 0, the end of life cycle, alate gynoparae and
males, apterous amphigonic females and fertilized diapausing
eggs. The thickness of the arrows indicates the approximate
population densities in the different periods. The broken
lines on the left hand side of Fig. 1 signifies rearing of
aphids on shoots in an isolator, on Fig. 2. a reconstruction
of the unstudied part of the cycle. V, VI... months;
1,2,3... generations of aphids, the numbers on Fig. 1 and 3
have been counted (by retaining the first-born nymphs) and
on Fig. 2 are approximate.

The populations that come from the same apple tree in Erevan
are the most similar: 26% and 33% of individuals were not
identified (Fig. 4). But using another index (the ratio of the
number of hairs on the hind part of the subgenital plate
relative to the degree of sclerotization) one can identify all
47 (23 + 24) individuals. This can be done with the aid of a
computer e.g. Stekolshchikov, in these proceedings.

Table 1

Character	D. chaerophyllina	D. brachycyclica
1. Colouration of secondary galls.	Red, sometimes yellow-green with red, or (in shade) pale green with pink.	Yellow, sometimes pale green, rarely (in the sun) with pink
2. Colouration of nymphs of emigrants	Grey-, olive-, or brown-green, when powdery-greenish or pinkish-grey	Yellow, greenish-yellow when powdery ochre-yellow.
3. Emigration from galls	In the 2nd & 3rd generation when 3-60% of the individuals are still apterous.	Complete in the 2nd generation.
4. Appearance of emigrants on the same twig.	Some days later than in the other species	Some days earlier than in the other species
5. Reproduction on C. maculatum.	Successful in nature and experiments, but in the latter case sometimes very weak and not long lasting.	Lacking in nature and experiments.
6. Reproduction on C. bulbosum	Successful as a rule in experiments but local in nature.	Succsessful in experiments and widespread in nature.
7. Appearance of alate exules on C. maculatum.	Exceedingly rare	Never lives on this plant
8. Appearance of alate exules on c. bulbosum	Rare	Abundant from the 4th generation onwards.
9. Remigration from C.maculatum	In September & October in nature, at a short photo-period (12-14hr, 20°C) in experiments.	Never lives on this plant
10. Remigration from C. bulbosum	Infrequent if at all, in experiments, in June, July & August. Found in nature in June.	In July-August, not earlier, after a definite number of generations (8th generation in experiments), in July-August found in nature too.
11. Photoperiodic reaction.	Present	Not present
12. Biological clock preventing remigration in early summer	Not present	Present

Interspecific and Intraspecific differences
in adaptive tactics

The main differences in the adaptive tactics of the two species is in the use of their secondary hosts. As the perennial Chaerophyllum maculatum is a universally resistant plant providing relatively bad food conditions while the annual Chaerophyllum bulbosum is a universally susceptible one suitable for many species, i.e. provides better food conditions (Shaposhnikov, 1961), the two aphid species show different adaptive tactics. In addition, as their secondary hosts complete growth at different times, the aphids have correspondingly different migration tactics.

As D. brachycyclica leaves its annual host in summer just as it ceases growth, the remigration is apparently stimulated by a deterioration in food quality (Fig. 3).

As shown by experiments, when a plant of C. bulbosum becomes unsuitable, alate morphs choose another individual of this plant species but not apple leaves and are therefore exules and not remigrants. Thus, a biological clock prevents remigration until most of the secondary host plants have been exploited.

The field observations show that up to 75% of C. bulbosum is colonized by D. brachycyclica. However, in spring, the species is extremely rare on the primary host. Thus, this aphid increases in abundance and spreads on the secondary host and almost the only function fulfilled on the primary host is amphimixis. This tactic is observed in most localities, but not in Armenia, where the species usually occurs on apple trees. It should be noted that Armenian populations also differ morphologically from northern populations.

D. chaerophyllina leaves its perennial host in autumn before it ceases growing when food conditions are still quite suitable (Shaposhnikov, 1959). The remigration therefore is stimulated by short photoperiod. (Fig. 1).

C. maculatum is the only or at least the main secondary host of this species in most localities. Experiments show that this aphid can also live on C. bulbosum, and the aphid is only

Isolation

Are these species reproductively isolated? In the Crimea
and in the north-western Caucasus and probably also in other
regions, these species are isolated because there is an interval
of a month or more between the end of reproduction of one
species and the beginning of reproduction in the other.
However, as D. chaerophyllina can sometimes produce an
amphigonic generation at the same time as D. brachycyclica
contact between females and males of two species is possible.
Unfortunately, cross mating experiments have not been made.

Fig. 4. Morphological differences between apterous exules (see the legend)
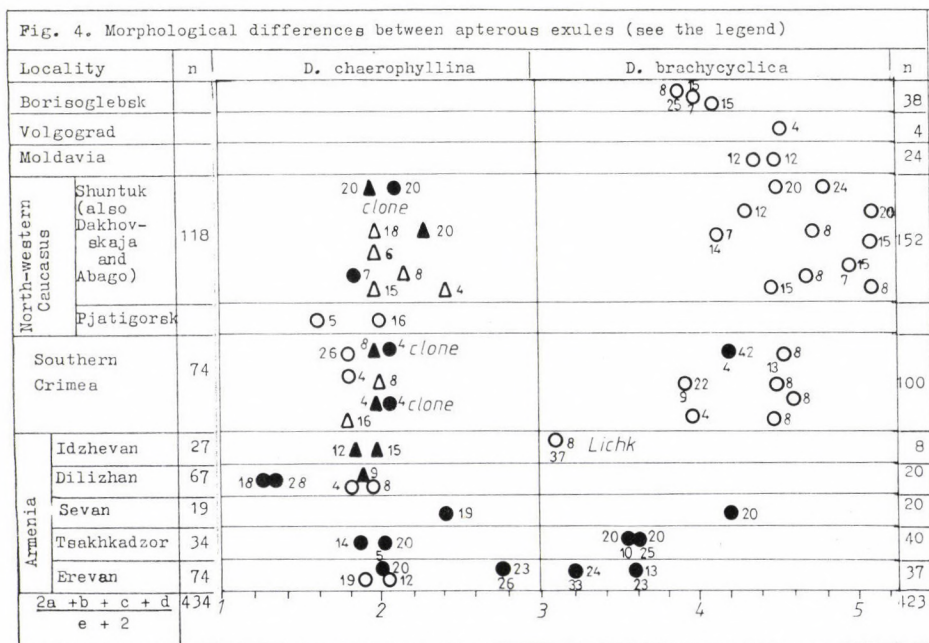
Fig.4.The OΔ aphid colonies were taken from plants in nature;
the O from C. bulbosum, the Δ from C. maculatum; the ●▲
aphid colonies were reared experimentally by transferring
emigrants from Malus and therefore their origin is known
(i.e. characters 1-6 in Table 1). The numbers beside
signs signifies the number of individuals in the sample,
the numbers below signs, the per cent of individuals not
identifiable by the universal index (if these individuals
are available), the numbers below the Figure - the scale -
gives the values obtained when using the index, and the
position of the signs relative to the scale, the
arithmetical mean of the sample.

found on this plant in nature in some localities. Because of the absence of a biological clock, remigration can be observed at anytime, usually too early for the aphids to colonise all C. bulbosum plants. There is a great number of emigrants of this species everywhere as there are many galls of this species on apple trees and the 2nd generation is apterous, which allows the production of an additional number of emigrants. The secondary host is settled sparsely probably because of its low food quality and alate exules are exceedingly rare. Thus the function of increasing in numbers and particularly that of dispersal is performed on the primary host.

Most probably some D. chaerophyllina have three hosts, successively changing from one to the other: Malus ——> C. bulbosum ——> C. maculatum ——> Malus. This three-host form has been studied in the Crimea (Fig. 2). But in the Crimea it is rare and in Shuntuk (near Majkop) they have not been found at all. These three-host forms are likely to be widely distributed in Armenia. In Armenia in 7 out of 19 cases emigrants from galls transferred to a set of plants established colonies on C. maculatum, 8 on C. bulbosum, and in 4 cases on both plants. Pure colonies of D. chaerophyllina on C. bulbosum have been found in the field 5 times and mixed with D. brachycyclica twice.

Thus there are a number of forms of D. chaerophyllina in Armenia: 1) the typical form, which chooses C. maculatum and is the most common aphid on Malus orientalis in the mountains; 2) forms that prefer C. bulbosum to various degrees and sometimes avoid C. maculatum, which are widely distributed but uncommon in the mountains; and at least some of which have three hosts: 3) an uncommon form (from Dilizhan) which biologically is similar to D. brachycyclica (the 1st, 2nd, 3rd and particularly the 5th characters in the table), but morphologically is "more D. chaerophyllina" like than all the other forms (1, 27-1, 34 in the scale, Fig. 4).

DISCUSSION

Comparison of the two species from different parts of their ranges shows that they are more similar in morphology, in adaptive tactics and in use of hosts in Armenia than anywhere else.   These facts allow me to suggest two interdependent hypotheses.

Firstly, it is highly probable that D. chaerophyllina has captured an additional host, C. bulbosum.   However, understanding the processes involved requires some preliminary explanation.

All modifications are a response of a genotype to the conditions of development, its reactive norm.   There is a wide spectrum of modifications in the reactive norm of every zygote. Some of them, which have been worked out historically and have an adaptive morphophysiological organisation, are adaptive norms, others that are not adaptive under normal conditions, are morphoses (Schmalhausen, 1983).   The morphoses are very labile and unstable inherited modifications, which are initiated by new factors capable of changing the normal way of development. The formation of a new adaptive norm proceeds by the substitution of external factors for internal ones (Schmalhausen, 1983) or, in other words, by the genetic assimilation of acquired characters (Waddington, 1957).

The clone of D. chaerophyllina from the Crimea exhibited two modifications, an adaptive norm for living on C. maculatum(Fig. 1) and a morphosis that preadapted it to the unusual plant C. bulbosum (Fig. 2).   The gradual transformation of the morphosis into the new adaptive norm is observed in Armenia, where C. bulbosum, becomes a complementary secondary host.   It is natural that a cluster of new forms has appeared that have different degrees of adaptation to the new host. Among them probably are some three-host forms and the unusual form found in Dilizhan, which possesses some of the biological characters of D. brachycyclica.

Secondly, it is quite possible that D. brachycyclica evolved from D. chaerophyllina in Armenia or elsewhere in the mountain forests of the Caucasus. One may consider the Dilizhan form of D. chaerophyllina as a natural model of one of the stages in the evolution of D. brachycyclica. The fact that the morphological changes have the opposite direction, does not make the model less important as it reflects a possible evolutionary pathway. Gradually the modification, which was labile in the past (morphosis), becomes increasingly more stable whereas the previous modification grows obsolete and tends to be lost. The more perfectly the aphids make use of the populations of the new secondary host plants the less they depend both on their previous sencondary host and their primary host. In Armenia D. brachycyclica produces approximately the same number of galls and generally retains the same adaptive tactics as D. chaerophyllina, using the primary host no less than the secondary one. However, in Armenia D. brachycyclica has made the first step towards the tactics shown by the more northern populations of the species: it has already lost the apterous second generation and as a result it produces somewhat fewer emigrants. Spreading to the more northern regions resulted in the origin of a new widely distributed form possessing different adaptive tactics and somewhat different morphology.

CONCLUSION

Study of two closely related species, Dysaphis chaerophyllina and D. brachycyclica, shows not only differences between them in many respects but also in the dynamics of the processes within each species. In particular the changes in adaptive tactics observed in different parts of the species ranges are accompanied by some morphological changes. Existance of several forms of D. chaerophyllina, some of which resemble D.brachycyclica, allows one to suppose that the latter originated from the former.

REFERENCES

Beketov, A.N. (1860): Harmony in the nature. Russk. vestnik, **30**. 197-240 (In Russian).

Dixon, A.F.G. (1985): <u>Aphid ecology</u>. Blackie. Glasgow, London. 457 pp.

Moran, N.A. & Whitham, T.G. (1988): Evolutionary reduction of complex life cycles: loss of host-alternation in Pemphigus (Homoptera:Aphididae). Evolution, **42(4)**. 717-728.

Schmalhausen, I.I. (1983): <u>Selected works</u>. <u>The ways and regularities of the evolutionary process</u>. "Nauka", Moscow. 360 pp. (In Russian).

Shaposhnikov, G. Ch. (1959): The initiation and evolution of the change of hosts and the diapause in plant-lice (Aphididae) in the course of the adaptation to the annual cycles of their host plants. Entom. obozr., **38**. 483-504. (In Russian, transl. into English in the U.S.A.).

Shaposhnikov, G. Ch. (1961): Specificity and appearance of adaptations to new hosts in aphids during the process of natural selection. Entom. obozr., **40**. 739-762. (In Russian, transl. into English in the U.S.A.).

Waddington, C.H. (1957): <u>The strategy of the genes</u>. Allen a. Univ, London. 262 pp.

RELATIONSHIPS BETWEEN HOST PLANT QUALITY AND REPRODUCTIVE INVESTMENT IN UROLEUCON JACEAE (L.) (APHIDIDAE)

Bernhard Stadler,
Department of Animal Ecology, University of Bayreuth
P.O.Box 10 12 51, D-8580 Bayreuth, F.R.G.

ABSTRACT

This paper examines the effects of different qualities of Centaurea jacea ssp. angustifolia (Schrank) Gremli on Uroleucon jaceae s. str. (L.). Aphids living on plants that were exposed to water stress and mechanical damage were compared in terms of alate production and reproductive investment (ovariole number, total no. of embryos and embryo developmental status) with control aphids on unstressed and undamaged plants. Aphids reared on water-stressed plants gave birth to a higher proportion of alatae than aphids on mechanically damaged or control plants. Alatae developing on water-stressed plants also showed the lowest investment in reproduction. Statistically significant relationships were found between reproductive investment and size of the aphids. U. jaceae also shows a marked seasonal trend in reproductive investment. Variability at two different levels of reproductive performance (ovariole number and embryo control) are discussed with regard to field observations.

INTRODUCTION

Aphids are known to be opportunistic and short-lived species, which often exploit resources that vary in space and time. Uroleucon jaceae, the aphid under investigation, is a non-host-alternating species, and it is thought to have evolved a secondary autoecy, which probably arose through the loss of woody winter hosts (Moran 1988). Mosbacher (1963) showed, that in spite of the wide potential host range of this species, it seems to be fairly restricted to Centaurea jacea in the field.

Recently, many attempts have been made to understand the relationship between investment in growth and investment in offspring (e.g. Dixon & Dharma 1980, Leather & Wellings 1981, Wellings et al. 1980, Ward & Dixon 1984, Dixon 1987, Leather 1987, Walters et al. 1988).

To assess the relationship between plant quality and reproductive performance, the influence of experimentally manipulated host plants on alatae of <u>Uroleucon jaceae s. str.</u> (L.) is investigated.

MATERIALS AND METHODS

Thirty potted plants of <u>Centaurea jaceae ssp. angustifolia</u> (Schrank) Gremli, were assigned to one of three groups, which were subjected to the following treatments:

A: Permanent water stress.
B: Slow death, induced by mechanical pressure of the basal plant leaves.
C: Control plants (no stress or damage imposed).

Every plant was infested with a single individual from a clone. After three weeks, the proportions of alatoid nymphs in their progenies were determined every two days. Several reproductive parameters (number of ovarioles, total number of embryos and number of sclerotized embryos) were evaluated by dissection of the adult alatae. The complete reproductive system was obtained by transferring the aphids into a droplet of water and by gently pulling the terminal abdominal segment with one pair of forceps, while holding the thorax with another pair of forceps. These dissections were done under a stereomicroscope.

RESULTS

The proportions of winged forms which developed during the period of observation (1.6.-1.7.88) is shown in Fig. 1. Aphids that were reared on water-stressed plants (A) gave birth to the highest proportion of alatae in mid June. In contrast, aphids from plants with treatment B and from the control C peaked at the end of June. No statistically significant difference was found in the relative crowding density (treatment A: 2.9 ± 1.8, treatment B: 3.4 ± 0.9, control C: 2.7 ± 0.3) (No. of aphids/cm length of the stem) (mean ± s).
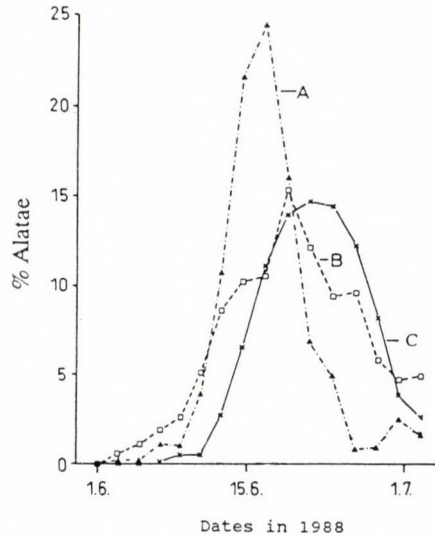
Fig. 1.
    Relative development of alatae on plants subjected to treatments A, B,
    and the control C, during the observation period (1.6. - 1.7.88).

    The analysis of the effects of different host qualities on
U. jaceae's reproductive system showed a statistically
significant decrease with time in the number of ovarioles, the
number of sclerotized embryos and the total number of embryos
in both treatments and even in the control (Fig. 2a, b, c).
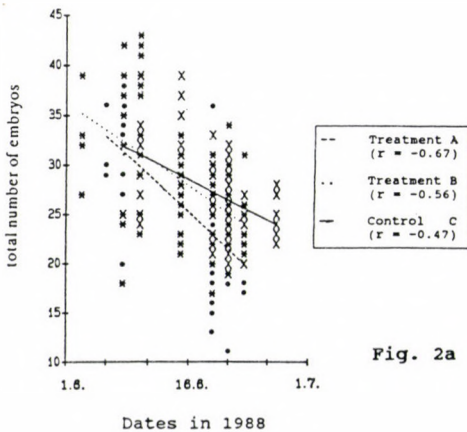
Fig. 2a
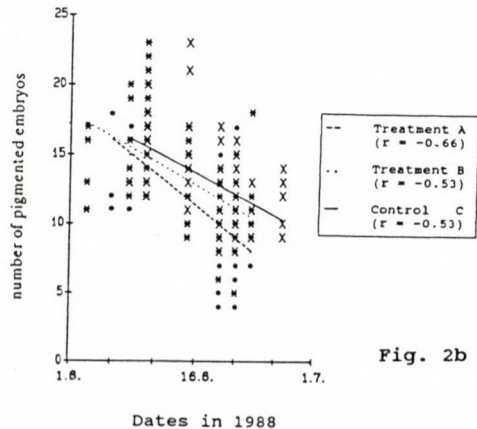
Fig. 2b

Fig. 2a, b, c.
    Changes in the total number of embryos
    (2a), number of sclerotized embryos (2b)
    and number of ovarioles (2c) in U. jaceae -
    alatae, reared on stressed plants (A, B)
    and on control plants (C).

    (. Treatment A, ✳ Treatment B, x Control C)
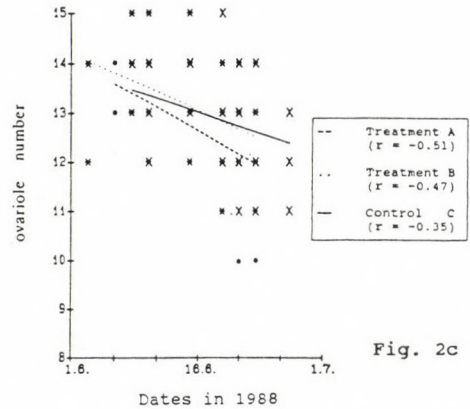
Fig. 2c

Although the variability of all these parameters was
relatively high, the strongest decline occured in aphids
living on water-stressed plants. In a comparison of the
regression lines in Fig. 2a, b, c the effect of water stress
on the total number of embryos (Fig. 2a) is statistically more
pronounced than the other relationships (ANCOVA: $F=3.04$;
$p=0.05$).

The decrease in reproductive investment occurs not only in
alatae, but in all morphs, during the course of the season.
The seasonal trend in ovariole number is given in Fig. 3.
Fundatrices and fundatrigeniae showed the highest reproductive
potential. The following generations showed a steady reduction
in the number of ovarioles.
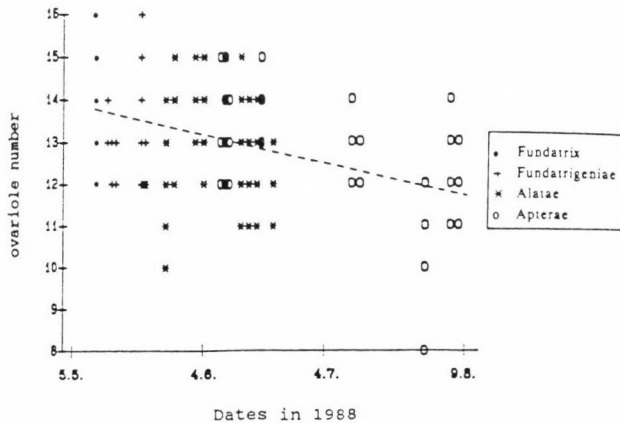
Fig. 3.
    Relation between ovariole number and time for four morphs in U.
    jaceae s. str. ($r = -0.368$; $p<0.001$; $n = 263$).

Since the weight of the mothers and the length of their hind tibia show a good relationship (r = 0.51; p<0.001; n = 196), this size parameter was used in regression analysis. Highly significant relationships were found between ovariole number and tibia length (r = 0.43; p<0.001; n = 278). But the explained variance is rather poor (18%). Mother's size can explain more of the variance in embryo parameters. It accounts for 47% of the variance in the number of sclerotized embryos and the total number of embryos (MULREG: r = 0.68; F = 121.46; p<0.001; df = 2; n = 278).

DISCUSSION

In recent years, two alternative explanations of aphid reproductive tactics have been put forward. On the one hand, many authors suggest that changes in the reproductive potential are genetically programmed and anticipate the seasonal decline in habitat quality (Dixon & Dharma 1980, Ward & Dixon 1984, Walters et al. 1988). On the other hand Wiktelius & Chiverton (1985) claim a direct response to varying plant quality with complete ovarioles being resorbed on poor quality plants. Since many investigations concentrate on apterae, little information is available on the effects of different plant qualities on alatae, especially of non-host-alternating species.

The results presented here point toward an aphid-plant relationship that is not directly bound to plant quality in the Wiktelius & Chiverton's sense. As the reproductive parameters decreased in all treatments, even in the control aphids living on good quality plants, and as the variation is equally high in all aphid groups, one can assume a programmed relationship between plant quality and reproductive investment in alatae of U. jaceae. If variation in the reproductive potential is a direct response to environmental heterogeneity, then there should be no or little variability when genetically identical aphids are reared under constant conditions (Walters et al. 1988). Furthermore there should be no decrease in the reproductive investment on good quality plants as shown in the control plants. However, field observations indicate that the appearance of alatae in U. jaceae coincides with the beginning of flowering of C. jacea plants. As blooming plants are rarely colonized by U. jaceae, alatae possibly settle on plants which are of lower quality than the one they left. Therefore, it seems reasonable to reduce the reproductive potential in

advance, to cope successfully with deteriorating habitat quality because it is well known that aphids with a high ovariole number suffer a higher mortality on low quality plants (Ward et al. 1983, Grüber & Dixon 1988). Nevertheless, it is advantageous for aphids to maintain a high variation in reproductive investment, since plant quality is heterogenous not only in a given area but also on individual plants. As a consequence, changes of feeding positions occur throughout the growing season and indicate a flexible response to variable phloem sap accessibility.

Although the size of the aphids is positively correlated with the reproductive investment, this relationship accounts for only a small proportion of the variance. The explained variation is especially small in the number of ovarioles, indicating a relationship which is not under control of the individual aphids. In contrast, variation in size accounts for a higher proportion of the variance in the total number of embryos and the number of sklerotized embryos (47%). This suggests that aphids control their reproductive investment by resorbing embryos when feeding on suboptimal plants as described for Aphis fabae Scop. and Megoura viciae (Buckton) by Dixon (1985) and Ward & Dixon (1982).

LITERATURE

Dixon, A.F.G., (1985): Aphid ecology. Blackie. Glasgow, New York, 157 pp.

Dixon, A.F.G., (1987): Aphid reproductive tactics. In: Population structure, genetics and taxonomy of aphids and Thysanoptera. Holman J., Pelikán J., Dixon A.F.G. & Weismann L. (eds.), SPB, The Hague, pp. 3-18

Dixon, A.F.G. & Dharma, T.R., (1980): Number of ovarioles and fecundity in black bean aphid Aphis fabae. Ent. exp. & appl., 28, 1-14

Grüber, K., & Dixon, A.F.G., (1988): The effect of nutrient stress on development and reproduction in an aphid. Ent. exp. & appl., 47, 23-30

Leather, S.R., (1987): Generation specific trends in aphid life history parameters. J. Appl. Ent., 104, 278-284

Leather, S.R. & Wellings, P.W., (1981): Ovariole number and fecundity in aphids. Ent. exp. & appl., 30, 278-284

Moran, N., (1988): The evolution of host plant alternation in aphids: evidence for specialization as a dead end. Am. Nat., 132, 681-706

Mosbacher, G.C., (1963): Über die Nahrungswahl bei Dactynotus Raf. (Aphididae) I. Die Wirtsspektren der Gruppe D. jaceae (L.) s. lat. und D. cichorii (Koch) s. lat. Z. angew. Ent., 51, 377-428

Walters, K.F.A., Brough, C. & Dixon, A.F.G., (1988): Habitat quality and reproductive investment in aphids. Ecol. Entomol., 13, 337-345

Ward, S.A. & Dixon, A.F.G., (1982): Selective resorption of aphid embryos and habitat changes relative to life-span. J. Anim. Ecol., 51, 859-864

Ward, S.A. & Dixon, A.F.G., (1984): Spreading the risk, and the evolution of mixed strategies: seasonal variation in aphid reproductive biology. Adv. Invert. Reprod., 3, 367-386

Ward, S.A., Wellings, P.W. & Dixon, A.F.G., (1983): The effect of reproductive investment on pre-reproductive mortality in aphids. J. Anim. Ecol., 52, 305-313

Wellings, P.W., Leather S.R. & Dixon A.F.G., (1980): Seasonal variation in reproductive potential: a programmed feature of aphid life cycles. J. Anim. Ecol., 49, 975-985

Wiktelius, S. & Chiverton, P.A., (1985): Ovariole number and fecundity for the two emigrating generations of the bird cherry-oat aphid (Rhopalosiphum padi) in Sweden. Ecol. Entomol., 10, 349-355

APHID SPECIES EATEN BY FROGS

L. Szalay-Marzsó,

University of Agriculture, H-2103 Gödöllő, Hungary

J. Török and T. Csörgő

Eötvös Loránd University, H-1088 Budapest, Hungari

ABSTRACT

The paper reports on the results of a faunistical survey
carried out in the Kis-Balaton Landscape Protection Area in the
southwest of Hungary. The stomachs of frogs /Rana arvalis L.,
R. esculenta L./ collected in the autumn of 1987 contained a
rather high number of aphids caught in the marshland. The mate-
rial consisted of 76 species, belonging to 46 genera and 5 fa-
milies. Of these 12 species were new for the Hungarian fauna.

Although the survey was not systematic enough to allow
further conclusions, it showed nevertheless the presence of a
variegated aphid fauna in the protected area and indicated
connections of the fauna with the ones of distant regions.
Based on the interesting data the survey will be continued.

INTRODUCTION

Since the early works of Szaniszló /1880/, Szépligeti
/1883/ and Horváth /1883, 1884, 1896, 1897/ more recent studies
have been made on the aphid fauna of Hungary by Pintera and
Szalay-Marzsó /1962/, Szalay-Marzsó /1961, 1962, 1965, 1969,
1989/, Andrásfalvy /1968, 1971/, Szalay-Marzsó and Andrásfalvy

/1970/, Halmágyi /1974/, Meszleny and Szalay-Marzsó /1981/,
but above all by Szelegiewicz /1966, 1968, 1977/ who also
summarized the earlier data. Although further valuable contri-
butions were made by various authors working in the field of
applied entomology, their detailed enumeration is not possible
here. Szelegiewicz /1968/ estimated the number of aphid species
living in Hungary at about 740, half of which had been known at
the publication of his paper.

An interesting opportunity to gain further data on the
aphid fauna of Hungary presented itself by examining the stomach
content of frogs /129 Rana esculenta L. and 83 R. arvalis L./
collected in the autumn of 1986. In the Landscape Protection
Area of Kis-Balaton /southwest Hungary/ regular zoological sur-
wey was carried out by a research team of the Eötvös Loránd
University /Budapest/, including the observation and ecological
study of birds and collection of the terrestrial and aquatic
fauna. As it turned out, the frogs had contained a rather
variegated aphid material, well perserved thanks to the feeding
habit of frogs that swallow their prey without chewing.

MATERIAL AND METHODS

The frogs were collected in the Kis-Balaton area, a
1403 hectare peat-bog marshland at the southwestern end of the
Leke Balaton. The marshland was originally a bay of the ancient
lake filled up in the historic times by the alluvial deposit
of the river Zala. The bay became thus a swamp, morass, then
a peat-bog with a few islands, like the Diás-island. The Zala
river was controlled by the end of the last century and as a

result of flood control measures the open water surface has
shrunk to 180 hectares. Some years ago the alarmingly progressing
eutrophization of the Balaton necessitated that the original
filtering function of Kis-Balaton be restored. The bank of the
Zala river was opened at some sections to flood large reservoirs
/70 sq.kilometers in total/ in which the suspended solids carried
by the water can be sedimented. To-day the Kis-Balaton is one
of the most valued protected marshlands of Hungary, a nesting
place of many rare birds.

The collection of frogs was carried out from the 5th of
September until 1st.of November by hand or hand-net, the captured
specimens were immediately sacrificed by chloroform, determined,
weighed, measured and dissected within hours. The whole digestive
tract of the animals was preserved in isopropyl alcohol until
further examination. The digestion of the stomach content could
be thus avoided. The aphids were then sorted out of the material
and preserved until determination in 75 per cent aethyl alcohol.

The frogs were collected at three localities:

A/ the Diás island, B/ the banks of the Zala river, C/ the
embankment of Reservoir No.1. As the aphids serving as prey
for the frogs were at least partly connected to the vegetation,
the biotopes are briefly characterized.

A/ Diás island.

A small island of some hectares, elevated only 2-3 meters
above the water level, covered py a plant community belonging
to the type Salicetum albae-fragilis. The sparse groups of
willow /Salix alba L. and S.fragilis L./ were intermixed

with alder /Alnus glutinosa L./ and birch /Betula pendula Roth./.
In the undergrowth of the trees and in the clearings among
dicotyledons /e.g. Eupatorium cannabinum L./ mostly sedges
/Carex acutiformis Ehrh., C.riparia Curt./ and grasses /Poa
palustris L., P.trivialis L., Dactylis glomerata L., Festuca
pratensis Huds., Arrhenatherum elatius L./ grew. The collections
were made about 100 meters from the shore.

B/ Bank of Zala river.

The steep bank of the slow river was covered by the
hydrophytes belonging to the community Caricetum acutiformis
ripariae, along the water among sparse reed /Phragmites com-
munis Trin./ and bulrush /Typha angustifolia L./ partly sub-
merged Polygonum amphibium L. and Ceratophyllum demersum L.
grew. The frogs collected in this biotope were captured along
the water's edge.

C/ Embankment of water reservoir No.1.

The steep embankment was covered by a vegetation belonging
to the community Scirpeto-phragmitetum glycerietosum /dominant
plant species: Glyceria maxima Holmbg./. Along the water's
edge sparse reed and partly submerged Hydrocharis morsus-ranae L.,
Polygonum amphibium and Ceratophyllum demersum grew. As the
embankment was built only some years ago, the open soil sur-
face became populated with adventitious plants, mostly segetal
weeds, like Bidens tripartitus L., Capsella bursa-pastoris L.,
Sonchus arvensis L., Cirsium arvense L., Polygonum aviculare L.,
Cichorium intybus L., Vicia cracca L.

Results and Discussion

The results of the study were summarized in Tables 1 and 2.

Table 1

Aphid species /apterae and alatae/ found in the stomach of frogs

/Kis-Balaton, September-October 1987/

Species	A arv. ap	A arv. al	A esc. ap	A esc. al	B arv. ap	B arv. al	B esc. ap	B esc. al	C arv. ap	C arv. al	C esc. ap	C esc. al
Chaitophoridae												
Atheroides doncasteri Oss.	.	.	.	.	.	.	.	.	.	.	1	.
Atheroides serrulatus Hal.	.	.	.	.	2	.	1	.	1	.	.	.
Laingia psammae Theob.	.	.	.	.	.	.	.	.	.	.	1	.
Sipha agropyrella HRL.	2	.	42	.	18	.	9	.	10	.	19	.
Sipha glyceriae Kalt.	4	.	20	2	.	.	1	.	1	.	.	.
Sipha maydis Pass.	.	.	.	.	.	.	.	.	.	.	4	.
Callaphididae												
Phyllaphis fagi Koch	.	.	.	.	.	.	.	1	.	.	.	.
Saltusaphis scirphus Theob.	.	.	.	.	.	.	.	.	.	.	1	.
Smynthurodes betae Westw.	.	.	.	.	2	.	.	.	.	.	.	.
Subsaltusaphis pallida HRL.	.	.	.	.	.	.	.	.	.	.	1	.
Symydobius oblongus Heyd.	.	.	1	.	.	.	.	.	.	.	.	1
Therioaphis ononidis Kalt.	.	.	3	.	.	.	.	.	.	.	.	.
Therioaphis trifolii Monell	.	.	3	.	.	.	.	.	.	.	2	.
Aphididae												
Acyrtosiphon pisum Harr.	.	4	41	4	11	2	11	2	6	.	14	.
Amphorophora rubi Kalt	.	.	.	3	.	.	.	.	.	.	.	.
Aphis craccivora Koch	.	.	.	.	.	.	1	1	.	.	.	.
Aphis fabae Scop.	.	2	8	19	.	.	.	1	.	.	.	.

Table 1 continued

Species	A				B				C			
	arv		esc		arv		esc		arv		esc	
	ap	al	ap	al	ap	al	ap	al	ap	al	ap	al
Aphis frangulae Kalt	.	.	2	.	.	.	1	.	.	.	.	.
Aphis nasturtii Kalt	.	.	14	1	.	.	.	.	.	.	2	.
Aphis pomi de Geer	.	.	1	.	.	.	.	.	.	.	.	1
Aulacorthum solani Kalt.	.	.	6	14	16	12	2	1	.	.	4	.
Capitophorus elaeagni del Gu.	.	.	4	2	.	.	.	.	.	.	.	.
Coloradoa artemisiae del Gu.	.	.	11	.	.	.	.	.	.	.	.	.
Corylobium avellanae Schrank	1	.	.	.	2	.	2	.	.	6	1	3
Cryptomyzus galeopsidis Kalt.	.	.	.	.	.	.	2	2	.	.	.	.
Cryptomyzus korschelti CB.	.	.	.	.	.	.	1	1	.	.	.	.
Cryptomyzus ribis L.	.	.	.	1	.	.	.	.	.	.	.	.
Dactynotus achilleae Koch	.	.	.	.	2	.	.	.	2	.	.	.
Dactynotus cichorii Koch	.	.	.	.	.	.	.	.	2	.	.	.
Dactynotus cirsii L.	.	.	.	.	.	.	.	.	3	.	.	.
Dactynotus jaceae L.	.	.	.	.	.	.	.	.	1	.	.	.
Dactynotus tussilaginis Walk.	.	.	.	.	.	.	1	.	.	.	.	.
Diuraphis frequens Walk.	.	.	.	.	5	.	26	.	3	.	1	.
Diuraphis holci HRL.	.	.	.	.	6	.	.	.	.	.	.	.
Dysaphis plantaginea Pass.	.	.	3	.	.	.	.	1	.	.	.	.
Hyadaphis foeniculi Pass.	.	.	.	8	.	1	.	.	.	.	.	.
Hyalopterus pruni Geoffr.	.	1	.	.	.	.	1	.	.	.	1	.
Hydaphias molluginis CB.	.	.	.	.	.	7	.	.	.	.	.	.
Hyperomyzus lactucae L.	.	.	.	.	.	2	.	.	.	.	.	.
Hyperomyzus picridis CB.	.	.	2	.	.	.	.	.	.	.	.	.

Table 1 continued

Species	A				B				C			
	arv		esc		arv		esc		arv		esc	
	ap	al	ap	al	ap	al	ap	al	ap	al	ap	al
Lipaphis erysimi Kalt.	.	.	.	2	.	.	.	.	.	.	.	.
Macrosiphoniella millefolii de Geer	.	.	.	.	1	.	.	.	.	.	1	.
Macrosiphum euphorbiae Thomas	.	.	.	.	.	.	.	.	1	.	.	.
Macrosiphum fragariae Walk.	.	.	1	.	.	1	.	1	.	2	.	.
Macrosiphum rosae L.	.	.	.	2	.	.	.	.	.	.	.	.
Metopolophium dirhodum Walk.	.	2	1	4	21	.	.	1	1	.	5	.
Microlophium evansi Theob.	.	.	1	.	.	.	.	.	.	.	.	.
Myzus ajugae Schout.	.	.	1	.	1	.	.	.	.	.	.	.
Myzus cerasi F.	.	.	.	.	10	1	3	1	.	.	.	.
Myzus certus Walk.	.	.	.	.	2	.	.	.	.	.	.	.
Myzus lythri Schrank	.	.	3	.	.	.	.	.	.	.	.	.
Myzus ornatus Laing	1	.	.	.	.	.	.	.	.	.	.	.
Myzus myosotidis CB.	1	.	.	.	1	.	.	.	.	.	.	.
Myzus persicae Sulz.	1	.	1	1	2	.	.	.	.	.	.	.
Nasonovia ribisnigri Mosl.	.	.	.	1	.	.	.	.	.	.	.	.
Pentatrichopus potentillae Walk.	1	.	1	.	.	.	.	.	4	.	.	.
Phorodon cannabis Pass.	.	.	.	.	.	.	.	1	.	.	.	.
Phorodon humuli Schrank	1	1	.	3	.	.	.	.	.	.	.	.
Pterocomma jacksoni Theob.	.	.	.	.	.	.	.	2	.	.	.	.
Pterocomma pilosum Buckt.	.	.	.	.	.	2	.	1	.	.	.	.
Rhopalosiphoninus latysiphon Dav.	.	.	.	2	.	.	.	.	.	.	.	.
Rhopalosiphoninus staphyleae Koch	1	.	1	.	.	.	.	.	.	.	.	.
Rhopalosiphum insertum Walk.	.	.	.	2	.	.	.	.	.	.	.	.
Rhopalosiphum maydis Fitch	.	.	12	2	3	.	.	.	.	.	.	.
Rhopalosiphum nympheae L.	.	.	.	.	6	.	.	.	.	.	.	.

　　　　　　　　SZALAY-MARZSÓ ET AL.

Table 1 continued

Species	A				B				C			
	arv		esc		arv		esc		arv		esc	
	ap	al	ap	al	ap	al	ap	al	ap	al	ap	al
Rhopalosiphum padi L.	.	6	9	21	.	2	.	4	.	.	34	.
Semiaphis dauci F.	.	.	.	.	8	.	.	.	.	.	.	.
Schizaphis graminum Rond.	.	.	.	.	11	7	7	5	.	.	3	.
Schizaphis typhae Laing	.	.	3	.	.	.	.	.	.	.	.	.
Sitobion avenae Fabr.	.	2	.	5	.	.	1	.	.	.	.	.
Thelaxidae												
Anoecia corni F.	.	3	.	20	.	6	4	22	.	2	3	6
Anoecia vagans Koch	.	.	.	6	.	.	.	.	.	.	.	.
Pemphigidae												
Eriosoma lanigerum Hausm.	.	.	.	2	.	.	.	.	.	.	.	.
Pemphigus bursarius L.	.	.	.	3	.	.	.	.	.	.	.	.
Pemphigus spirothecae Pass.	.	.	.	1	.	1	.	.	.	.	.	.
Tetraneura ulmi L.	.	.	.	.	2	.	.	.	.	.	.	.

Abbreviations: A = Diás island, B = Bank of Zala river,
　　　　　　　　C = Embankment of reservoir No.1
　　　　　　　　arv = Rana arvensis, esc = R. esculenta,
　　　　　　　　ap = apterae, al = alatae

As shown in Tables 1 and 2 the frogs collected in the Kis-Balaton contained quite variegated aphid material, consisting of 76 species, belonging to 42 genera and 5 families. From the aphids further 84 specimens were injured beyond the possibility of identification and could be determined only to genus. From these

Table 2

Number of aphids found in the stomach of frogs /Kis-Balaton,
September-October 1987/, determined only to genus /injured
exemplars/. For abbreviations see Table 1.

	arv	esc
Acyrtosiphon	1	1
Amphorophora	1	1
Anoecia	-	1
Aphis	15	16
Cavariella	-	1
Chaitophorus	-	1
Coloradoa	1	10
Corylobium	-	1
Cryptomyzus	5	-
Dactynotus	-	4
Diuraphis	-	1
Forda	-	1
Galiobium	1	-
Macrosiphum	1	2
Myzus	-	7
Pentatrichopus	1	-
Rhopalosiphum	3	2
Subsaltusaphis	-	3
Tetraneura	1	1
Therioaphis	1	2

genera, however, 4 are not mentioned in Table 1 /Cavariella,
Chaitophorus, Forda and Galiobium/, so the total number of
genera represented in the material is 46. From the species
12 were new for the Hungarian fauna, not mentioned either in
the faunistical records or in the comprehensive list of Szele-
giewicz /1968/: <u>Sipha agropyrella</u> HRL., <u>Sipha glyceriae</u> Pass.,

Caspitophorus elaeagni del Gu., Coloradoa artemisiae del Gu.,
Cryptomyzus galeopsidis Kalt., Cryptomyzus korschelti CB.,
Diuraphis holci HRL., Hydaphias molluginis CB., Lipaphis
erysimi Kalt., Myzus certus Walk., Myzus myosotidis CB.,
Pterocomma pilosum Buct. and Schizaphis Typhae Laing. As the
host plant data are unknown it seems to be quite unnecessary
to enumerate the known hosts even of the monoecious aphids.
Some interesting cases, however, like the presence of Phyllaphis
fagi Koch, Eriosoma lanigerum Hausm. /monoecious on beech and
apple, resp./ or of Rhopalosiphoninus latysiphon Dav. /living
on potato shoots in cellars/ in the material show the connections
of the Kis-Balaton aphid fauna with more distant regions. The
number of Hyalopterus pruni Geoffr. caught by the frogs was
unexpectedly low as the alienicolae of this species appear in
large colonies on reed also in the Balaton area.

As far as the number of aphids caught by the frogs in the
differenc biotopes is concerned, the Diás island yielded the
most aphids, followed by the bank of the Zala river. The method
of survey was hardly suitable to draw conclusions on the preying
efficiency of the two frog species, but Rana esculenta seemed
to be a more efficient predator of aphids: from the 891 aphids
615 specimens were caught by the 129 R. esculenta and 276 by
the 83 R. arvalis.

The data in present paper indicate that it would be
worthwhile to continue the aphidological studies in the
Kis-Balaton area with reference to the host plants.

REFERENCES

Andrásfalvy P. /1968/: Contribution a la connaissance des aphides des plantes fruitieres. Rovartani Közl. 1. 179-188.

Andrásfalvy P. /1971/: A magyar faunában ismeretlen vagy kevéssé ismert levéltetvek /Hom.: Aphidoidea/. Folia Ent. Hung.24. 229-238.

Halmágyi L./1974/: Adatok a hazai fák és cserjék levéltetveinek ismeretéhez. Folia Ent. Hung. 27. 85-90.

Horváth G. /1883/: Sur les migrations des Pucerons. Rev. d'Ent. 2. 64-67.

Horváth G. /1884/: Zabpusztitó levéltetvek. Rovartani Lapok l. 143-145.

Horváth G. /1896/: Eine alte und drei neue Aphiden-Gattungen. Wien.Ent. Zeitung, 15. 1-7.

Horváth G. /1897/: Homoptera /Fam. Aphididae/. In: Fauna Regni Hungariae, Term. Tud. Társ. pp 64.

Meszleny A.-Szalay-Marzsó L./1981/: A Myzus ascalonicus Donc. és egyéb, a hazai faunára nézve uj levéltetüfajok felbukkanása. Növényvédelem, 1. 45-46.

Pintera, A.-Szalay-Marzsó L./1962/: Neuere Angaben zur Kenntnis der Blattlaus /Aphidoidea/Fauna Ungarns. Acta Zool. Ac. Sci. Hung., 1-2. 127-133.

Szalay-Marzsó L. /1961/: A burgonyatáblák levéltetüfaunája és a burgonya virusos leromlása. Növénytermelés, 10. 351-360.

Szalay-Marzsó L. /1965/: A hajtatóházakban, pincékben élő levéltetvekről. M.Mezőg. 12. 13-14.

Szalay-Marzsó L. /1969/: Levéltetvek a kertészetben. Mezőg. Kiadó, Bp. pp.187.

Szalay-Marzsó L. /1989/: Levéltetvek /Aphidoidea/. In: Jermy T. and Balázs K./ed./: Növényvédelmi Állattan kézikönyve Akad. Kiadó, p. 88-193.

Szalay-Marzsó L.and Andrásfalvy P./1970/: Faunistical data on Hungarian Aphids living on fruit trees and shrubs. Folia Ent. Hung. 23. 133-140.

Szaniszló A. /1880/: Egy uj levéltetü faj, amely buza- és árpa-
gyökéren élődik. Természetr. Füz. 4. 192-196.

Szelegiewicz, H. /1966/: Ergänzungen zur Blattlaus-Fauna /Hom.
Aphididae/ von Ungarn. Acta Zool. Ac. Sci. Hung. 12. 181-192.

Szelegiewicz, H. /1968/: Faunistische Übersicht der Aphidoidea
/Homoptera/ von Ungarn. Acta Zool. Ac.Sci. Hung. 7. 58-98.

Szelegiewicz, H. /1977/: Levéltetvek - Aphidoidea. Fauna Hung.
Akad. Kiadó pp. 128.

Szépligeti Gy. /1883/: Adatok a Budapest-vidéki növénytetvek
faunájának isemretéhez. Rovarász. Lapok, 1. 1-5 and 17-20.

SEASONAL CHANGES IN THE FEEDING SITES OF CAPITOPHORUS CARDUINUS (WALKER): RELATION TO PLANT MORPHOLOGY

Wolfgang Völkl

Department of Animal Ecology, University of Bayreuth
P.O.Box 10 12 51, D-8580 Bayreuth, F.R.G.

ABSTRACT

The feeding sites of the non-host alternating aphid Capito-
phorus carduinus (Walker) varied throughout the season on its
two host plants Cirsium arvense (L.)Scop. and Cirsium palustre
(L.)Scop.. On C. arvense, the upper main stem was preferred
early in the season, while the aphid concentrated on the
peduncles and leaves of older plants. On C. palustre, the
entire stem area was colonized throughout the season, with
feeding on peduncles and leaves of minor importance. These
different distributions were caused mainly by differences in
the depth of the phloem elements and in the lignification of
the surrounding sclerenchymatic tissue.

INTRODUCTION

The choice of feeding sites in aphids is determined by two
major factors: (a) the nutritional quality of the plant or a
certain part of it and (b) the accessibility of the phloem ele-
ments. Previous studies of the accessibility of nutrients for
aphids dealt mainly with the relationship between stylet length
and depth of the phloem elements (Gibson 1972, Dixon 1985,
Völkl 1989). However, other morphological plant characters such
as trichomes, hardened tissue (Hennig 1962) or a cuticle bar-
rier (Birch 1984) are also important in determining the
accessibility of phloem elements.

The present study demonstrates the influence of morpho-
logical characters of the plants on the distribution of the
aphid Capitophorus carduinus (Walker) on two thistles, Cirsium
arvense (L.)Scop. and Cirsium palustre (L.)Scop..

MATERIAL AND METHODS

a) Biology of Capitophorus carduinus

The non host-alternating aphid C. carduinus is oligophagous on thistles of the genera Cirsium and Carduus (Börner 1953). It overwinters in the egg stage either on the rhizomes of the perennial C. arvense or on the roots of the biennal C. palustre). Fundatrices appear in mid May and population peaks occur in the last half of June (Völkl 1989). The first oviparae were observed in mid September.

b) Field samples

Field observations were carried out in Upper Franconia, West Germany, at 8 sites with dense stands of C. arvense and 6 sites with dense stands of C. palustre. At each site, colony numbers and feeding sites of C. carduinus were recorded at weekly intervals from mid May to mid September.

c) Measurement of morphological parameters of the host plant

The seasonal variation in the depth of the phloem elements and in the lignification of the sclerenchymatic tissue around the phloem elements was measured for C. arvense and C. palustre at two phenological stages in early June and late July. The depth of the phloem elements and the breadth of the sclerenchymatic tissue around the vascular bundles were measured from free-hand cross-sections using a binocular microscope (magnification 50x). Lignified sclerenchymatic tissue was identified by its yellow colouration after treatment with the chemical "reactif lactique" (Gazet du Chatelier 1948).

RESULTS

a) Seasonal variation in feeding sites

Table 1 shows the distribution of C. carduinus on C. arvense and C. palustre in early June and late July. The upper main stem and the side branches of C. arvense were mainly colonized early in the season, while the aphids concentrated on peduncles, leaf veins and leaf laminae on older plants. On

Table 1   Seasonal variation in feeding sites (relative fre-
quency of occurrence) of C. carduinus on C. arvense (based on
125 colonies) and on C. palustre (based on 268 colonies).
*: data for C. arvense from Völkl (1989).

	lower main stem	upper main stem	side branch	ped- uncle	leaf peti- ole	leaf main vein	leaf lami- na	flower head
C.arvense,*								
early June	–	0.06	0.18	0.14	0.22	0.40	–	–
late July	–	–	0.06	0.30	0.11	0.25	0.22	0.06
C.palustre								
early June	0.28	0.39	0.07	0.02	0.21	0.12	0.01	–
late July	0.14	0.16	0.34	0.06	0.18	0.09	0.03	–

C. palustre, the entire stem area - where the aphid was nor-
mally found between stem ribs - and the side branches were the
main feeding sites throughout the season. Feeding on the
peduncles, leaf veins and leaf laminae was of minor importance
on this plant.

b) Accessibility of phloem elements
     The depth of the phloem elements and the diameter of the
lignified "sclerenchymatic cap" covering the vascular bundles
depended on plant species, stem diameter and phenology (Fig.
1). Early in the season, the phloem elements were more super-
ficial, and the sclerenchymatic cap was not as marked as late
in the season. The only plant parts where the phloem was not
protected by scelerenchymatic tissue throughout the season were
the peduncles, leaf veins and leaf laminae.
     As the average stylet length is 0.35 mm in L_1 (Völkl 1989),
all phloem elements embedded up to this depth should be
potentially accessible. But on C. arvense, no feeding C.
carduinus   were   found   if   the   maximum   diameter   of   the
sclerenchymatic cap exceeded approximately 0.075 mm, even if
the phloem elements were potentially reachable (e.g. on upper
stem parts).
     In C. palustre, the phloem elements in the stem ribs are
also covered by a thick sclerenchymatic cap, but can be reached

easily if the aphid inserts its stylet from the side of the
ribs (Fig. 1). An average of 20% of the phloem elements of all
stem parts, even of the lower main stem, are accessible in this
way. But in this host plant, thin stems, peduncles and leaf
laminae are protected by a dense cover of trichomes, which may
hinder at least L_1 and L_2 from feeding.

DISCUSSION

The ability to penetrate host tissues and to reach the
phloem elements is one factor that determines the exploitation
of a resource (Klingauf 1987). Due to its short stylets C.
carduinus can utilize only plant parts where the phloem is near
the surface (Völkl 1989). Therefore, two important reasons for
the different distribution on the two thistles (Tab. 1) are
differences in the depth of the phloem elements and in the
amount of   lignification of the surrounding sclerenchymatic
tissue.

In the main stems of C. arvense, the phloem is deeply em-
bedded and cannot be reached. Upper stem parts can be exploited
early in the season. Late in the season, the utilization of su-
perficial phloem elements that are within the reach of the
stylets is prevented by the thick sclerenchymatic tissue that
surrounds each vascular bundle and that probably cannot be
penetrated by C. carduinus. Therefore, the aphids are forced to
feed on peduncles, leaf veins or leaf laminae, where the phloem
elements are not protected by a sclerenchymatic cap.

Stems of C. palustre provide feeding sites throughout the
season, since some of the phloem elements in and between the
stem ribs are always accessible from the side where, they are
not protected by the sclerenchymatic cap (Fig. 1). In very
thick stems, even in the stem ribs, the phloem is deeply
embedded and out of reach. On the other hand, peduncles and
leaf veins of young plants with superficial phloem are not
colonized because of their dense coverings of hair.

In addition to earlier studies on the importance of morpho-
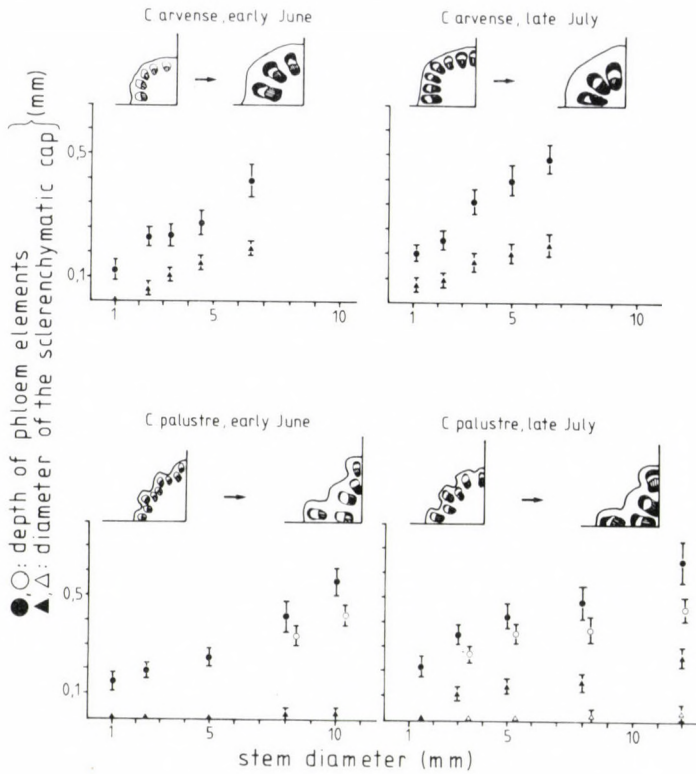
Figure 1: Relationship between stem diameter and depth of phloem elements and diameter of the sclerenchymatic cap, respectively, in C. arvense and C. palustre in two phenological stages. Filled circles = depth of phloem elements in C. arvense and C. palustre (outside of stem ribs); open circles = depth of phloem elements within stem ribs of C. palustre; filled triangles = maximum diameter of the sclerenchymatic cap in C. arvense and C. palustre (outside of stem ribs); open triangles = minimum diameter of the scelerenchymatic cap in stem ribs of C. palustre. The drawings above the graphs elucidate the structure of the vasculars at low and high stem diameters. Black = sclerenchymatic cap, hatched = xylem, white = phloem.

logical constraints for the choice of feeding sites by aphids
(e.g. Gibson 1972, Dixon 1985) this example shows that the
depth of the phloem elements in some cases is not the only
important factor determining their accessibility. In some host
plants, especially perennials, the presence of lignified scle-
renchymatic tissue should also be considered.

ACKNOWLEDGEMENT

LITERATURE
Birch, N. (1984): Resistance of three species of aphids in wild
    relatives of the Faba bean (genus Vicia); taxonomy and
    possible mechanisms. IOBC, WRPS Bull. 1984, VII/4: 35-36.

Börner, C. (1953): Aphidae Europae Centralis. Mitt. Thür. Bot.
    Ges. 4 (3): 488 pp.

Dixon, A.F.G. (1985): Aphid ecology. Blackie: Glasgow & London.
    157 pp.

Gibson, R.W. (1972): The distribution of aphids on potato
    leaves in relation to vein size. Entomol. Exp. & Appl. 15:
    213-223.

Hennig, E. (1962): Neuere Untersuchungen über die Bedeutung der
    sogenannten Probesaugstiche bei Aphiden. Z. Pflanzenkr.
    Pflanzensch. 69: 321-330.

Klingauf, F. (1987): Feeding, Adaptation and excretion. In:
    Minks, A.K. & Harrewijn, P. (eds.): Aphids. Their biology,
    natural enemies and control. Vol. A. Elsevier, Amsterdam.
    pp. 225-253.

Gazet du Chatelier, G. (1948): Un nouveau reactif pour
    l`analyse des poudres et des coupes vegetales. Ann. Pharmac.
    franc. 35: 1-5.

Völkl, W. (1989): Resource partitioning in a guild of aphid
    species associated with creeping thistle Cirsium arvense.
    Entomol. Exp. & Appl. 51: 41-47.

DO APHIDS SPECIATE SYMPATRICALLY?

S.A.Ward

Department of Zoology, La Trobe University, Bundoora,
Victoria 3083, Australia.

ABSTRACT

A number of authors have argued that speciation in aphids
(Homoptera: Aphididae) and other plant-parasitic insects does
not require that the incipient species be geographically isolat-
ed. Instead, aphids on different host-plants may mate assorta-
tively and, ultimately, populations adapted to different hosts
may diverge to become separate species.

Here I discuss the barriers to sympatric speciation in aphids
and suggest an alternative explanation for the emergence and
maintenance of distinct host races. I show that published data
on a range of aphid species support the hypothesis that the
separation of uniform populations into host races results from
self-fertilisation or the loss of the sexual generations, rather
than from assortative mating with respect to host preference, as
is normally assumed.

INTRODUCTION

Many aphid species are composed of "biotypes", host races, or
subspecies (Müller 1971, Eastop 1972). These races may be fully
interfertile, or partially isolated by post-zygotic barriers to
gene flow (Müller 1985, 1986). One common feature of such races
is that they differ in their preference for, and ability to
survive on, the various host plants in the species' range (e.g.
the numerous sympatric races of Acyrthosiphum pisum [Müller
1971, 1980; Müller & Steiner 1985]). Müller (1985) has argued
persuasively that these races have arisen by sympatric diver-

gence of populations with differences in host preference, and that they are incipient species; i.e., that aphids may commonly speciate without geographical isolation.

Sympatric speciation has been the focus of lively debate for many years. While several authors argue that phytophagous insects may speciate sympatrically (ie. without geographical isolation) via the formation and divergence of host races (Müller 1971, 1985a; Bush 1975), others contend that the conditions for sympatric speciation are too stringent for the process to be important in nature (Futuyma & Mayer 1980; Paterson 1981).

Here I consider some of the assumptions forming the basis of current models of sympatric speciation, and propose a more realistic model. I then propose an alternative explanation for the emergence of biotypes and host races in aphids.

SYMPATRIC SPECIATION

The main steps in this process are often modelled as follows (Maynard Smith 1966; Bush 1975; Pimm 1978; Kondrashov 1983; Rausher 1984). (1) In a population of insects specializing on host HA, mutants arise which prefer host HB. (2) The mutation spreads, perhaps because host HB is an "empty niche", so individuals preferring HB escape from competition. (3) A mutation at another locus causes an increase the insect's fitness on HB, at a cost to its performance on HA. With polymorphisms at both loci (preference and viability), selection may result in linkage disequilibrium: most individuals prefer the host to which they are best adapted. (Alternatively, the HB-preference allele has the pleiotropic effect of increasing fitness on HB, while reducing survival on HA.) (4) Mating occurs on the host, so it is assortative with respect to host preference. (5) Ultimately, assortative mating and selection against maladaptive genotypes (hybrids, or individuals which prefer the host to which they are least well adapted) lead to a complete separation of the two host races: speciation is completed.

Thus, sympatric speciation may be possible if mating is assor-

tative with respect to a character showing stable underdominance (i.e. with disruptive selection on a stably polymorphic character).

Stable underdominance requires that the extreme phenotypes (or homozygotes) are selected for in different habitats, in each of which density-dependent processes regulate the population (Levene 1953; Maynard Smith 1966, 1970). Mating will be assortative if the character under disruptive selection is correlated with host preference. The original generalist species may then split into two specialists if selection eliminates those individuals whose habitat preference is inappropriate - those that prefer the habitat in which they are least fit, or in which they are likely to produce maladapted hybrids.

MODELS FOR APHIDS

The existing models of sympatric speciation contain two important implicit assumptions. First, "preference" is assumed to be a single character, often controlled by alleles at a single locus. Aphids, however, encounter one plant at a time, and "preference" results from between-plant variation in the chance that the aphid will settle. The fact that there are generalists means that mutants which accept HB do not necessarily reject HA: the responses to the two hosts must be free to evolve independently - they must be controlled by genes at different loci.

Second, the models assume that all dispersers find hosts: that there is no cost of specialization. In fact, however, perhaps fewer than 1% of aphids find hosts (Taylor 1977), so there are considerable benefits to be gained by accepting several hosts.

The above considerations suggest that a more realistic model for speciation in aphids must include changes in allele frequencies at at least three loci: one determining the aphid's readiness to settle on host HA, another its readiness to settle on HB, and a third which determines its fitness on HA and HB. Analysis of such a model (Ward in press, Ward in prep.) shows that the conditions for sympatric speciation are far more strin-

gent than is the case for two-locus models.

In particular, it shows that to avoid genetically unsuitable mates aphids must reduce their host range, and run the risk of failing to find hosts at all. This means that for such speciali-zation to be favoured by selection, hybrids between host races must be extremely unfit on both hosts; indeed, if 1% of migrat-ing aphids find hosts, then for sympatric speciation to occur the hybrids' fitnesses on both hosts must be less that 1.01% of the fitnesses of the well-adapted specialists (Ward in press).

A second major barrier to sympatric speciation is that of gene flow via matings on a third, fourth, etc., host. Unless the races have non-overlapping host ranges they cannot become repro-ductively isolated. In fact, however, aphids' host races do share hosts - e.g. Acyrthosiphum pisum (Müller 1971).

What this means is that we must be extremely cautious in invoking disruptive selection and assortative mating to explain the divergence of host races or biotypes; some other mechanism is required.

ALTERNATIVE MECHANISMS

In aphid species with apterous males, particularly if the hosts are small herbaceous plants unlikely to receive more than one migrant, males will usually mate with their genetically identical sisters: self-fertilisation is prevalent. This may limit gene flow through the population, and permit the temporary divergence of races whose host preference matches their ability to survive on the various available hosts. Indeed, self-fertili-sation may result in permanent divergence (i.e. speciation) if mutants arise with abnormal karyotypes; here, if structural heterozygotes are eliminated then new karyotypes can persist only as a result of self-fertilisation.

If self-fertilisation has been important as an isolation mechanism, and thus as a factor contributing to sympatric diver-gence, the majority of host races should appear in autoecious (non-host alterating) aphids with apterous males, or in second-

arily autoecious strains of species that normally show host alternation - i.e. mutant clones that have lost the autumn migration to the primary host.

The second, and simpler, isolation mechanism is the loss of the sexual generations. Clearly this results immediately in complete reproductive isolation from the parent population, and should thus permit sympatric divergence of the new race.

Table 1 summarises the relevant features of 39 well-documented "biotypes" in 12 species (or species groups) (Ward in press). As predicted, most of these produce apterous males or have abandoned sex altogether. These cases can thus be explained without invoking the classical models involving assortative mating.

Table 1   The mechanisms by which 39 biotypes in 12 species are isolated or separable from conspecific biotypes.

	Biotypes	Species/groups
Isolation by:		
Anholocycly	5	4
Primary host	4	2
Secondary host	8	3
Self-fertilisation		
autoecious	19	6
secondary autoecy	3	3
total selfing	22	8

The puzzling instances of races differing in their secondary hosts (on which they do not mate) clearly cannot result from assortative mating with respect to host choice, so the only remaining candidates for classical sympatric speciation are the races separated by differences in primary host range (in Brachycaudus prunicola [Thomas 1962] and Myzus cerasi [Dahl 1968]). It remains to be shown whether these diverged sympatrically or have instead regained sympatry since diverging in allopatry. The theoretical considerations discussed above suggest the latter.

In conclusion, while there is strong evidence for the

existence of sympatric host races in aphids, the classical models for sympatric speciation seem inappropriate. Published data support the alternative hypothesis that self-fertilisation and anholocycly are more important than disruptive selection and assortative mating in the evolution of aphid host races.

ACKNOWLEDGEMENTS

REFERENCES

Bush GL (1975) Modes of animal speciation. Ann. Rev. Ecol. Syst. 6: 339-364.

Dahl ML (1968) Biologische und morphologische Untersuchungen über den Formenkreis der schwarzen Kirschenlaus Myzus cerasi (F.) (Homoptera: Aphididae). Dtsch. Ent. Z. 15: 281-312.

Eastop VF (1972) Biotypes of aphids. pp.40-51 in Lowe AD (ed) Perspectives in aphid biology. Ent. Soc. N.Z. Bull. 2: 40-51.

Futuyma DJ, Mayer GC (1980) Non-allopatric speciation in animals. Syst. Zool. 29: 254-271.

Kondrashov AS (1983) Multilocus model of sympatric speciation. Theor. Popul. Biol. 24: 121-135, 136-144.

Levene H (1953) Genetic equilibrium when more than one niche is available. Am. Nat. 87: 331-333.

Maynard Smith J (1966) Sympatric speciation. Am. Nat. 100: 637-650.

Maynard Smith J (1970) Genetic polymorphism in a varied environment. Am. Nat. 104: 487-490.

Müller FP (1971) Isolationsmechanismen zwischen sympatrischen bionomischen Rassen am Beispiel der Erbsenblattlaus Acyrthosiphon pisum (Harris) (Homoptera, Aphididae). Zool. Jb. Syst. 98:131-152.

Müller FP (1980) Wirtspflanzen, Generationenfolge und reproduktive Isolation intraspezifischer Formen von

Acyrthosiphon pisum. Ent. exp. appl. 28: 145-157.

Müller FP (1985a) Biotype formation and sympatric speciation in aphids (Homoptera: Aphidinea). Entomol. Gener. 10: 161-181.

Müller FP (1985b) Genetic and evolutionary aspects of host choice in phytophagous insects, especially aphids. Biol Zbl. 104: 225-237.

Müller FP, Steiner H (1985) Das Problem Acyrthosiphon pisum (Homoptera: Aphididae). Z. ang. Zool. 72: 317-334.

Paterson HEH (1981) The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. S. Afr. J. Sci. 77: 113-119.

Pimm SL (1978) Sympatric speciation: a simulation model. Biol. J. Linn. Soc. 11: 131-139.

Rausher MD (1984) The evolution of habitat preferences in subdivided populations. Evolution 38: 596-608.

Taylor LR (1977) Migration and the spatial dynamics of an aphid, Myzus persicae. J. Anim. Ecol. 46: 411-423.

Thomas KH (1962) Die Blattläuse des Formenkreises Brachycaudus prunicola (Kalt.). Wiss. Z. Univ. Rostock 11: 325-342.

Ward SA (1987a) Optimal habitat selection in time-limited dispersers. Am Nat 129: 568-579.

Ward SA (1987b) Cyclical parthenogenesis and the evolution of host range in aphids. pp 39-44 in Holman J, Pelikan J, Dixon AFG, Weisman L (eds) Population structure, genetics and taxonomy of aphids and thysanoptera. SPB Academic Publishing, The Hague.

Ward SA (in press) Reproduction and host selection by aphids: the importance of "rendez-vous" hosts. In Bailey WJ, Ridsdill-Smith TJ (eds) Reproductive Behaviour in Insects: Individuals and Populations. Chapman & Hall, London.

THE APPLICATION OF MITOCHONDRIAL DNA ANALYSIS IN APHID SYSTEMATICS

R. Foottit[1], C. Galvis[2] & L. Bonen[2]

[1]Biosystematics Research Centre, Agriculture Canada, Research Branch,

Central Experimental Farm, Ottawa, Canada K1A 0C6

[2]Department of Biology, University of Ottawa, 30 Somerset St.E., Ottawa,

Canada K1N 6N5

ABSTRACT

The identification and classification of certain aphid groups is limited by a lack of distinctive characteristics and a high degree of morphological plasticity. Because the analysis of DNA restriction fragment length polymorphisms (RFLPs) has proven to be a powerful tool in taxonomic studies, we have begun to apply these molecular techniques in aphid systematic studies. We have developed methods for the rapid isolation of aphid DNA that is enriched for mitochondrial (mt) DNA. This DNA, when cleaved by appropriate restriction endonucleases and hybridized with cloned *Drosophila* mtDNA probes, reveals the presence of RFLPs among aphid species. This approach has been used to examine DNA from various aphid species including *Acrythosiphon pisum* (Harris) and *Sitobion avenae* (Fabricius), using amounts of tissue ranging from 200 mg to 6 grams.

INTRODUCTION

The cyclical parthenogenetic mode of reproduction of aphids has placed constraints on the genetic analysis of this group of organisms.

Classical approaches are difficult to use and although enzyme
electrophoresis has been used extensively, the relatively low levels of
polymorphic loci that have been detected limit its usefulness at the
population level (Eggers-Schumacher, 1987).

Recently, the use of molecular techniques such as the analysis of
DNA restriction fragment length polymorphisms (RFLPs) has proven to be
an extremely powerful tool in the taxonomic studies of a wide variety of
organisms (Lansman et al., 1981). This method allows the detection of
DNA sequence changes (in the form of the altered electrophoretic
mobility of DNA restriction fragments) that have occurred during
evolution. Animal mitochondrial (mt) DNA, which is a small, circular,
maternally-inherited molecule of 15,000 to 20,000 base pairs, has been
used extensively in such analyses, in part because mtDNA often shows
more intra-and inter-specific variation than its nuclear counterpart
(Attardi, 1985). Such studies have provided insight into population
structure and gene flow, historical biogeography, and phylogenetic
relationships for a number of different organisms (cf. Moritz et al.,
1987; Avise, 1986).

The usefulness of mtDNA analysis in aphid systematics will depend
on a practical (rapid and inexpensive) method for the isolation and
detection of mtDNA from small quantities of aphid material. Recently,
several such protocols have been developed for Diptera (Cockburn &
Seawright, 1988; Afonso et al., 1988; Tamura & Aotsuka, 1988) as well as
other animal (Jones et al., 1988) and plant (Wilson & Chourey, 1984)
groups. Here we describe a method that allows the detection of mtDNA
variation among different aphid groups.

MATERIALS AND METHODS

Aphid DNA was isolated using a modification of the Wilson & Chourey

(1984) protocol for plant mitochondrial DNA. Aphids (200 mg - 6 gm),

that had been quick-frozen in an ethanol-dry ice bath, were ground by

mortar and pestle for several minutes in cold homogenizing buffer

[0.44 M sucrose, 50 mM Tris-HCl (pH 8.0), 3 mM EDTA,1 mM

mercaptoethanol, 0.1% bovine serum albumin] at a concentration of

approximately 0.5 ml buffer/g aphids. The volume of buffer was

increased approximately 20-fold prior to filtration through cheesecloth

and then Miracloth (Calbiochem, LaJolla, California, USA). After two

centrifugations at 500 x g for 5 min. to remove the nuclear fraction and

cellular debris, the mitochondria were pelleted from the supernatant by

centrifugation at 12,000 x g for 25 min. A purer mitochondrial fraction

can be made with additional differential centrifugations.

The mitochondrial pellet (from 600 mg aphids) was resuspended in

200 ul 50 mM Tris-HCl (pH 8.0), 20 mM EDTA before the addition of 400 ul

lysis buffer [0.2 M Tris-HCl (pH 8.0), 0.1 M EDTA, 0.2 M NaCl, 2% SDS,

0.02 M mercaptoethanol]. After the sample was incubated at 65°C for 20

min., 200 ul 5 M potassium acetate were added and the mixture placed on

ice for 30 min. The samples were then microcentrifuged for 3 min. and

the DNA precipitated by adding 40 ul 5 M ammonium acetate and 400 ul

cold isopropanol and placing at -20°C for 30 min. The pellets were

recovered by microcentrifugation, washed with 70% ethanol and dried

under vacuum before being resuspended in 225 ul 50 mM Tris-HCl (pH 8.0),

20 mM EDTA. A second rapid precipitation was carried out by the

addition of 25 ul 3M sodium acetate and 166 ul isopropanol at room

temperature. After several minutes of gentle mixing, the DNA was

recovered by centrifugation for 30 sec. The pellet was washed and dried

before being resuspended in 60 ul 10 mM Tris-HCl (pH 7.5), 1 mM EDTA and stored at -20°C.

Restriction endonuclease digestions, agarose gel electrophoresis, Southern blotting and hybridizations were carried out according to standard procedures (Maniatis et al., 1982). After electrophoresis in 1% or 2% agarose gels in Tris-borate-EDTA buffer [89 mM Tris-HCl, 89 mM boric acid, 8 mM EDTA, (pH 8.2)], the restricted DNA fragments were transferred to nylon membranes (Biotrans, ICN, Cleveland, Ohio, USA) by capillary blotting and bound by ultraviolet crosslinking. ^{32}P-labelled DNA probes were prepared from *Drosophila yakuba* Burla mt DNA clones using the oligomer labelling method (Feinberg & Vogelstein, 1983). Three clones (pdyHB, pdyHC and pdyHD) containing HindIII fragments of 4.8 kb, 2.3 kb and 1.5 kb, respectively, in pBR322 plasmid vectors (Clary & Wolstenholme, 1984) were used. Blots were prehybridized in 5 x SSC (1 x SSC: 0.15 M NaCl, 0.015 M sodium citrate), 5 x Denhardt's solution [0.1% ficoll, 0.1% polyvinylpyrrolidone, 0.1% bovine serum albumin], 0.5% SDS, 50 mM sodium phosphate buffer (pH 7.0) and 250 ug/ml sheared denatured calf thymus DNA for several hours. Hybridization was carried out for approximately 36 hr. at either 46°C or 50°C. Blots were washed first in 2 x SSC at room temperature and then extensively at 37°C in 2 x SSC prior to autoradiography at -80°C. For the detection of aphid mtDNA by this method, the amount of DNA loaded per gel lane corresponded to approximately 15-30 mg of aphid biomass.

RESULTS

The protocol outlined above has been used to isolate DNA from a number of different aphids including *Acyrthosiphon pisum* (Harris) and *Sitobion avenae* (Fabricius). Aphid mtDNA was detected by hybridization

analysis using cloned *D. yakuba* mtDNA as probe (Fig. 1). Relatively

little mtDNA was detected in the nuclear fraction (lanes 1 & 2), whereas

strong hybridization to an EcoRI fragment of approximately 1.4 kb was

seen for both the crude mitochondrial fraction (lanes 3 & 4) and the

more extensively purified mitochondrial fraction (lanes 5 & 6) that had

undergone two additional rounds of differential centrifugation. In lane 6

(Fig. 1A), discrete bands can be seen superimposed on the nuclear DNA

profile. Since the sum of their lengths greatly exceeds that of insect

mt genomes (that is, 16 kb, Clary & Wolstenholme, 1984), they presumably

include other abundantly represented types of DNA in addition to mtDNA.
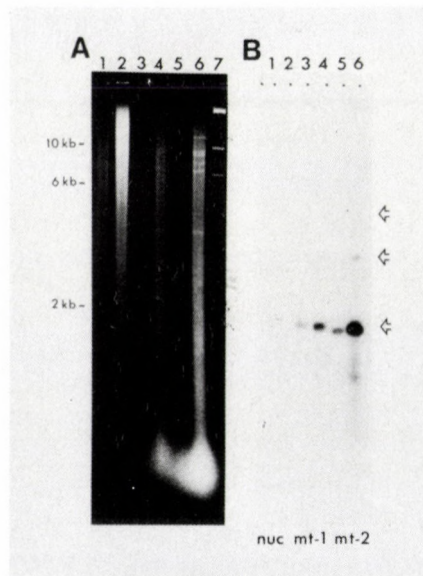
Fig. 1. (A) UV fluorescence pattern of ethidum bromide stained aphid DNA:
Acyrthosiphon pisum nuclear DNA (lanes 1 & 2), crude mtDNA (lanes 3 & 4) and
enriched mtDNA (lanes 5 & 6) fractions, digested with EcoRI. Approximately
twice the amount of DNA was loaded in lanes 2, 4 and 6 compared to lanes 1, 3
and 5. Size marker (lane 7): (lambda DNA x HindIII. (B) Southern blot
analysis using cloned *Drosophila yakuba* mtDNA probe (pdyHB). Arrowheads
indicate positions of hybridizing fragments.

Although the intensity of the hybridization signals indicate strong sequence similarity between aphid and fruit fly mtDNA, it appears that not all regions of the *D. yakuba* 4.8 kb probe hybridize equally well with aphid mtDNA (cf. only one major hybridizing EcoRI fragment of approximately 1.4 kb and two very minor bands of approximately 2.6 and 4.0 kb; Fig. 1B).

When hybridizations were carried out at 46°C instead of 50°C in order to detect less closely-related sequences, results were somewhat
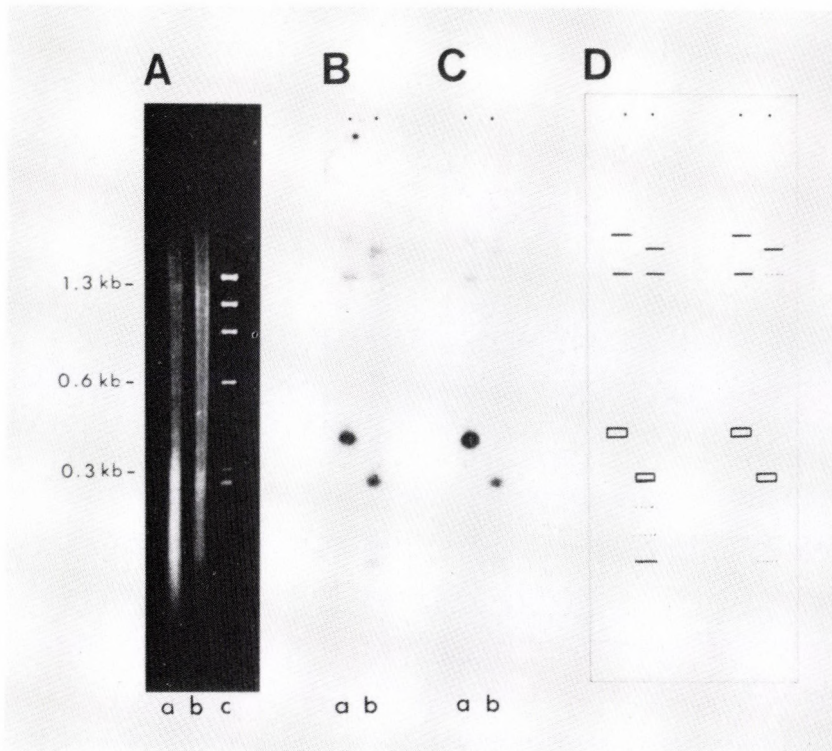
Fig. 2. (A) UV fluorescence pattern of A. *pisum* (lane a) and *S. avenae* (lane b) mtDNA digested with AluI. Size marker (lane c): phiX174 DNA x HaeIII. (B & C) Autoradiograms of hybridizations conducted at 46°C (B) or 50°C (C) using *D. yakuba* mtDNA probes (pdyHB, pdyHC and pdyHD). (D) Schematic of hybridization results shown in (B) & (C).

variable with respect to signal intensity and background levels. Figure 2 shows the results of such an experiment for AluI digests of A. *pisum* and S. *avenae* DNA, and it also illustrates differences in the hybridization patterns for the two aphid species. *Acyrthosiphon pisum* mtDNA shows three hybridizing fragments of approximately 1.9 kb, 1.3 kb and 0.4 kb, the latter being the most prominent one. The S. *avenae* mtDNA hybridization pattern shows a prominent signal of approximately 0.3 kb and five additional ones (of approximately 1.3 kb, 0.2 kb, 0.15 kb and 0.1 kb, of differing intensities depending on the temperature of hybridization). Only the 1.3 kb AluI fragment is held in common between the A. *pisum* and S. *avenae* mtDNA.

DISCUSSION

We report on the isolation of aphid DNA and the detection of mtDNA variation between A. *pisum* and S. *avenae*. This DNA isolation procedure reproducibly yields DNA that can be cleaved easily with restriction enzymes and stored over long periods of time in aqueous solution at -20°C. Quick-frozen aphids can be stored at -80°C prior to DNA isolation. The protocol can be scaled down for smaller biomasses; to date 200 mg - 6 gm quantities have been used. The method is relatively rapid and inexpensive, for the most part being carried out in microfuge tubes, and it does not involve the use of organic solvents or ultracentrifugation. The level of contaminating nuclear DNA is low enough that detection by Southern hybridization analysis is feasible using DNA probes from organisms as distantly related as *Drosophila*. To increase the sensitivity of RFLP detection, it will be advantageous to use cloned aphid mtDNA probes.

The examination of DNA from a variety of aphid species to determine the extent of mtDNA restriction fragment divergence will give a clearer picture of the utility of this approach and of the range of taxonomic levels at which this information can be applied. Since different regions of the mtDNA molecule are known to be subject to different evolutionary constraints (cf. the rapidly-evolving D-loop region vs. the conservative ribosomal RNA genes; Attardi, 1985), appropriate probes and restriction enzymes should allow the examination of very broad phylogenetic relationships as well as close ones such as maternal lineages among clonal populations of aphids. Recently, genetic differentiation in the mtDNA among biotypes of *Schizaphis graminum* (Rondani) was observed using such restriction enzyme analysis (Powers et al., 1989).

REFERENCES

Afonso, J.M., Pestano, J. & Hernandez, M. (1988): Rapid isolation of mitochondrial DNA from *Drosophila* adults. Biochem. Genet., **26**. 381-386.

Attardi, G. (1985): Animal mitochondrial DNA: An extreme example of genetic economy. Int. Rev. Cytol. **93**. 93-145.

Avise, J.C. (1986): Mitochondrial DNA and the evolutionary genetics of higher animals. Phil. Trans. R. Soc. Lond. B., **312**. 325-342.

Clary, D.O. & Wolstenholme, D.R., (1984): The *Drosophila* mitochondrial
   genome. In: N. Maclean (Editor). Oxford Surveys on Eukaryotic Genes.
   Vol.1. Oxford University Press, Oxford, pp 1-35.

Cockburn, A.F. & Seawright, J.A. (1988): Techniques for mitochondrial
   and ribosomal DNA analysis of anopheline mosquitoes. J. Amer. Mos.
   Control Assoc. **4.** 261-265.

Eggers-Schumacher, H.A. (1987): Enzyme electrophoresis in biosystematics
   and taxonomy of aphids. In: J. Holman, J. Pelikan, A.F.G. Dixon &
   L. Weismann (Editors). Population Structure, Genetics and Taxonomy of
   Aphids and Thysanoptera. SPB Academic Publ., The Hague, pp 63-70.

Feinberg, A. & Vogelstein, B. (1983): A technique for radio-labelling
   DNA restriction endonuclease fragments to high specific activity.
   Anal. Biochem. **132.** 6-13.

Jones, C.S., Tegelstrom, H., Latchman, D.S. & Berry, R.J. (1988): An
   improved rapid method for mitochondrial DNA isolation suitable for use in
   the study of closely related populations. Biochem. Genet. **26.** 83-88.

Lansman, R.A., Shade, R.O., Shapira, J.F. & Avise, J.C. (1981): The use
   of restriction endonucleases to measure mitochondrial DNA sequence
   relatedness in natural populations. III. Techniques and potential
   applications. J. Mol. Evol. **17.** 214-226.

Maniatis, T., Fitsch, E.F. & Sambrook, J. (1982): Molecular Cloning: a
   Laboratory Manual. Cold Spring Harbor Laboratory, New York, 545 pp.

Moritz, C., Dowling, T.E. & Brown, W.M. (1987): Evolution of animal
   mitochondrial DNA: relevance for population biology and systematics.
   Ann. Rev. Evol. Syst. **18.** 269-292.

Powers, T.O., Jensen, S.G., Kindler, S.D., Stryker, C.J. & Sandall, L.J.
   (1989): Mitochondrial DNA divergence among greenbug (Homoptera:
   Aphididae) biotypes. Ann. Entomol. Soc. Am. **82.** 298-302.

Tamura, K. & Aotsuka, T. (1988): Rapid isolation method of animal
   mitochondrial DNA by the alkaline lysis procedure. Biochem. Genet.
   26. 815-819.

Wilson, A.J. & Chourey, P.S. (1984): A rapid inexpensive method for the
   isolation of restrictable mitochondrial DNA from various plant
   sources. Plant Cell Rep. **3.** 237-239.

USING A COMPUTER TO IDENTIFY THE MORPHS

OF TWO CLOSELY RELATED SPECIES

A.V. Stekolshchikov,

Zoological Institute of the USSR Academy of Sciences,

Leningrad, 199034, USSR

ABSTRACT

Nontraditional diagnostic methods, such as complex indices and
discriminant functions, are used to identify two aphid species in the
genus *Dysaphis* Börner.

INTRODUCTION

One of the characteristics of aphids is the presence of taxa that
are distinct biologically but are morphologically very similar; i.e.,
they cannot be distinguished by individual characteristics or with the
help of simple indices (correlations of two characteristics). This
makes the identification of specimens with unknown biologies difficult.
One way to approach this problem is to combine, by complex indices or by
discriminant analysis, several quantitative characteristics into one
complex, defined for each taxa by a successful selection of basic
characteristics that may not cris-cross at all or only slightly.
Compiling complex index selection and combination of characteristics
(arrangement of coefficients determining participation of each one in a
final formula) can be done empirically by sorting out possible
combinations and selecting the best one (Scott & Shepard, 1976;

Shaposhnikov, 1986), because discriminant analyses permit the use of a computer for selection of characteristics and for their unification. This was accomplished with the help of the analytical methods worked out by Fisher (1936).

The use of these methods for aphid identification is becoming more wide spread (Eastop, 1985; Blackman & Paterson, 1986). The aim of this paper is to compare and analyze the possibility of using complex indices and discriminant analyses for the identification of two closely related species of aphids in the genus *Dysaphis* Börner.

MATERIALS AND METHODS

The two aphids studied were *Dysaphis chaerophyllina* Shaposhnikov and *D. brachycyclica* Shaposhnikov. The biologies of these species are well studied (see Shaposhnikov in this book). Characteristics of all morphs of these species have been used in this research.

From the various methods of discriminant analyses, the linear discriminant analysis has been selected; because, in this case, discriminant functions are obtained that correspond with the following requirements: taxa can be diagnosed with a high degree of accuracy, characters can be used in a dichotomous key, and special calculations are not required in the diagnoses. A.L. Lobanov (Zoological Institute of the USSR Academy of Sciences), with this author's help, has developed for the BESM-6 computer a special software package that provides a comprehensive study of an initial set of characteristics and that includes both interactive programs and completely automatic ones. In all programs, a standard algorythum of discriminant analysis for separation of two apriori groups has been used. The initial set included 42 quantitative characteristics.

RESULTS

From the data obtained, a key was constructed that permits the identification of all morphs of *D. chaerophyllina* and *D. brachycyclica*. Thus, despite close morphological similarity in these species, separate characteristics and simple indices can be used to identify the alate exules and males. For all other morphs, discriminant functions have been devised that include from 3 to 6 characteristics. For example, the function for apterous exules can be presented as

− 1.53d − 1.89e + 0.56f (d = number of hairs on the cauda; e = degree or extent of sclerotization as illustrated in Fig. 1; f = number of hairs on the posterior margin of the subgenital plate). If the value of the function is less than 13, the specimen belongs to *D. chaerophyllina*, if more than 13, to *D. brachycyclica*. Functions obtained are universal, and by using them we can diagnose species throughout their distributional area. Unfortunately, in some samples up to 25% of the specimens were determined incorrectly. the data on a number of specimens and samples used for each morph and the percentage of specimens determined correctly by the key are given in Table 1.
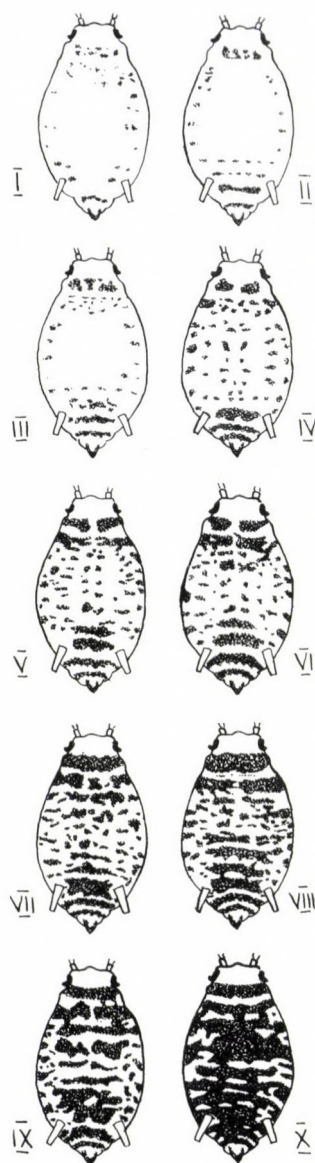
Fig. 1.   Degree of sclerotization of cuticle of apterous exules (Shaposhnikov, 1965). I-X = conditional classes.

Table 1   Characteristics of the key for identification of all morphs of
           Dysaphis chaerophyllina and *D. brachycyclica*.

		Fundatrix	Emigrant	Apterous exule	Alate exule	Gynopara	Male	Amphigonic female
D. chaerophyllina	number of specimens	27	151	434	17	61	40	54
	number of samples	21	15	33	7	6	3	6
	% identified correctly	96.3	96.9	98.4	100	98.4	100	94.4
D. brachycyclica	number of specimens	13	101	423	21	68	18	65
	number of samples	5	7	30	3	7	3	4
	% identified correctly	100	97.0	95.5	100	95.6	100	93.8

INTRASPECIFIC FORMS

Biological differences occur between the Armenian and northern
populations of *D. brachycyclica* and between certain populations of
D. chaerophyllina and some samples of this species from Dilizhan (the
Dilizhan form) (see Shaposhnikov in this book). With discriminant
analysis it was possible to develop functions that permited the
identification of all known morphs of these intraspecific forms with an
accuracy of 95-100%.

To study the degree of similarity between apterous exules of
different populations of the species, the phenotypic similarity measure
"r" was calculated using the Zhivotovsky (1979) method. Two sets of
characters were used in the calculations. One set consisted of 33
unbroken and meristic characters; and the other consisted of an

abbreviated set of 11 meristic characters, only. Results are given in

Table 2 and Fig. 2.

Table 2   Value of the phenotype similarity measure "r" for intraspecific
forms of *Dysaphis chaerophyllina* and *D. brachycyclica*. [Above
the diagonal, the values for "r" are for 33 characters. Below
the diagonal, the values for "r" are for 11 characters.]

		D. brachycyclica		*D. chaerophyllina*	
		Armenian populations	Northern populations	Dilizhan form	All other forms
D. brachycyclica	Armenian populations	–	0.66	0.78	0.85
	Northern populations	0.84	–	0.48	0.74
D. chaerophyllina	Dilizhan form	0.74	0.60	–	0.81
	All other forms	0.83	0.75	0.88	–

The differences between dendrograms A and B in Fig. 2 occur because

individuals of *D. chaerophyllina* and the Armenian populations of *D.*

brachycyclica have smaller sizes than those of the Northern populations of

D. brachycyclica. Using only meristic characters (Fig. 2B), intraspecific

forms unite in groups corresponding to their species. When using meristic

characters only (Table 2), Armenian populations of *D. brachycyclica* merge

to *D. chaerophyllina*--the value of "r" for the Armenian population of

D. brachycyclica and all forms of *D. chaerophyllina,* except the Dilizhan

form, is equal to 0.83 and is a bit less than the mean "r" (0.84) for the

Armenian and Northern populations of *D. brachycyclica*.

The mean value of this discriminant function for apterous exules

shows the existence of morphological differences between the Dilizhan form

(2.7 - 2.8) and all other forms of *D. chaerophyllina* (5.0 - 10.6).
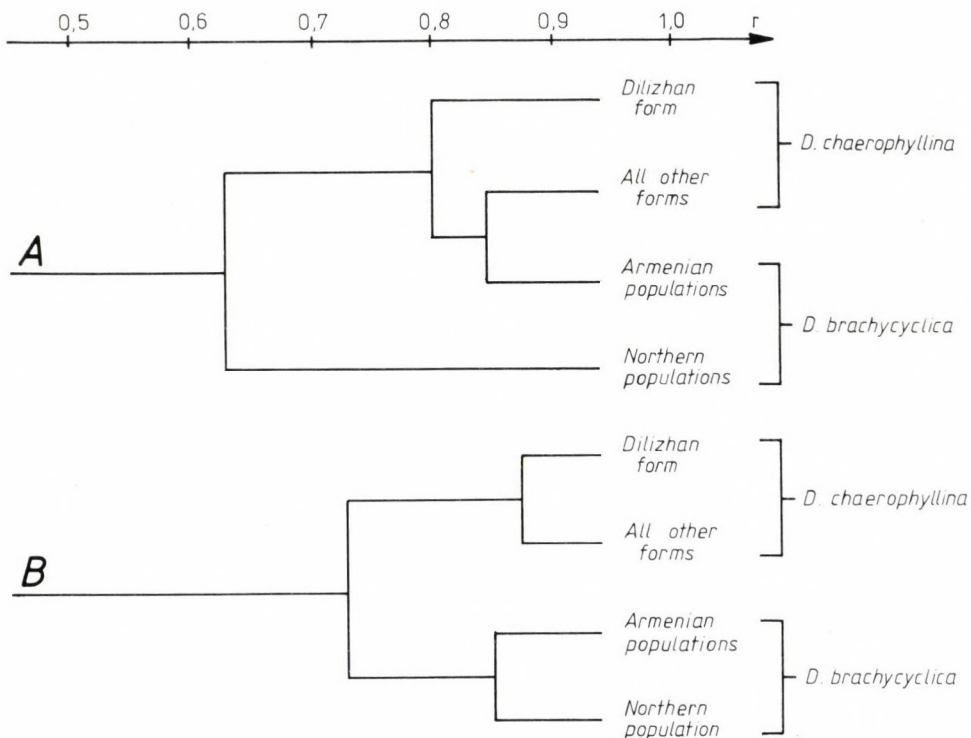
Fig. 2.   Dendrograms of similarity between intraspecific forms of
          Dysaphis chaerophyllina and *D. brachycyclica*.   [A = set with 33
          characters; B = set with 11 characters.]

DISCUSSION

Comparison of complex indices (see Shaposhnikov in this book) and
discriminant function is of some interest, but it cannot be done
objectively because in the same individuals of the same species,
different characters were used.   Nevertheless, an attempt to compare the
two methods may be useful.   Using all the individuals studied in both
species (434 +423), the percent correctly identified is 98.4% for
D. chaerophyllina and 92.7% for *D. brachycyclica* by complex index and

correspondingly 98.4% and 95.5% by discriminant function. Complex index

has some advantage over discriminant function because of its nonlinear

function. But, because the complex index is made empirically, the

results depend on the skill and qualification of the specialist. The

quality of the index depends on morphological similarity of the species

studies--the higher the index, the more difficult it is to find

characters to separate the species. The possibility of using a computer

for discriminant functions gives important advantages to indices because

it does not depend on the specialist's qualifications and it lacks

subjectivity and permits the selection of the best set and the fewest

number of characters.

CONCLUSION

Our data indicate that discriminant functions and empirically

derived complex indices can be used successfully for the diagnosis of

morphologically close species. One can conclude that complex indices

are more effective for unrelated species and discriminant functions give

better results for closely related species.

These methods prove that intraspecific forms of *D. chaerophyllina* and

D. brachycyclica differ not only biologically but also morphologically.

ACKNOWLEDGEMENT

REFERENCES

Blackman, R.L. & Paterson, A.J.C. (1986): Separation of *Myzus
   (Nectarosiphon) antirrhinii* (Macchiati) from *Myzus (N.) persicae*
   (Sulzer) and related species in Europe (Homoptera: Aphididae).
   Systematic Entomol., **11**. 267-276.

Eastop, V.F. (1985): The acquisition and processing of taxonomic data.
Evolution and Biosystematics of Aphids. Proc. International
Aphidological Symposium at Jablonna, 5-11 April 1981. Wroclaw, Poland,
pp. 245-270.

Fisher, R.A. (1936): The use of multiple measurements in taxonomic
problems. Ann. Eugenics, **7**. 179-188.

Scott, J.A. & Shepard, J.H. (1976): Simple and computerized discriminant
functions for difficult identifications: a rapid nonparametric method.
Pan-Pac. Entomol., **52**. 23-28.

Shaposhnikov, G.Ch. (1965): Morphological divergence and convergence in
an experiment with aphids (Homoptera, Aphidinea). Entomol. Obozr.,
44. 1-12.

Shaposhnikov, G.Ch. (1986): New species of the genus *Dysaphis* Borner
(Homoptera, Aphidinea) and peculiarities of the taxonomic work with
aphids. Entomol. Obozr., **65**. 535-550.

Zhivotovsky, L.A. (1979): Population similarity measure for polymorphic
characters. Zhur. Obshch. Biol., **40**. 587-602.

THE NORTH AMERICAN SPECIES IN AND RELATED TO *DIURAPHIS* AIZENBERG

M.B. Stoetzel

Systematic Entomology Laboratory, Room 6, Building 004, PSI, BARC-West,

Agricultural Research Service, U.S. Department of Agriculture,

Beltsville, Maryland 20705 U.S.A.

ABSTRACT

Species in the aphid genus *Diuraphis* Aizenberg (1935) and species in
related genera are discussed. Emphasis is placed on three pest species;
namely, *Diuraphis (Holcaphis) tritici* (Gillette, 1911), the western
wheat aphid; *Brachycorynella asparagi* (Mordvilko, 1929), the asparagus
aphid; and *Diuraphis noxia* (Mordvilko, 1913), the Russian wheat aphid.

INTRODUCTION

Species in the aphid genus *Diuraphis* Aizenberg (1935) and related

genera listed in Eastop and Hille Ris Lambers (1976) are a diverse group

and were described under several generic names: *Aphis* Linnaeus (1758),

Brachycolus Aizenberg (1935, nec Mabil 1833), *Brachycorynella* Aizenberg

(1956), *Brachysiphoniella* Takahashi (1921), *Cavahyalopterus* Mimeur

(1942), *Cuernavaca* J. M. Baker (1934), *Holcaphis* Hille Ris Lambers

(1939), *Hyalopterus* Koch (1854), *Lipaphis* Mordvilko (1929), *Semiaphis*

van der Goot (1913), *Siphocoryne* Passerini (1860), *Thripsaphis* Gillette

(1917), and *Uhlmannia* Boerner (1952).

The description in 1911 of *Brachycolus tritici* Gillette, commonly

known in the United States as the western wheat aphid, and the

introduction into the United States in 1969 of *Brachycolus asparagi*

Mordvilko (1929), commonly known in the U.S. as the asparagus aphid, brought attention in the U.S. to this group of spindle-shaped, short-cornicled, and waxy covered aphids previously grouped in the genus *Brachycolus*. But the introduction of *Diuraphis noxia* (Mordvilko, 1913), the Russian wheat aphid, into South Africa in 1978 (Dürr, 1983), into Mexico in the early 1980s (Pena-Martinez, 1987), and into the U.S. in 1986 (Stoetzel, 1987) has brought world-wide attention to these aphids.

MATERIALS AND METHODS

Taxonomic and host information was obtained from specimens in the collections of the U.S. National Museum of Natural History, Washington, DC, USA and of Agriculture Canada, Ottawa, Ontario, Canada and from the literature.

DISCUSSION AND CONCLUSIONS

In 1929 when Mordvilko described *asparagi,* he placed the species in the genus *Brachycolus*. While *asparagi* Mordvilko is spindle-shaped, has short cornicles, and is covered with a waxy coating, it differs from the other aphids in this group because its cornicles are barrel-shaped and have a distinct flange, the dorsal abdominal setae are short and blunt or spatulate, and the antennae are longer than half the length of the body. Because of these differences, *asparagi* Mordvilko is separated from those species in *Brachycolus* and is retained in the monotypic genus *Brachycorynella*.

In the U.S., *B. asparagi* is found in most of the states along the eastern seaboard and west to the Mississippi River. In 1979, it was collected in the northwestern state of Washington where it has become a

serious pest. It was collected in Oregon in 1981 and in California in 1984. Toxins injected into the plants during feeding cause a shortening of the nodes and produces what is called "witches' broom." Heavy infestations can kill seedlings and severely dwarf mature plants. Males are winged.

Diuraphis noxia (Mordvilko) was first detected in the United States in a Texas wheat field in March 1986; and, by the end of 1986, it also had been collected in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, and Wyoming. Infested wheat plants in some fields showed a characteristic purple streaking, trapped heads, and prostrate growth pattern. *Diuraphis noxia* has been collected in the U.S. on wheat, barley, oats, triticale, and numerous grasses. By 1989 it also had been collected in Arizona, California, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, and Washington. Thus, it has now been collected in every western state in the U.S. Males are wingless.

After the detection of *Diuraphis noxia* in the United States, attention was turned to *D. mexicana* (J.M. Baker, 1934) and *D. nodulus* (Richards, 1959), two species of *Diuraphis* previously recorded from North America but uncollected since their original descriptions. Populations of *D. mexicana* were located in 1987 in Mexico on *Bromus unioloides* (Peña-Martinez, 1987), and laboratory coloies have been established.

Diuraphis nodulus was collected by Richards on *Dactylis glomerata* in British Columbia, Canada. To date *D. nodulus has not been recollected*. Peña-Martinez (1987) stated that similarities in the descriptions and type specimens led her to conclude that *mexicana J.M. Baker and nodulus Richards* are synonyms. Host transfer experiments and further morphological studies are needed to validate this opinion.

Diuraphis (Holcaphis) tritici (Gillette) can be a pest on wheat where it forms colonies on the leaves and in the heads. It has also been reported to colonize *Agropyron occidentale*. This and the other five species - *agrostidis* Muddathir 1965, *bromicola* Hille Ris Lambers 1959, *calamagrostis* Ossiannilsson 1959, *frequens* Walker 1848, and *holci* Hille Ris Lambers 1956 - placed with it in *Diuraphis (Holcaphis)* are all elongate, spindle-shaped aphids found on various species of grasses. They lack a process on the 8th abdominal tergite, and their cornicles are poriform without a flange. Further research on these species probably will help to substantiate giving generic status to *Holcaphis*.

REFERENCES

Aizenberg, Y.Y. (1935): New aphid genera and species (Aphididae). Zap. Bol'shevsk. Biol. St., **7-8**. 151-160.

Aizenberg, Y.Y. (1956): New genera and nes species of Aphididae. Horae Soc. Entomol. Ross. **45**. 128-166.

Baker, J.M. (1934): Algunos afidos Mexicanos. An. Inst. Biol. Univ. Mex. **5**. 209-222.

Boerner, C. (1952): Europae centralis Aphides. Die Blattlause
    Mitteleuropas. Namen, Synonyme, Wirtspflazen, Generationszyklen.
    Mitt. Thur. Bot. Ges. **3**. 1-488.

Dürr, H.J.R. (1983): *Diuraphis noxia* (Mordvilko) (Hemiptera:
    Aphididae), a recent addition to the aphid fauna of South Africa.
    Phytophylactica **15**. 81-83.

Eastop, V.F. & Hille Ris Lambers, D. (1976): Survey of the world
    aphids. W. Junk Publ., The Hague, 573 pp.

Gillette, C.P. (1911): A new genus and four new species of Aphididae
    (Rhynch.). Entomol. News **22**. 440-444.

Gillette, C.P. (1917): Two new aphid genera and some new species.
    Can. Entomol. **49**. 193-199.

Hille Ris Lambers, D. (1939): On some western European aphids.   Zool.
    Mededel. **22**. 79-119.

Hille Ris Lambers, D. (1956): On aphids from the Netherlands with
    descriptions of new species (Aphididae, Homoptera). Tijdschr.
    Entomol. **98**. 229-249.

Hille Ris Lambers, D. (1959): Notes on European aphids with descriptions
    of new genera and species (Homoptera, Aphididae). Mitt. Schweiz.
    Entomol. Ges. **32**. 271-286.

Koch, C.L. (1854): Die Pflanzenlause Aphiden, getreu nach dem Leben
    abgebildet und beschrieben. Murnberg. Hefts **I-IV**. 135-236.

Linnaeus, C. (1758): II. Hemiptera.   Systema Naturae. Edito decima,
    reformata. **1**. 1-824.

Mimeur, J.-M. (1942): Aphididae Nord-Africains.   Bull. Soc. Sci. Natur.
    Maroc **21**. 67-70.

Mordvilko, A.K. (1913): Aphidoidea. In, Kurdyumov, N. V., The more
    important insects injurious to grain crops in Middle and Southern
    Russia. Studies from the Poltava Agricultural Experiment Station,
    No. 17. Dept. Agric. Entomol. No. VI, 42-43.

Mordvilko, A.K. (1929): Aphidoidea, pp.163-204. In, Philipgew, J.N.,
    Keys for the identification of Russian insects.

Muddathir, K., (1965) A new species of *Holcaphis* (Homoptera:
    Aphidoidea) together with a key to the British species. Ann. Mag.
    Natur. Hist. **8**. 477-485.

Ossiannilsson, F. (1959): Contributions to the knowledge of Swedish
    aphids. I.   Descriptions of some apparently undescribed forms.
    Kungl. Lantbrukshogsk. Ann. **25**. 1-46.

Passerini, G. (1860): Gli Afidi con un prospetto dei generi ed alcune
    specie nuove Italiane. Parma **1860**. 1-40.

Peña-Martinez, R. (1987): Notas taxonomicas sobre el genero *Diuraphis*
    Aizenberg (Homoptera: Aphididae) en Mexico. Resumenes XXII Cong.
    Nac. Entomol. 19-23 April 1987, Mexico.

Richards, W.R. (1959): A new genus and three new species of Aphididae
    (Homoptera). Can. Entomol. **91**. 248-253.

Stoetzel, M.B. (1987): Information on and identification of *Diuraphis*
    noxia (Homoptera: Aphididae) and other aphid species colonizing
    leaves of wheat and barley in the United States. J. Econ. Entomol.
    80. 696-704.

Takahashi, R. (1921): Aphididae of Formosa. Part I. Agric. Exp. Stn.
    Govt. Formosa Rep. **20**. 1-97.

van der Goot, P. (1913): Zur Systematik der Aphiden. Tijdschr. Entomol.
    56. 69-155.

Walker, F. (1848): Descriptions of Aphides. Zool. **6**. 2217-2221.

A MORPHOLOGICAL STUDY OF THE POPULATIONS OF UROLEUCON ON PICRIS

AND ANDRYALA (HOMOPTERA, APHIDOIDEA).

E.J. Tizado-Morales and J.M. Nieto Nafría

Departamento de Biología Animal, Facultad de Biología,

Universidad de León, 24071 León, Spain.

ABSTRACT

Aphids identified as Uroleucon (U.) picridis (Fabricius) had ultimate rostral segments longer than 1.5 times the length of their hind tarsal segment II and were collected from the compositae genera Picris and Andryala.

Fourteen characters were measured on 84 apterous viviparous females, and an analysis showed that Uroleucon (U.) picridis living on these two composites can be separated morphologically into two groups consistent with the differences in the host plant. However, until further biological information is obtained, these two groups can not be given separate taxonomic status.

INTRODUCTION

Uroleucon (U.) picridis (Fabricius) is a species which has been found in practically all Europe, Central Asia, Japan, Turkey, and Israel. It can be separated from the rest of the species of Uroleucon by its very long ultimate rostral segment which is between 1.51 and 1.85 times longer than the length of the second segment of the hind tarsus (Hille Ris Lambers, 1939). At first it was thought to be monophagous on Picris hieracioides (Hille Ris Lambers, 1939). However, it has also been recorded on Picris pyrenaica in France

(Remaudière, 1951), Picris echioides in Portugal and the Middle East (Ilharco, 1979; Eastop, 1985), Cichorium and Lactuca in Turkey (Tuatay and Remaudière, 1964) and Sonchus and Leontodon in Madeira (Ilharco, 1974).

The presence of one Uroleucon species on Andryala spp. in southeastern Europe was reported by Nieto (1974) and Mier (1978) in Spain, by Ilharco (1973) on the island of Porto Santo (Portugal), and by Starý et al. (1975) in Corsica (France). In all cases, it was identified as Uroleucon (U.) picridis.

However, when Nieto Nafría and Remaudière (personal communication) found sexual morphs, including winged males, on Andryala spp. in the province of Cuenca and when it was realized that Andryala has a tomentose stem while Picris has hispid hairs on its stem, we began to wonder if there were differences between the populations on Andryala and those on Picris. This study was started to find out if differed morphologically these two populations of Uroleucon.

MATERIAL AND METHODS

The aphids used in this study were 53 parthenogenetic apterae field collected as follows: 6 from Picris hieracioides, 10 from P. echioides, and 34 from Andryala spp. Additionally, two Uroleucon samples collected on Leontodon hispidus and one on Hispidella hispanica, in the Department's collection, were classified as U. picridis and were included in this study. Overall, 84 specimens were measured.

The samples were mainly collected in Spain (47 from 13 Spanish provinces) although 3 were from Algeria, 2 from France and one from Italy (Sardinia).

Each aphid was measured for fourteen variables, including those normally used in the separation of Uroleucon species.

The characters used were the length of the following: (1) body, (2) antenna, (3) hind tibia, (4) hind femur, (5) siphunculus, (6) cauda, (7) antennal segment III, (8) antennal segment IV, (9) antennal segment V, (10) basal part of antennal segment VI, (11) processus terminalis of antennal segment VI, (12) apical segment of rostrum, (13) hind tarsal segment II, and (14) antennal segment I.

The data were analyzed using various statistical methods to find variables to characterize both populations and afterwards to find a discriminant function between both of them.

RESULTS AND DISCUSSION

Figure 1 shows a plot of the scores of the first two canonical variables, which together account for 76.5% of the total variation of the individuals. They were obtained by the principal component method using the 84 specimens and the 14 variables. The specimens segregate into two groups, one formed by the Picris hieracioides, P. echioides and Leontodon hispidus (Picris group) samples and the other formed by the Andryala spp. and Hispidella hispanica (Andryala group) samples.

The first canonical variable evaluated as a linear combination of the 14 variables, is interpreted as the general size of the individuals and equally influenced for all the variables. The second canonical variable has a higher discriminatory value and is basically correlated to the length of the apical segment of the rostrum and, to a lesser extent, to the length of the processus terminalis of antennal segment VI.

The next step consisted in analysing the biometric variables and the possible differences between both groups using univariate statistical and regression test. Figures 2 and 3 represent frequency histograms for some of

the more significant variables such as the lengths of the apical segment of the rostrum and the antennal segment IV, and the normal curves associated with these distributions. Histograms of the lengths of the hind tarsal segment II (Fig. 4) has also been included because it is a character normally used in the separation of this species.

No particular variable (with exception of the length of the apical segment of the rostrum) is clearly discriminate in either group, and we had to resort to using pairs of variables (Fig. 5) or proportions between pairs (Fig. 6) in order to define the Picris and Andryala groups.

In the relationship between pairs of variables, the rostrum and the tarsus were studied in more detail (Fig. 7) as they are used in identifying U. picridis, although in this paper they show a lower discriminatory value than other pairs of variables. When comparing our values with the limits given by Hille Ris Lambers (1939), it is shown that all of the specimens of the Picris group are included within these limits. However, these limits exclude 88% of the specimens of the Andryala group, which fall within the limits given to U. picridis and to U. cichorii (Koch, 1955), and other Uroleucon species that have a fairly long rostrum. Another author, Eastop (1985), gives 1.4 and 1.7 as the extreme values for the proportion between the rostrum and the tarsus, with in which a high percentage of the specimens fall (68%), although 21% of the Picris group and 40% of the Andryala group remain outside, which also suggests that 22% of the specimens of the Andryala group would fall within the limits given by Eastop to Uroleucon cichorii s.lat.

Lastly, Wald-Anderson's linear discriminant function was calculated using the 14 variables and obtaining a linear combination equation of the original variables, which has a 0.1% margin of error. Other discriminant

functions were calculated with the pairs of variables which best separated both groups and good results were achieved, the formula is $7.569*r=IV+1.276$ (Fig. 5), which has a 1% margin of error.

CONCLUSION

All the populations of one species have a set of general adaptations that enable them to survive under certain conditions. While a population is usually adapted to a particular biogeocenosis, a species is adapted, as a rule, to a system of homocenoses, i.e. biogeocenosis of the same type. Hence, we can speak of species adaptations typical of all populations of a species as well as of population adaptations promoting the well-being of the species within the limits of local conditions (Shaposhnikov, 1981).

In the Picris and Andryala groups there exist morphological differences which allow their separation. But, it is not wise to give a taxonomic status to these groups, in the absence of biological data that could decide whether these differences are only adaptations of the same species to different host or whether they are characteristic of two independent species.

We will not give taxonomic status to these groups until biological tests have been carried out to prove whether each one of the groups can complete their biological cycle on Picris hieracioides or P. echioides, and Andryala spp.

ACKNOWLEDGEMENTS
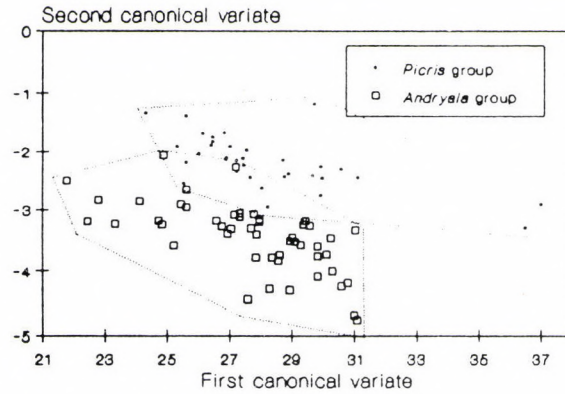
Figure 1.- Principal components
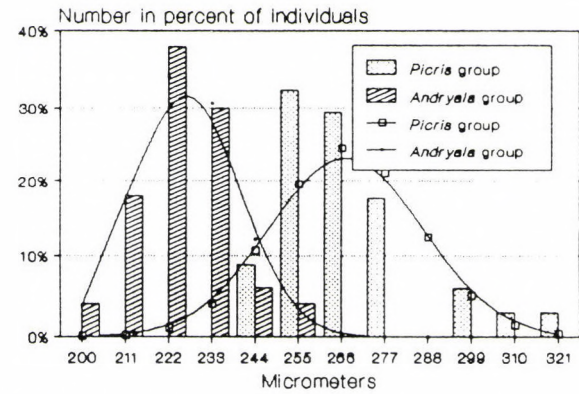
Figure 3.- Length of apical segment of rostrum
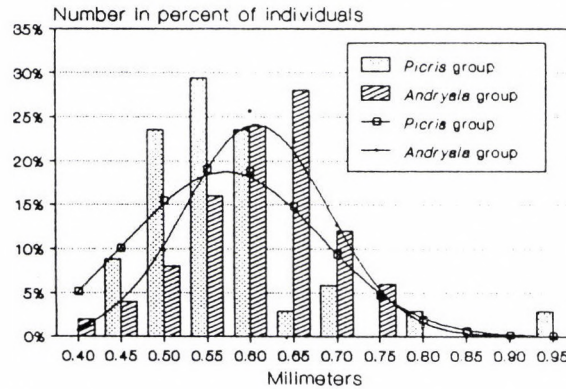
Figure 2.- Length of antennal joint IV
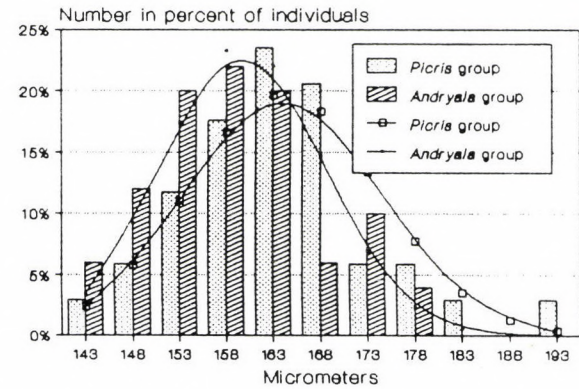
Figure 4.- Length of hind tarsal segment II
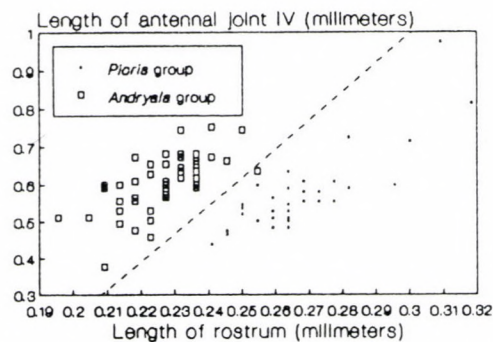
Figure 5.- (see text)
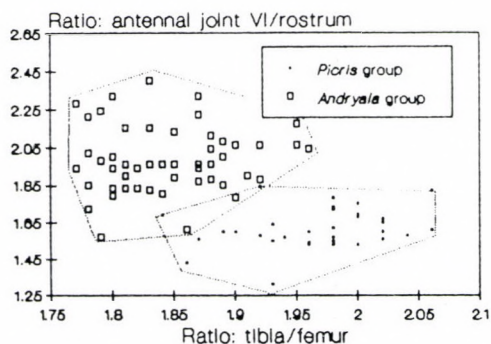
Figure 6.- (see text)
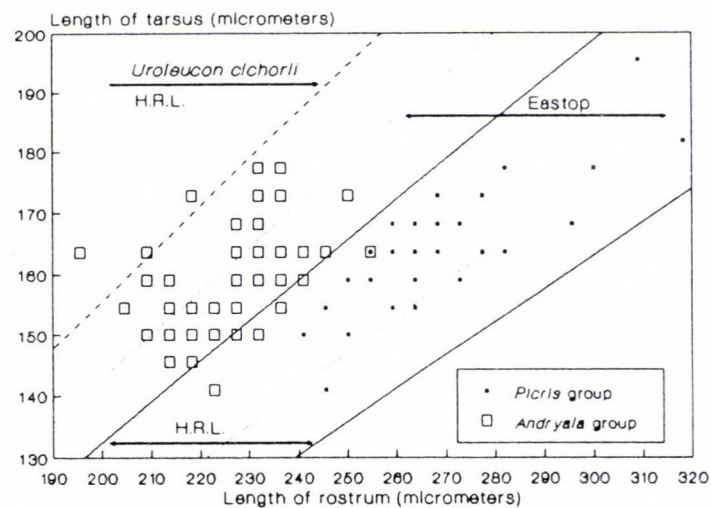
Figure 7.- (see text)

REFERENCES

Eastop, V.F. (1985): Key to the Middle Eastern species of Uroleucon Mordvilko (Aphididae: Homoptera). Systematic Entomology 10: 395-404.

Hille Ris Lambers, D. (1939): Contributions to a monograph of the Aphididae of Europe. II. Temminckia, 4: 1-134.

Ilharco, F.A. (1973): Afídeos de ilha de Porto Santo (Homoptera, Aphidoidea). Agr. Lus. 34(3): 219-254.

Ilharco, F.A. (1974): List of the aphids of Madeira Island. (Homoptera, Aphidoidea). Bocagiana, 35: 1-44.

Ilharco, F.A. (1979): 1º Aditamento ao catálogo des afídeos de Portugal continental (Homoptera, Aphidoidea). Agr. Lus. 39(4): 253-294.

Mier Durante, M.P. (1978): Estudios afidológicos de la provincia de Zamora. Publicaciones Caja de Ahorros Provincial de Zamora. 226 pp.

Nieto Nafría, J.M. (1974): Aphidinea de la Cordillera Central y provincia de Salamanca. Monogr. INIA, 8, 168 pp.

Remuadière, G. (1951): Contribuiton a l'etude des Aphidoidea de la faune française Aphididae: Dactynotinae et Myzinae. Rev. Path. veg. Ent. agr. Fr., 30(2): 125-144.

Shaposhnikov, G.CH. (1981): Population and species in aphids and the need for a universal species concept. Agriculture Canada, Research Banch, Ottawa, 62 pp.

Starý, P., F. Leclant and J.P. Lyon (1975): Aphidiides (Hym.) et aphides (Hom.) de Corse I. Les aphidiides. Ann. Soc. ent. Fr. (N.S.) 11(4): 745-762.

Tuatay, N. and G. Remaudière (1964): Première contribution au catalogue des Aphididae (Hem.) de la Turquie. Rev. Path. veg. Ent. agr. Fr., 43: 243-278

EVOLUTIONARY LOSS OF THE SECONDARY HOST

IN HETEROECIOUS APHIDS: PHYLOGENETIC EVIDENCE

C.D. von Dohlen,

Department of Zoology, University of Maryland,

College Park, Maryland, 20742 USA

ABSTRACT

Host alternation in aphids probably evolved from a single-host life cycle on the ancestral primary host. Extant subfamilies with host-alternating species also contain species with autoecious cycles confined to the primary host, which may resemble the ancestral cycle that gave rise to heteroecy. If host alternation arose convergently several times within each subfamily, these autoecious cycles could be the most primitive members of their taxa and closely related to the single-host ancestor. Recent literature has suggested, however, that 1) origins of heteroecy were few, and mostly restricted to the root ancestor of each subfamily, and 2) autoecious cycles on the primary host were secondarily derived from host-alternating cycles. I have employed the techniques of phylogenetic systematics on morphology to reconstruct the phylogeny of the subfamily Hormaphidinae, in order to determine the evolutionary positions of autoecious species. The estimated trees suggest that these species are highly derived, and that heteroecy is likely ancestral to the subfamily.

INTRODUCTION

Aphid subfamilies characterized by complex, host-alternating life cycles (Hormaphidinae, Pemphiginae, Anoeciinae, and Aphidinae) also contain species with simple, single-host cycles. In one type of autoecious life cycle, species persist year-round on the secondary hosts of their heteroecious relatives, often with no sexual generation. Such taxa unquestionably were derived from host-alternating ancestors that discarded the primary host.

Less clear is the origin of those aphids that live solely on the primary host and always incorporate a sexual generation. Recently, several researchers have suggested that such autoecious life cycles were derived from host-alternating ancestors via loss of the secondary host and most of its attendant generations (Heie, 1979; Aoki & Kurosu, 1986, 1988; Akimoto, 1985; von Dohlen & Gill, 1989). Moran (1988) proposed that if the Aphidinae clade and the Hormaphidinae-Pemphiginae-Anoeciinae clade are monophyletic groups, respectively, then the occurrence of heteroecy in aphids can be explained by as few as two origins, i.e., in the ancestor of each clade. It follows then that autoecious cycles on primary hosts would have evolved many times independently.

Although it is likely that a complicated feature such as heteroecy had few origins within the aphids, the possibility remains that autoecious species on primary hosts could be relicts of primitive autoecious lines that spawned host-alternating offshoots several times (Mordvilko, 1930). Such a case has been shown for rust fungi (Hart, 1989). Only an estimation of phylogeny below the subfamily level can tell us what has been the pattern of life cycle evolution in these insects.

The work presented here addresses the evolution of life cycles in the subfamily Hormaphidinae from a phylogenetic perspective. I test the hypothesis that host alternation is ancestral and autoecious primary-host cycles are multiply derived. Using morphological characters, I have applied the methods of phylogenetic systematics based on parsimony to reconstruct the phylogeny of part of the subfamily. I show that the autoecious species occupy positions toward the terminal parts of the tree, and conclude that they have evolved many times independently.

MATERIALS AND METHODS

Slide-mounted specimens of 16 Hormaphidinae species were obtained from the U.S. National Collection and from scientists in Japan and Europe. These included most holocyclic members of the tribes Hormaphidini and Nipponaphidini, and one Cerataphidini species. Three outgroup species were chosen from the Pemphiginae to root the tree; six of the 19 total species were autoecious (Table 1). Specimens were alate fundatrigeniae from the primary-host gall except for two anholocyclic species, which were alates from the secondary host.

All specimens were examined under a compound microscope and scored for a predefined set of attributes. Continuous and meristic measurements were made with a Zidas digitizer attachment. The simple gap-coding procedure of Mickevich & Johnson (1976) was applied to these quantitative data to distinguish the character states, which were then coded as integers (Table 2). In several cases, ratios of continuous measurements were used to try to eliminate the confounding effects of size. Qualitative attributes were assigned integers as required. Life cycle features were deliberately omitted.

Table 1   Sample sizes (N), life cycles, and collection locations for
species scored.

Species	N	Life Cycle	Location
Hormaphidini:			
Hamamelistes betulinus (Horvath)	5	anholocyclic	Europe
H. kagamii (Monzen)	3	heteroecious	Japan
H. miyabei (Matsumura)	7	autoecious	Japan
H. spinosus Shimer	5	heteroecious	N. America
Hormaphis hamamelidis (Fitch)	6	heteroecious	N. America
Hormaphis n. sp.	7	autoecious	N. America
Nipponaphidini:			
Dinipponaphis autumna (Monzen)	4	autoecious	Japan
Metanipponaphis cuspidatae (E. & K.)	2	heteroecious	Japan
M. rotunda (Takahashi)	4	heteroecious	Japan
Monzenia globuli (Monzen)	10	autoecious	Japan
Nipponaphis distychii Pergande	2	heteroecious	Japan
N. distyliicola Monzen	8	heteroecious	Japan
Neothoracaphis yanonis (Matsumura)	4	heteroecious	Japan
Quadrartus yoshinomiyai Monzen	5	heteroecious	Japan
Sinonipponaphis monzeni (Takahashi)	6	heteroecious	Japan
Cerataphidini:			
Ceratovacuna lanigera Zehtner	2	anholocyclic	Japan
Outgroup species (Pemphiginae):			
Eriosoma lanigerum (Hausmann)	5	heteroecious	N. America
E. rileyi (Thomas)	4	autoecious	N. America
Pemphigus monophagus Maxson	4	autoecious	N. America

PHYLOGENETIC COMPUTER PROGRAMS AND RESULTS

A. PHYSYS

The first analysis was performed with PHYSYS (Farris & Mickevich,
1985). The routine /DWAGNER.S/ applied branch-swapping to an initial
shortest tree to find the most parsimonious arrangement of taxa. This
analysis treated character states additively, as fixed transformation
series with each state arising from only one other state. All
characters were weighted equally.

Table 2   Characters scored and states for qualitative and meristic
characters.   Continuous data were transformed to natural logs, and count
data to square roots for gap analysis.

---

0. Rostrum length:body length 0) .044-.023 1) .018 2) .013-.003
1. # Sensoria on antennal segment III 0) 4-6 1) 10-12 2) 15-19
   3) 21-26 4) 28-37
2. # Antennal segments 0) 6 1) 5 2) 4 3) 3
3. Type of sensoria 0) wide elongate 1) annular
4. # Antennal projections 0) 6 1) 5 2) 4 3) 3
5. Branch of medius in forewing 0) present 1) absent
6. Base of cubitals in forewing 0) fused 1) close 2) apart
7. Cubitus in hindwing 0) absent 1) present
8. # Hooklets on hindwing 0) 2 1) 3-4 2) 5-6
9. # Setae tarsal segment I fore-mid-hindleg 0) 3-3-2 1) 3-3-3
10. Siphunculi 1) present   2) absent
11. # Pairs spiracles 0) 7 1) 5 2) 4
12. Shape of cauda 0) broad rounded 1) narrow rounded 2) knobbed
13. # Setae on cauda 0) 2 1) 8 2) 10 3) 12 4) 14
14. # Setae on anal plate 0) 7-9 1) 10 2) 12 3) 14 4) 16 5) 20-24
15. Shape of anal plate 0) entire 1) bilobed
16. Base of medius and cubitus in hindwing 0) fused with
    pterostigma 1) fused, common trunk 2) separate but close 3) wide
    separation 4) very widely separated
17. # Setae on femur 0) 59-61 1) 51-52 2) 45-47 3) 25-27
    4) 19-20 5) 12-14 6) 8-10 7) 4-5
18. # Setae on tibia 0) 111-128 1) 94-109 2) 85-86 3) 39-50
    4) 28-34 5) 22-24
19. # Short setae tarsal segment II 0) 12-18 1) 4
20. Pattern of long setae tarsus II 0) 4 thin, short 1) 2 long,
thick/2 shorter, thinner 2) 4 long, thick
21. Trunk of cubitals forewing 0) absent 1) trunk very short
    2) trunk 1/4 length cu-1b 3) trunk > 1/2 cu-1b
22. Length antennal projection:width antennal segment III
23. Dorsal seta length:head width
24. Apical segment rostrum width:length
25. Tarsus segment II width:length
26. Tibia width:length
27. Length of medius branch:total length medius
28. Length tibial seta:head width
29. Length short setae on tarsal II segment:head width
30. Length empodial hair:head width
31. Length seta on anal plate:head width
32. Length seta on genital plate
33. Caudal setae shortest:longest
34. Apical rostral segment seta length:width head
35. Genital plate width:length
36. Cauda width:length
37. Siphunculus width aperture:width base
38. # Sensoria ant. segment IV 0) 2 1) 3-4 2) 5-9 3) 10-13 4) 14-20
39. # Sensoria ant. segment V 0) 4-5 1) 5-6 2) 6-7 3) 8 4) 9-15
40. Basal width ant. segment III:width below basal-most sensorium
41. Length base to 1st sensorium ant. segment III:width of segment

---

In the second analysis, a successive weighting procedure was applied
to the first tree. Characters were weighted by their individual
consistency indices (CI) on the initial tree, the tree recalculated,
characters reweighted, etc. until the tree length, CI, and character
weights remained unchanged. Thus, successive weighting favored the
cladistically most reliable characters.

A single most parsimonious tree was generated from the additive
character-state matrix with all characters weighted equally (Figure 1a).
The tribe Hormaphidini is a monophyletic group. *Hamamelistes kagamii*
clusters with the two *Hormaphis* species rather than the other
Hamamelistes. The Nipponaphidini are not a monophyletic group, but all
the species except *S. monzeni* and *N. distichii* cluster together. These
two (which I suspect are synonyms) are placed closest to the root. The
sole representative of Cerataphidini is between the root and the two
other tribes, suggesting that Hormaphidini and Nipponaphidini are sister
groups and therefore more closely related to each other than either is
to Cerataphidini. Most significantly, all the autoecious species in the
study group occupy highly derived positions on the phylogeny; 3 out of 4
are terminal taxa.

The successive weighting procedure in PHYSYS produced exactly the
same topology as the first tree. As expected the CI increased (to 50)
as more reliable characters were given greater weight.

B. HENNIG86

The powerful microcomputer program HENNIG86 turns off character
additivity when a given transformation series is not presumed; thus,
each state can arise from any other (Farris, 1988). With non-additive
characters weighted equally, the shortest tree was found by applying
branch-swapping to an initial tree (Figure 1b). As expected,
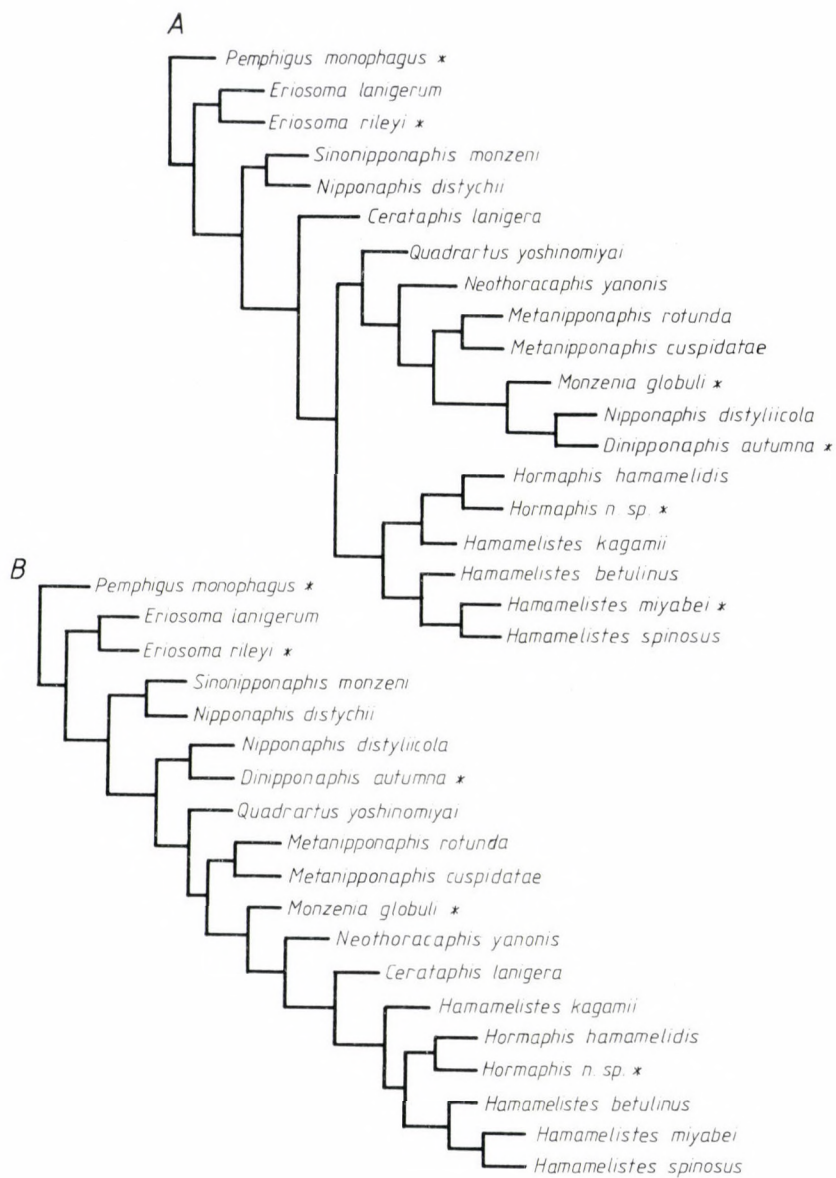
Figure 1.   A. The most parsimonious tree found by PHYSYS with characters additive and weighted equally. Length = 255, consistency index (CI) = 44, * = autoecious. B. The most parsimonious tree from HENNIG86 with characters non-additive and weighted equally. Length = 204, CI = 56, * = autoecious.

the consistency index increased when the constraint of additivity was relaxed. As with PHYSYS, this tree defines the Hormaphidini as a monophyletic group. All the Nipponaphidini, however, now cluster together. In addition, the Cerataphidini and Hormaphidini are sister groups deriving from the Nipponaphidini and are therefore most closely related. As before, none of the autoecious species occupy positions near the root or form a monophyletic group.

The successive weighting procedure in HENNIG86 produced a tree very similar to the first, except for the positions of a few host-alternating taxa within the Nipponaphidini.

DISCUSSION

The results from all analyses support the hypothesis that auto-ecious species are multiply derived from host-alternating ancestors, and indeed that host alternation was ancestral to the subfamily. No tree placed the autoecious species in basal positions or collected them into a monophyletic group. If the character of life cycle were superimposed on any tree, the shortest length would be attained only when all hypothetical ancestors were heteroecious. It is possible, but not expected, that the inclusion of more taxa (especially in the Cerataphidini) or other life stages could change the topology.

An intriguing question yet to be answered is: How often did heteroecy evolve in the entire Hormaphidinae-Pemphiginae-Anoeciinae clade? Is it ancestral to the whole clade or did it evolve independently in each subfamily? More taxa need to be evaluated to confirm that autoecious species in the Pemphiginae and Anoeciinae occupy derived positions as they do in Hormaphidinae.

Because aphids have relatively few good qualitative morphological characters, and because of some problems using continuous characters, molecular data may give more reliable estimates of phylogeny for these insects. Molecular methods can at least provide independent tests of phylogeny, which may be compared to those derived from morphology. Electrophoresis of proteins, restriction fragment-length polymorphisms of mitochondrial DNA (treated not as phenetic distance measures but phylogenetically as presence/absence of alleles or restriction sites), or even DNA sequencing may prove fruitful.

CONCLUSIONS

The most parsimonious phylogeny of part of the subfamily Hormaphidinae, reconstructed from morphological characters, agrees that autoecious life cycles on the primary host are derived from host-alternating ancestors. It is likely that heteroecy is ancestral to the entire subfamily. Thus, aphids with complex cycles may give rise to simple cycles in two different ways: either by discarding the ancestral primary host and existing solely on the secondary host (a frequent event), or by rejecting the secondary host and several generations to live exclusively on the primary host. The latter simplification appears to be a rare event.

ACKNOWLEDGEMENTS

REFERENCES

Akimoto, S. (1985): Taxonomic study on gall aphids, *Colopha*,
    Paracolopha, and *Kaltenbachiella* in East Asia, with special reference
    to their origins and distributional patterns. Insecta Matsumurana,
    n.s. **31**:1-79.

Aoki, S. & Kurosu, U. (1986): Soldiers of a European gall aphid,
    Pemphigus spirothecae (Homoptera: Aphidoidea): Why do they molt?
    J. Ethol. **4**:97-104.

Aoki, S. & Kurosu, U. (1988): Secondary monoecy of a North American gall
    aphid, *Pemphigus monophagus* (Homoptera, Aphidoidea). Kontyu
    56:394-401.

Farris, J.S. & Mickevich, M.F. (1985): Computer program for
    phylogenetics. Published by the authors.

Farris, J.S. (1988): HENNIG86 Reference, version 1.5.

Hart, J.A. (1989): Rust fungi and host plant coevolution: Do primitive
    hosts harbor primitive parasites? Cladistics **4**:339-366.

Heie, O.E. (1979): Revision of the aphid genus *Nasonovia* Mordvilko,
    including *Kakimia* Hottes & Frison, with keys and descriptions of the
    species of the world (Homoptera: Aphididae). Ent. scand. Suppl.
    9:1-105.

Moran, N.A. (1988): The evolution of host-plant alternation in aphids:
    Evidence for specialization as a dead end. Amer. Nat. **132**:681-706.

Mordvilko, A.K. (1930): About the origin of heteroecy in plant-lice.
    Comp. Rend. Acad. Sci. URSS **1930**:256-262.

von Dohlen, C.D. & Gill, D.E. (1989): Geographic variation and evolution
    in the life cycle of the witch-hazel leaf gall aphid, *Hormaphis*
    hamamelidis. Oecologia **78**:165-175.

RECENT ADVANCES IN PALAEOAPHIDOLOGY

O.E.Heie

Institute of Biology, Royal Danish School of Educational Studies,
Emdrupvej 101, DK-2400 Copenhagen N.V., Denmark.

ABSTRACT

Recent additions to the list of fossil aphids are commented on.
Oligocallis hakolampii sp.n. is described from Baltic amber. No
recently found fossil belongs to Aphididae or Lachnidae. A survey of
the composition of the faunas of the Cretaceous, the Tertiary and
today is given, and the reasons for the differences, especially the
remarkable difference in species-richness of Aphididae in the Tertiary
and now, are discussed.

RECENT ADDITIONS TO THE LIST OF FOSSIL APHIDS

More than 900 fossils have been found, belonging to about 150
species: Triassic 1, Jurassic 3, Cretaceous 37, Tertiary 115. Among
the recent findings are more representatives of Oviparosiphidae from
the Cretaceous in USSR (Shaposhnikov & Vengerek in press),
Elektraphididae, Mindaridae, Anoeciidae, Hormaphididae, Pemphigidae
and Drepanosiphidae from Bolshaya Svetlovodnaya, USSR, probably Late
Oligocene (Heie 1989) and Elektraphididae (Steffan 1981), Pemphigidae
and Drepanosiphidae from Baltic amber, among the latter a species
described below. For the first time an aphid fossil has been found in
Africa; it is from the Cretaceous and consists of a wing similar to
that of Siphonophoroides (Drepanosiphidae), previously known from the
Tertiary of North America and Europe (Rayner & Waters in press). A
relative of Lizerius, a primitive drepanosiphid genus, today
represented in the Neotropical region, is the first aphid found in
Dominican amber, age Late Eocene. It differs little from some recent
South American species (Heie & Poinar 1988).

DESCRIPTION OF <u>OLIGOCALLIS</u> <u>HAKOLAMPII</u> SP. N.

The piece of amber containing this aphid was bought in Poland by Kari Hakolampi and sent to me by Dr. Kauri Mikkola, Helsinki. All measurements are given in 1/100 mm.

Body 140 long, head 21, pronotum 13, pterothorax 33, abdomen 71. Longitudinal diameter of the large protruding eye 14, vertical diameter 15-16; ocular tubercle built into posterior margin of eye. Antenna 6-segmented, 227 long, with a gradual transition between base of segm.VI and processus terminalis carrying roundish rhinaria in a row (primary and accessory rhinaria); diameter of III in the middle 1.5-2; lengths: I 9, II 7, III 52, IV 48, V 43, VI about 24 + about 44; basal 60% of III with 6 subcircular rhinaria; the other segments without secondary rhinaria. Rostrum reaching to 2nd coxae; apical segm. blunt, about 7, 0.8-0.9 x segm.II of hind tarsus. Fore legs thick, developed for jumping, diameter of femur in the middle 1.7 x diameter of hind femur; lengths: fore femur 50, middle femur 41, hind femur 62, fore tibia 60, hind tibia ab. 80, tarsi 12-13 incl. claws; diameter in the middle: fore femur 10, middle femur 4.5, hind femur 6, fore tibia 2, middle tibia 1.5, hind tibia 2.5; trochantera well defined. Fore wing about 225 long; Cu-branches leaving main vein at separate points 14 apart, darker than other veins, Cu_{1a} curved; M with 2 forks; Rs leaving distal half of the pointed pterostigma close to its middle, not as distinct as the other veins; distance from wing base to base of Cu_{1b} 64. Siphunculi truncate, without constriction, about 7 long, width at base about 9, at apex 2.5-3.0, without distinct flange. Cauda not visible.

In my key to genera related to <u>Drepanosiphum</u> (Heie 1967) it goes to <u>Oligocallis</u>. Three species from Baltic amber have been described (Heie 1967 and 1972): <u>O. debilis</u> has longer antennae, relatively shorter processus terminalis and fewer secondary rhinaria; <u>larssoni</u> differs by having fore femur longer than or as long as hind femur; differences between <u>hakolampii</u> and <u>saltatorius</u> are small. The new species is larger, with shorter siphunculi without constriction and thicker fore femora.

The holotype is in the collection of the Zoological Museum,

University of Helsinki, Finland.

COMPOSITION OF APHID FAUNAS OF THE PAST COMPARED WITH TODAY

The new finds have not changed our image of the faunas of the past. It becomes more and more clear that their composition until the Miocene or perhaps even Pliocene was remarkably different from today, first of all in being deficient in species of Aphididae (s.str.), the family richest in species (59%) in modern time, and also deficient in representatives of Lachnidae.

The geological history of aphids consists of at least three very different phases (Heie 1987):

1) From the Triassic to the Cretaceous: The fossils belong to extinct, more or less specialized families, at the end of the Mesozoic also to extant families.

2) The Eocene-Oligocene and perhaps also the Miocene: The aphids mainly belonged to Drepanosiphidae, Pemphigidae and Elektraphididae.

3) From the end of the Tertiary or the beginning of the Quaternary until now: Most aphids belong to Aphididae.

Whereas Adelgidae are known only from the Pliocene, and no fossils of Phylloxeridae have been found, the related extinct family Elektraphididae made up 11% of the Cretaceous fauna and 9% of the Tertiary fauna.

Drepanosiphidae and Pemphigidae were richest in species in the Tertiary, 36% and 22% respectively, and the percentages of species of Anoeciidae, Greenideidae, Hormaphididae and Thelaxidae were not very different from today, while Mindaridae declined from Early Tertiary till the present day.

Longistigma caryae (Harris) from the Miocene broadleaved forest of Iceland, that survives in similar recent ecosystems, is still the only known lachnid fossil. The absence of a family from Tertiary deposits does of course not mean that it evolved recently. If the interpretation of the phylogeny (Heie 1987) is correct, then most or all recent families must have appeared in Upper Cretaceous because Cretaceous representatives of themselves or their supposed sister groups have been found. Fossils cannot tell that taxa did not exist at a certain time. They can however tell if taxa were abundant or not, on

the assumption that fossils are numerous and representative. The latter condition probably exists now with regard to Tertiary fossils. Both Aphididae and Lachnidae were small families until the last part of that period. The origin and evolution of Aphididae is a mystery, and so is the phylogeny of the major tribes of Aphidinae, Aphidini and Macrosiphini. Only one species of uncertain systematic position and different from supposed ancestors of Aphididae has been described from the Cretaceous. The few Tertiary Aphididae belong to Baltichaitophorinae, are related to the primitive and isolated Parachaitophorus, and to Aphidini and Macrosiphini.

DISCUSSION

The transitions between the three phases are connected with changes in host associations; in the Cretaceous from gymnosperms to woody angiosperms, in the Tertiary from woody plants to herbs. These changes were not made by all, but by some not too specialized species, which then became the ancestors of most of the species in the next phase. Many families became extinct during the first transition, probably because they were too specialized and they fed on plants that became extinct. Only one family, Elektraphididae, disappeared during the second transition, being replaced by Adelgidae.

Transition number two is difficult to understand. Today, successful groups such as Aphis and the tribe Macrosiphini are mainly, though not totally, associated with herbs, and several macrosiphine genera consist of numerous species feeding on only one family or even genus of advanced herbaceous angiosperms. Gymnosperms, ferns and other old plant groups have also been acquired as hosts by members of these successful groups, but rather recently. The related family Lachnidae is rich in species today because many of these live on gymnosperms. This family evolved from one or a few ancestors, which in Late Tertiary moved from broadleaved to coniferous trees. Association with woody angiosperms is a primitive character of Lachnidae. The genera feeding on conifers form together a monophyletic group according to Lampel & Burgener (1987).

We have two questions 1) Why are the Aphididae so successful? and 2) why did it happen in Late Tertiary?

1) The reason why many species-rich aphidid genera developed during the end of the Tertiary may not only be accessibility of many new plants, but also an ability of these aphids, the special life cycle developed by their ancestors making a new type of host alternation possible, different from the types developed earlier in other families, and also making re-establishment of the holocycle possible on originally secondary herbaceous hosts alone. Moran (1988) explains why host-alternating aphids maintain their host alternation even if their primary hosts are not the optimal food resources. They do so because the fundatrices are specialized, adapted for feeding on the primary hosts and unable to live on better resources found by migrants. The specialization of the fundatrices has generally not gone as far in Aphididae as in other host-alternating families. That may be the reason for their successful acquisition of many new hosts.

2) Since the Late Tertiary climatic oscillations may have contributed to the richness of species of Aphididae in the Holarctic region. According to Dixon et al. (1987) the number of aphid species is negatively correlated with the diversity of plant species in a certain area, because alate aphids can survive without food only for at short time, have a high degree of host specificity and locate their hosts with a low efficiency. This explains the species-poverty of tropical regions compared with temperate regions. It may also explain the species-poverty of Aphididae in the Tertiary compared with the Quaternary. The northern parts of America and Eurasia lost during glacial periods plant species, which reinvaded them more or less completely during warmer intervals. So there must have been low plant species diversity several times and favourable possibilities for alatae to find the right host not too far away from where they were born. Similar favourable conditions may have been absent in the warm part of the Tertiary.

The evolution of Aphididae must have been rapid towards the end of the Tertiary, with a radiation that produced the huge number of genera and species that dominate the aphid fauna today. A contemporary evolution of the angiosperms, especially herbs, ability to acquire new hosts, and decreasing plant diversity in the northern parts of the

Holarctic region may explain this radiation, but the real evolutionary history of the Aphididae and the full explanation of the events are still unknown.
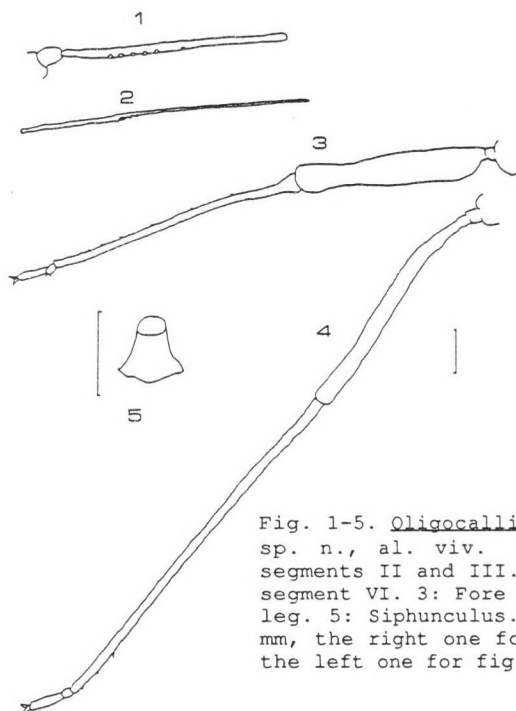
Fig. 1-5. Oligocallis hakolampii sp. n., al. viv. 1: Antennal segments II and III. 2: Antennal segment VI. 3: Fore leg. 4: Hind leg. 5: Siphunculus. Scales: 0.1 mm, the right one for figs. 1-4, the left one for fig. 5
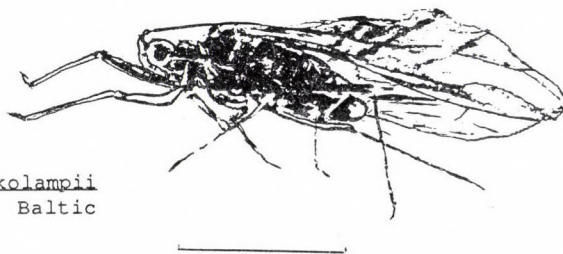
Fig. 6. Oligocallis hakolampii sp. n., al. viv. in Baltic amber. Scale: 1 mm. Photo: Reijo Tyynelä.
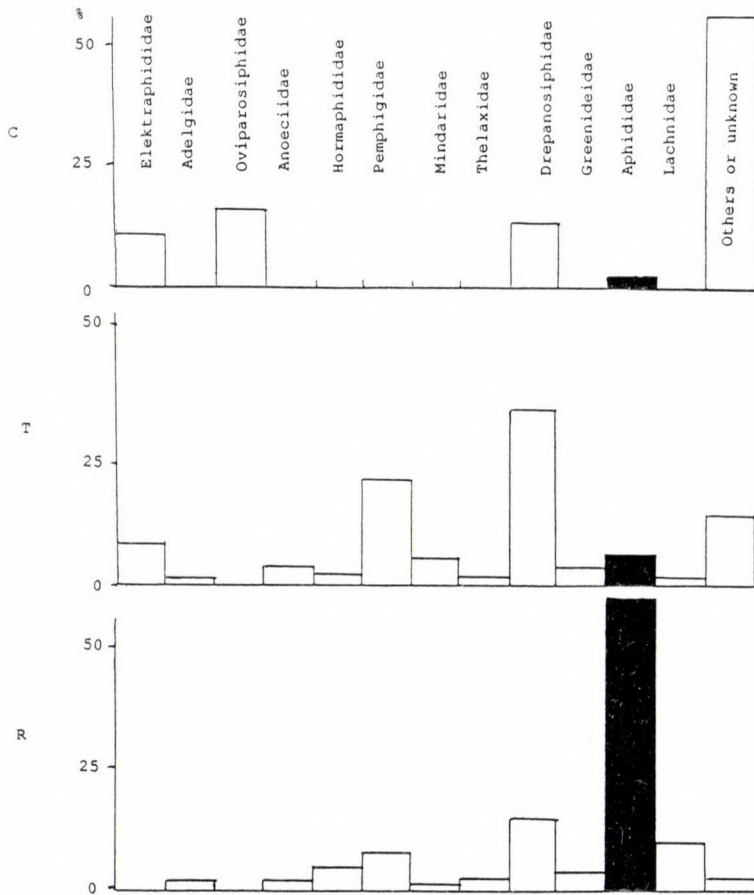
Fig. 7. Number of species of various families (percentages of total number of known species) from the Cretaceous (C, N = 37), the Tertiary (T, N = 115) and today (R, N = 4300).

REFERENCES

Dixon, A.F.G., Kindlmann, P., Leps, J. & Holman, J. (1987): Why there are so few species of aphids, expecially in the tropics. American Naturalist **129**: 580-592.

Heie, O.E. (1967): Studies on fossil aphids. Spolia zool. Mus. haun. **26**:1-274.

- (1972): Some new fossil aphids from Baltic amber in the Copenhagen collection. Steenstrupia **2**:247-262.

- (1987): Palaeontology and phylogeny. In: Minks & Harrewijn (ed.): Aphids. World Crop Pests vol.2A, Elsevier, pp. 367-391.

- (1989): Fossil aphids (Insecta, Homoptera) from the Tertiary deposits of Bolshaya Svetlovodnaya, the USSR. Ent.scand.19: 475-488.

- & Poinar, G.O. (1988): _Mindazerius dominicanus_ nov. gen., nov. sp., a fossil aphid (Homoptera, Aphidoidea, Drepanosiphidae) from Dominican amber. Psyche **95**: 153-165.

Lampel, G. & Burgener, R. (1987): The genetic relationships between lachnid taxa established by enzyme-gel-electrophoresis. Proc. Intern. Symp. Smolenice Sept. 1985, pp. 71-95.

Moran, N. (1988): The evolution of host plant alternation in aphids: Evidence for specialization as a dead end. American Naturalist **132**: 681-706.

Rayner, R.J. & Waters, S. (in press): A fossil aphid wing from Orapa, South Africa. Palaeontology.

Shaposhnikov, G.H. & Vengerek, P. (in press): New Oviparosiphidae. (In Russian).

Steffan, A.W. (1981): Further evidence for egg-laying plant lice in Early Tertiary (Homoptera: Aphidina: Elektraphididae). Entom. Gen. **7**: 5-15.

THE DIGESTIVE SYSTEM OF *HYALOPTERUS* AND ITS BEARING ON THE EVOLUTION OF THE STRUCTURE OF THE DIGESTIVE SYSTEM IN THE APHIDOIDEA

M. B. Ponsen

Department of Entomology, Agricultural University, P.O.Box 8031, 6700 EH Wageningen, The Netherlands.

ABSTRACT

The digestive system of *Hyalopterus* consists of a foregut, oesophageal valve, stomach, intestine, hindgut, rectum, and an epidermal invagination which terminates at the anal opening. In about 15% of the specimens of *Hyalopterus* on *Prunus* and in about 50% of those on *Phragmites* the anterior part of the stomach is encapsulated by the anterior part of the hindgut, forming a concentric filtersystem. This phenomenon is described in detail and is discussed in the context of the several forms of the digestive system within the Aphidoidea.

INTRODUCTION

The genus *Hyalopterus* belongs to the family Aphididae sensu Börner (1952). Within the genus *Hyalopterus* there are two species, viz. the mealy peach aphid, *Hyalopterus amygdali* (Blanchard), and the mealy plum aphid, *H. pruni* (Geoffray). Detailed studies carried out by Basky and Szalay-Marszó (1987) revealed no morphological features for separating these species, nevertheless, they are distinct species as they can not live on each other's primary hosts (Table 1), and the males do not copulate with females of the other species. In summer both species migrate to the secondary host, *Phragmites australis*.

The digestive system of *H. pruni* feeding on *Prunus domestica* and *Phragmites communis* (= *Phragmites australis*) consists of a foregut, a dilated stomach, a tubular intestine, and a hindgut

(Janiszewska, 1932), but lacks a filterchamber (Kunkel and Kloft, 1977).

Investigations of the anatomy of the digestive system of *Hyalopterus* was carried out as dissections of aphids of this genus revealed the presence of a primitive filtersystem in some specimens.

MATERIALS AND METHODS

Specimens of the species listed in Table 1 were collected randomly from the host plant and put in Duboscq-Brasil's fluid.After fixation the larvae were dehydrated in a graded series of ethanol transfered to methyl benzoate, then into methyl benzoate celluidin (2%) for three days or longer, and then into toluene and finally embedded in paraplast. Serial sections, 8μm thick, were stained in a 1% aqueous solution of methylgreen rinsed in tap-water, dehydrated in methanol and methyl benzoate, cleared in xylene, and finally mounted in xylene-dammar.

In order to dissect the digestive system aphids were placed on self-adhesive tape attached to a black plastic plate. Under a dissecting microscope each aphid was covered with a drop of Levy solution and dissected using watchmakers forceps.

RESULTS

The alimentary tract starts with the food canal that is formed by the interlocked maxillary stylets. This food canal leads into the pharyngeal duct formed by the epipharynx and the hypopharynx lip. The pharyngeal duct is separated from the pharyngeal pump by a valve, of which both the dorsal and ventral walls are marked by two cuticular dome-shaped prominences. The structure of the pharynx, including the muscles of the valve and the pump, is similar to that of *Myzus persicae* (Sulzer) (Ponsen, 1987).

The pharyngeal pump passes into the foregut, oesophageal
valve, midgut, hindgut, and rectum terminating at the anal
opening. The midgut is the longest part of the alimentary tract
and consists of the stomach and intestine. In dissections the
hindgut is a transparent, sac-like structure that shows vigorous
peristaltic movements generated by circular and longitudinal
muscles. The stomach and intestine are opaque, show slow
peristaltic movements, and have only circular muscles.

The foregut runs posteriad from the tentorium, between the
salivary glands, follows the median dorsal furrow of the
suboesophageal ganglion and terminates in the oesophageal valve.
It is a uniform thin tube made up of simple squamous epithelium
of which the nuclei protrude into the narrow lumen.

The oesophageal valve is an invagination of the foregut into
the lumen of the stomach. It consists of two layers of non
muscular epithelium that forms an intravalvular space. The inner
layer is a continuation of the foregut, whereas the outer layer
is built up of cuboidal cells, each with a relatively large
spherical nucleus. The cells of both the foregut and the outer
layer of the valve secrete a chitinous intima.

The stomach starts in the mesothorax or metathorax and joins
the intestine in the first, second, or third abdominal segment.
It has a dilated structure and lies centrally in the dorsal
region of the aphid. The maximum diameter of the stomach is
situated just behind the oesophageal valve.

The stomach wall is made up of two forms of cells. The
anterior region consists of triangular cells with spherical
nuclei and an apocrine secretion. The epithelial cells of the
posterior region of the stomach are cuboidal with oval nuclei
and a merocrine secretion. These stomach cells secrete
continuously throughout larval and adult life. The stomach lumen
is completely full of solid material, which is not present in
the intestinal lumen. Both cell forms contain small vacuoles and
granules, and the basal cell membranes are invaginated. The
striated border of the apocrine cells is much narrower than that
of the merocrine cells.

The intestine is the tubular part of the midgut and can be divided into two histologically distinct regions. The first runs from the stomach to the abdominal loop situated in the fifth, sixth, or seventh abdominal segment, from where it gradually broadens, forming the second region of the intestine. Before reaching the hindgut, the second region of the intestine forms one or two additional loops situated between the mesothorax and the third abdominal segment. The transition from the stomach to the intestine is marked by a sharp loop.

In the second region of the intestine the cells and nuclei are bigger, and the cytoplasm more vacuolated than in the first. Moreover, the second region of the intestine is characterized by the presence of groups of three cells; triplets. The apical cell membranes of the triangular intestinal cells are distinctly striated.

The middle cell of each triplet is very large and has a large nucleus, whereas the other two cells are smaller and have relatively small nuclei. The cytoplasm of these cells contains numerous minute vacuoles; the apical cell membrane has a small striated zone and the basal cell membrane is strongly invaginated. The number of triplets varies from 6 to 8, with the majority occuring singly at irregular intervals among the triangular epithelial cells.

The hindgut starts in the meso- or metathorax and runs directly caudad to open into the rectum. It consists of simple squamous epithelial cells with elliptical nuclei. The irregular apical cell membrane is covered with a delicate intima, which dissolves at each moult. The cells contain large irregular vesicles, clusters of basophilic material, and waxy droplets. The waxy droplets originate from fat cells and are released by the hindgut cells into the lumen.

In a number of specimens the anterior region of the stomach is completely encapsulated by the anterior region of the hindgut forming a concentric filtersystem (Fig. 1A). On the other hand, there are specimens in which the stomach is not encapsulated by the hindgut which is completely separate from the stomach and is

more or less spherical in cross section (Fig. 1B). In dissections the two parts of the filtersystem are so intimately fused that they cannot be separated easily from each other.

The segment of the hindgut which envelopes the stomach is the filterchamber. The filterchamber is lined with both endodermal and ectodermal epithelial cells arranged so that the endodermal cells are situated on the side adjacent to the stomach and the squamous ectodermal cells on the opposite side (Fig. 1A, 1-7). The endodermal cells in the filterchamber are a continuation of those of the second region of the intestine, and their number gradually decreases until the hindgut consists of only squamous cells (Fig. 1A, 7).

In those specimens in which the stomach is not encapsulated by the hindgut (Fig. 1B), the epithelial lining of the anterior part of the hindgut is identical to that of the specimens with a filtersystem (Fig. 1A). Although the hindgut is separate from the stomach and has a more or less spherical structure, the endodermal cells are also situated on the side adjacent to the stomach and the ectodermal cells on the opposite wall (Fig. 1B, 1-7).

The presence of a filtersystem is independent of the morph, the hostplant, the locality, the number of additional loops in the second region of the intestine, and the colour of the aphids. The percentage of specimens with a filtersystem is significantly higher on reed than on *Prunus* sp.(G-test, P< 0.0001). Moreover it appears, that adults with or without a filtersystem can produce both types of progeny, i.e., with or without a filtersystem.

In the seventh abdominal segment the hindgut passes into the rectum, which is made up of small columnar cells with elliptical nuclei. The rectum joins an invagination of epidermal cells the structure of which is similar to those of the forgut. This invagination opens to the exterior via the anus, which is opened by six dorsal muscles and closed by two pairs of lateral muscles.

DISCUSSION

According to Hille Ris Lambers (1964) and Heie (1967) the Adelgidae may be considered as the phylogenetically oldest family of the Aphidoidea. Their digestive system consists of a short foregut, a tubular stomach situated in the middle of the aphid, and a descending intestine. The first region of the intestine lies in a direct line with the stomach (Fig. 2). In the Thelaxidae the tubular stomach is situated centrally, close to the dorsum of the aphid, whereas the intestine runs from the stomach directly ventrally and then passes posteriorly to the abdominal loop. The digestive system of the Chaitophoridae is similar to that of the Thelaxidae, however, in the Chaitophoridae there are genera and even individuals of some species that have or lack an additional loop in the second region of the intestine (Ponsen, 1987). In the genera *Greenidea* and *Israelaphis* of the family Greenideidae, the stomach bends ventrally to join the intestine (Fig. 2). The most characteristic structure of the *Aphis*-group is the transition from the dilated stomach to the intestine, which could have evolved from the type (I and III) seen in the Thelaxidae and Chaitophoridae, via a weak loop being an intermediate form (II and IV) to the evolutionary final form, marked by a sharp loop (V) (Fig. 2). The most advanced form of gut in *Aphis* (V) is also seen in the Anoeciidae, with or without an additional loop.

Within the family Drepanosiphidae there are certainly three, and possibly six anatomically distinct groups of aphids. In the first group the tubular stomach lies ventrally, and starts in one of the first five abdominal segments (Fig. 2, A-B). In *Drepanosiphum acerinum* and *D. aceris* the stomach starts in the sixth abdominal segment and is curved (Fig. 2C). The second group (Fig. 2E) has two transparent hindguts, a descending intestine and a blind ectodermal hindgut. Both hindguts form a filtersystem: a concentric filtersystem in which the stomach is encapsulated by the ectodermal hindgut and a parallel filtersystem in which the anterior region of the ascending

Table 1   Source and number of specimens of *Hyalopterus* with (+) and without (-) a filtersystem

Aphid	Hostplant	Total number of aphids		Apterous viviparous		Alate viviparous		Apterous oviparous		Alate males	
		Dis-sected	Sec-tioned	F i l t e r s y s t e m							
				+	–	+	–	+	–	+	–
Hyalopterus pruni	*Prunus domestica*	570	28	36	239	21	302				
	Prunus spinosa	417	26	70	130	45	198				
	Prunus insititia	290		37	103	33	117				
Hyalopterus amygdali	*Prunus persica*		37	1	0	11	25				
Hyalopterus sp.	*Phragmites australis*	564	108	219	65	76	66	5	1	58	182
	Phragmites mauritianus		20	12	2	5	1				

Table 2   List of aphid genera belonging to the family Aphididae of which the transition from the stomach to the intestine is marked by a sharp loop and the hindgut is of ectodermal origin.

GENUS	NUMBER OF SPECIES STUDIED	GENUS	NUMBER OF SPECIES STUDIED	
Acyrthosiphon	3	*Megoura*	1	
Amphorophora	1	*Metopeurum*	1	
Aulacorthum	2	*Metopolophium*	2	
Brachysiphum	1	*Microlophium*	1	
Brevicoryne	1	*Myzus*	3	
Cavariella	2	*Nasonovia*	1	
Cryptosiphum	1	*Ovatus*	1	
Diuraphis (Holcaphis)	1	*Pentatrichopus*	1	
Dysaphis	3	*Phorodon*	1	
Hayhurstia	1	*Pleotrichophorus*	1	
Hyadaphis	1	*Rhopalomyzus (Judenkoa)*	1	
Hyperomyzus	1	*Rhopalosiphum*	3	
Idiopterus	1	*Sitobion*	1	
Illinoia (Masonaphis)	1	*Tubaphis*	1	
Impatientinum	1	*Uroleucon*	7	
Liosomaphis	1	*Xerophilaphis*	1	
Lipaphis	1	*Acaudinum*	1	filtersystem
Longicaudus	1	*Capitophorus*	1	filtersystem
Macrosiphoniella	5	*Cryptomyzus*	2	filtersystem
Macrosiphum	3	*Hyalopterus*	2	(filtersystem)

intestine is fused with the posterior region of the descending intestine. *Paoliella terminaliae*, a representative of the third group, lacks a filtersystem (Fig. 2D). The other three groups are hypothetical (Fig. 2, F-H). They are likely to have either a concentric filtersystem or a parallel filtersystem, with or without a blind ectodermal hindgut.
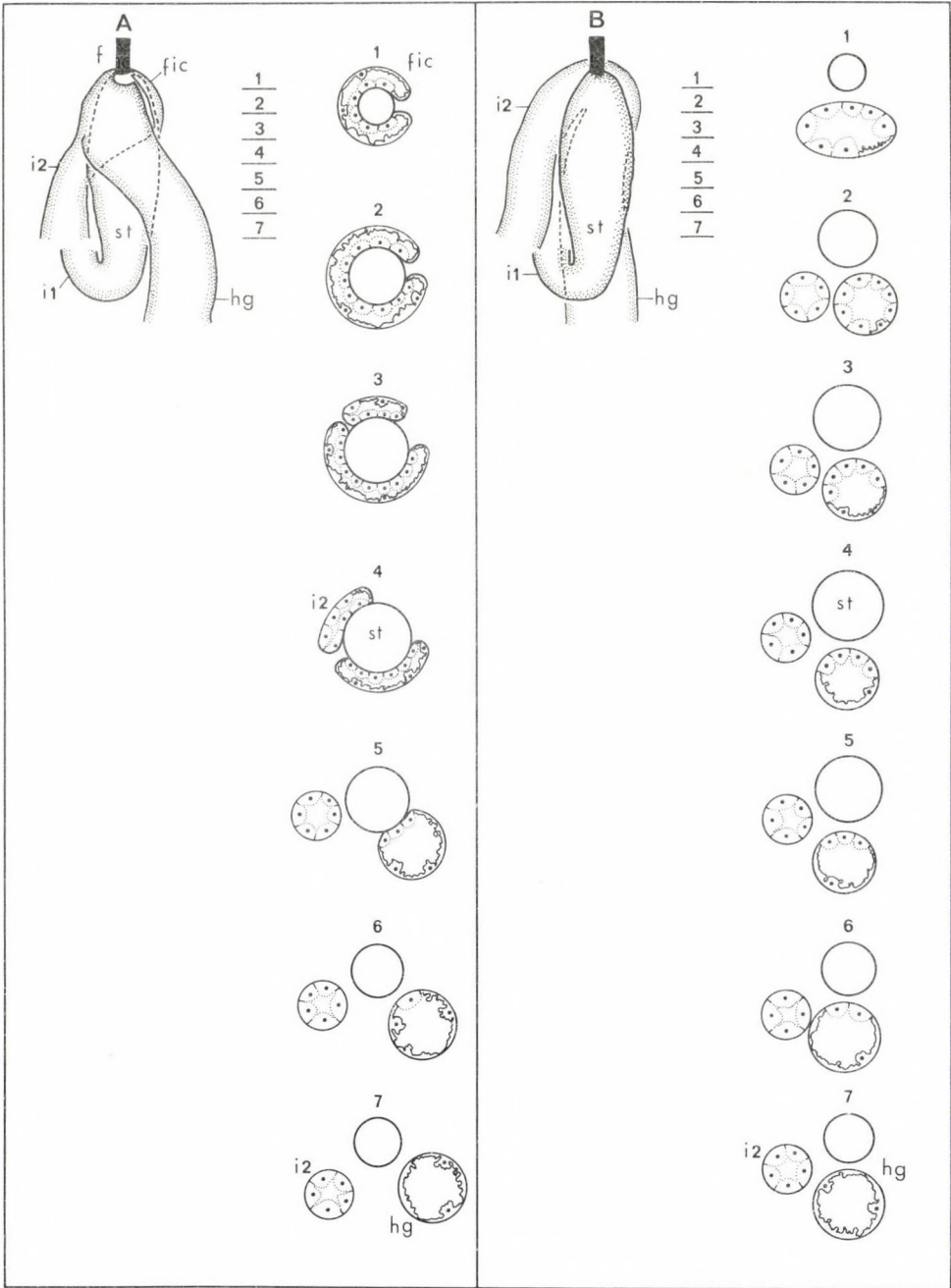
Histologically there are two types of hindgut, ectodermal or endodermal (descending intestine). The ectodermal hindgut has a simple squamous epithelial lining the cells of which have elongated or elliptical nuclei. The cells contain irregular vesicles and their apical cell membrane is folded and coated with a delicate intima. The descending intestine consists of either cuboidal or triangular cells with more or less spherical nuclei, cytoplasmic vacuoles, and a very thin apical striated zone. In dissections, both the ectodermal hindgut and the descending intestine is transparent and exhibits vigorous peristaltic movements generated by circular and longitudinal muscles. The transition from the second region of the intestine to the descending intestine is marked by a gradual increase of 2-4 strongly vacuolated intestinal cells followed by an abrupt change to the typical cellular structure of the descending intestine. Species belonging to the families Adelgidae, Thelaxidae, Chaitophoridae, Greenideidae, Drepanosiphidae, Anoeciidae, and the genus *Aphis* all have a descending intestine.

During evolution the descending intestine was presumably replaced by the ectodermal hindgut, but with the retention of the concentric filtersystem. Species with such a structure occur in the family Lachnidae, and the genera *Acaudinum*, *Capitophorus*, and *Cryptomyzus* (Fig. 2). In these species the anterior part of the midgut, namely the filtergut, is encapsulated by the anterior part of the ectodermal hindgut.

A similar structure occurs in *Hyalopterus*, where the anterior part of the stomach is encapsulated by the anterior part of the hindgut. This concentric filtersystem occurs in about 19% of the specimens of *Hyalopterus* on *Prunus* and about

Fig. 1. Semi-schematic representation of the gut of individuals of *Hyalopterus* with (A) and without a filtersystem (B). The transverse serial sections 1-7 are from the region of the stomach and illustrate the relationship between the stomach and hindgut in those individuals that have (A) and lack a filterchamber (B). ai, ascending intestine; di, descending intestine; f, foregut; fic, filterchamber; fig, filtergut; hg, hindgut; i1, first region of intestine; i2, second region of intestine; st, stomach.

54% of those on *Phragmites* (Table 1). In the other individuals
the stomach is not encapsulated by the hindgut but the latter is
completely separate from the stomach and more or less spherical
in cross section (Fig. 1).

The anterior region of the hindgut that envelopes the
anterior region of the stomach is the filterchamber (Fig. 1A).
It is lined with both endodermal and ectodermal epithelia, but
arranged so that the endodermal cells are situated on the side
adjacent to the stomach while the squamous ectodermal cells are
on the opposite wall of the filterchamber. The endodermal cells
are a continuation of those of the intestine and the number
gradually decreases until the hindgut consists of only squamous
cells (Fig. 1A, 1-7). This cellular arrangement also occurs in
the anterior part of the hindgut of those specimens of
Hyalopterus that lack a filtersystem (Fig. 1B, 1-7). An
identical cellular arrangement is present in the filterchamber
of *Cryptomyzus* and *Eulachnus* (Lachnidae).

It appears that all aphid genera with a filtersystem have an
ectodermal hindgut. On the other hand, there are genera that
have an ectodermal hindgut but lack a filtersystem, as depicted
in Table 2. In these genera the cellular arrangement in the
anterior part of the hindgut is identical to that in *Hyalopterus*
with a filtersystem. Probably all the species in Table 2 that
have an ectodermal hindgut may have had a filtersystem but this
has been lost during evolution. To this group belong *Phloeomyzus
passerinii* and genera of the family Aphididae, excluding
Anuraphis, *Aphis*, *Brachycaudus*, *Plocamaphis*, and *Pterocomma*,
which have a descending intestine.

Fig. 2. Diagrams illustrating the existing and hypothetical (?) forms of the digestive
system within the Aphidoidea. The dashed line represents the endodermal hindgut or
descending intestine, and the dotted line the ectodermal hindgut. For explanation of
abbreviations see Fig. 1.
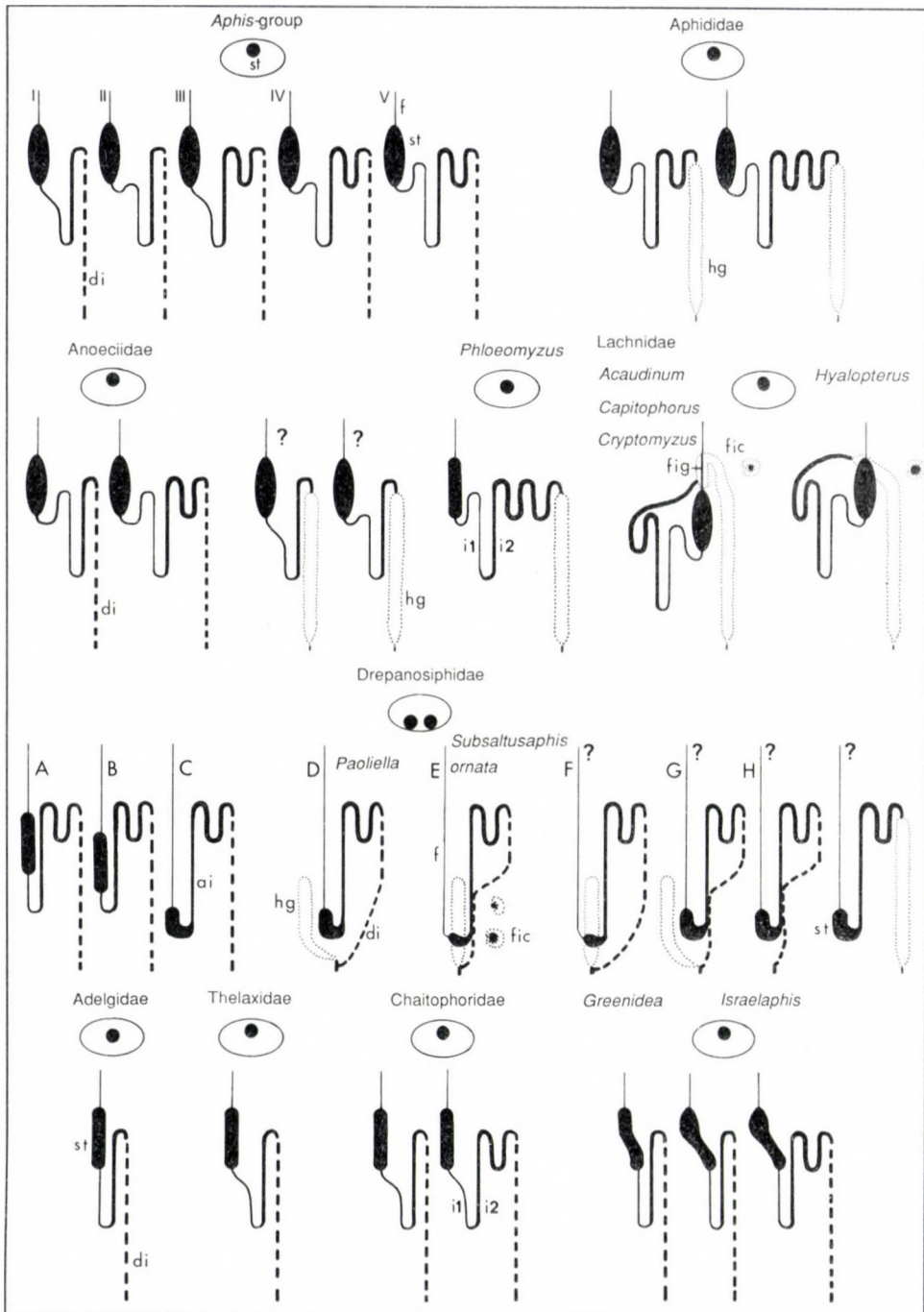
ACKNOWLEDGEMENTS

LITERATURE

Basky, Z. and Szalay – Marszó, L., (1987): Study of isolation mechanisms in the *Hyalopterus pruni* and *Hyalopterus amygdali* complex. Proc. Int. Symposia, Smolenice (Czechoslovakia), 1985.

Börner, C., (1952): Europae centralis Aphides. Mitt. thüring. bot. Ges., Beiheft **3**, 484 pp.

Heie, O.E., (1967): Studies on fossil aphids (Homoptera: Aphidoidea). Spolia zool. Mus. Haun., **26**, 274 pp.

Hille Ris Lambers, D., (1964): Higher categories of the Aphididae. In: Heie, O.E., (1967).

Janiszewska, J., (1932): Untersuchungen über die Hymenoptera *Aphidius* sp., Parasiten der Blattlaus *Hyalopterus pruni* Fabr. Bull. int. Acad. pol. Sci. Lett., **7BII**, 277-293.

Kunkel, H. and Kloft, W., (1977): Fortschritte auf dem Gebiet der Honigtau-Forschung. Apidologie, **8**, 369-391.

Ponsen, M.B., (1987): Alimentary tract. In: Aphids their biology, natural enemies and control (Eds. Minks, A.K. and Harrewijn, P.). Elsevier, Amsterdam, **2A**, 79-97.

THE CHROMOSOMES OF LACHNIDAE

Roger L. Blackman

Department of Entomology, Natural History Museum, Cromwell Road, London,

SW7 5BD, UK

ABSTRACT

Some features of the cytogenetics and cytotaxonomy of Lachnidae are
discussed, with particular attention to differences in chromosome number
between closely related species, the system of sex determination and the
behaviour of the X chromosomes during spermatogenesis, and the occurrence
and distribution of "B chromosomes" and constitutive heterochromatin.

INTRODUCTION

Karyotypes of more than 60 species of Lachnidae are known, of which more
than 40 are Cinara species. Despite the generally large size of the aphids
in this family, their chromosomes are often rather small and difficult to
resolve. This is especially so in the case of Lachninae and Traminae,
which mostly do not provide well-spread metaphase preparations. Neverthe-
less, lachnids show a number of features of cytogenetic and cytotaxonomic
interest, which are described in this paper.

MATERIALS AND METHODS

Satisfactory squash preparations of somatic cell nuclei can generally be
obtained from young embryos dissected out of aphids fixed directly in 3
parts methanol: 1 part glacial acetic acid, and kept for several months

in this fixative, provided that the embryos are hydrolysed with 1N hydro-chloric acid for 5 min at 65 C prior to squashing in 45% propionic acid (for details see Blackman, 1980a).

However, with Lachninae (notably Lachnus and Stomaphis) and Traminae, pretreatment of living tissue in a mildly hypotonic solution (e.g. 0.75% potassium chloride, or 1% sodium citrate) for 5-10 min prior to fixation is generally necessary in order to prevent late prophase and metaphase chromo-somes from clumping together. Freshly-fixed material (left only 15-30 min in methanol/acetic acid fixative) can be squashed directly in propionic acid without prior treatment in hydrochloric acid, although acid hydrolysis will give a cleaner preparation with less cytoplasmic background.

Squashes made with freshly-fixed material can be "C-banded" to reveal constitutive heterochromatin (sections consisting mainly of highly repetitive DNA sequences). The method involves denaturation of DNA with strong alkali, followed by incubation in a saline solution that selectively renatures highly repetitive sequences (for details see Blackman, 1985).

Spermatogenesis occurs in the testes of 1st and 2nd instar males, and is virtually complete by the 3rd instar. Squash preparations of testis tissue can be made in the same way as for embryonic cells.

RESULTS AND DISCUSSION

Lachninae   Somatic cell chromosomes of Stomaphis and Lachnus are particularly difficult to resolve, which is a pity because their karyotypes are potentially useful as taxonomic characters. Most European populations of Stomaphis quercus (L.) examined, collected from both Quercus and Betula,have a 2n(female)=10 karyotype like that of S. japonicus Takahashi (Fig. 1b). A sample from Quercus petraea in Czechoslovakia, however, had 2n=8 (Fig. 1a), lacking the the two smallest chromosomes. By analogy with

S. japonicus (see below), the missing elements are probably X chromosomes,

although X chromosome numbers are usually very stable in aphids. S.

cupressi (Pintera) is very different with 2n=14 (Fig. 1c), and S. yanonis

Takahashi has 2n=?16 (but Honda, 1921, recorded a haploid number of 10 for

yanonis).

Karyotype	Provenance of samples
2n= 7?	Q. robur, W. Germany (2 samples)
2n= 8 (7+1B)	Q. cerris, Czechoslovakia; Q. robur, W. Germany (2)
2n= 9 (7+2B)	Q. robur, Czechoslovakia, Denmark, Poland
2n=10	Castanea sativa, Portugal, ?UK
2n=11 (10+1B)	Q. robur, Sweden (1), UK (4)
2n=12?	Q. borealis, Portugal
2n=14	Castanea sativa, ?UK; Q. robur, UK
2n=15 (13+2B?)	Q. pyrenaica, Q. suber; both Portugal
2n=16	Q. ilex, Portugal (2)
2n=17?	Q. ilex, Portugal

Table 1   Karyotype variation in the Lachnus roboris group (23 samples)
   (uncertain karyotype determinations are indicated by "?")

Lachnus roboris (L.) (Fig. 1d-f) shows great variation in chromosome

number, some of which may be intraspecific and due to variable numbers of

accessory heterochromosomes ("B chromosomes"). Table 1 summarises the

available data and shows the difficulty of demonstrating any particular

association between karyotype and host plant. A more intensive study,

integrating karyotypic data with biological, morphometric and possibly

enzyme/DNA studies, is needed to clarify the taxonomy of these aphids. L.

tropicalis (van der Goot) in Japan and China shows similar variability

(2n=12, 13 and 16 in 6 samples). One sample of L. iliciphilus (del Guercio)

from West Germany had 2n=8.

In both $\underline{S.}$ $\underline{quercus}$ and $\underline{L.}$ $\underline{roboris}$, males have two chromosomes less than females, so sex determination is $X_1X_1X_2X_2/X_1X_2O$. In $\underline{S.}$ $\underline{japonicus}$, X_2 is much smaller than X_1 (Fig. 1g), whereas in the $\underline{L.}$ $\underline{roboris}$ group X_1 and X_2 are more similar in size (Fig. 1h). "B chromosomes" behave like X chromosomes on the anaphase I spindle, although their number is unreduced in the male.

$\underline{Maculolachnus}$ $\underline{submacula}$ (Walker) yields much better preparations than other Lachninae studied. There are 10 chromosomes in female somatic cells; C-banding reveals interstitial blocks of constitutive heterochromatin on all the longer chromosomes (Fig. 1i). Male somatic cells have 9 chromosomes (Fig. 1j), so sex determination is XX/XO. The X chromosome is quite short, and there are two small "B chromosomes", one of which has a constriction (arrowed in Fig. 1i).

$\underline{Tuberolachnus}$ $\underline{salignus}$ (Gmelin) has "2n=20" in all populations so far examined (from India, Iran, Japan and the UK) (Fig. 1k). The X chromosomes, if they still exist in this permanently parthenogenetic aphid, are unidentifiable. $\underline{Pterochloroides}$ $\underline{persicae}$ (Cholodkovsky) also has 2n=20.

Spermatogonial divisions in the testes of 1st instar males show 9 chromosomes (Fig. 2a), the two "B chromosomes" appearing as dots. In prophase I and metaphase I of spermatogenesis (Figs 2b,c), the autosomes are paired to form bivalents, but the two "B"s are unpaired and situated close to the unpaired X chromosome. At anaphase I, the X and the two "B"s are stretched along the axis of the spindle as the autosomes move to the poles (Fig. 2d-j). Late anaphase (Fig. 2k) shows considerable attenuation of the X (and B) chromosomes, before they all pass into one of the daughter cells. At this stage the autosomes in the nucleus of the daughter cell that will eventually receive the X and the "B"s are already decondensed, whereas those in the other nucleus are still strongly condensed. Only the
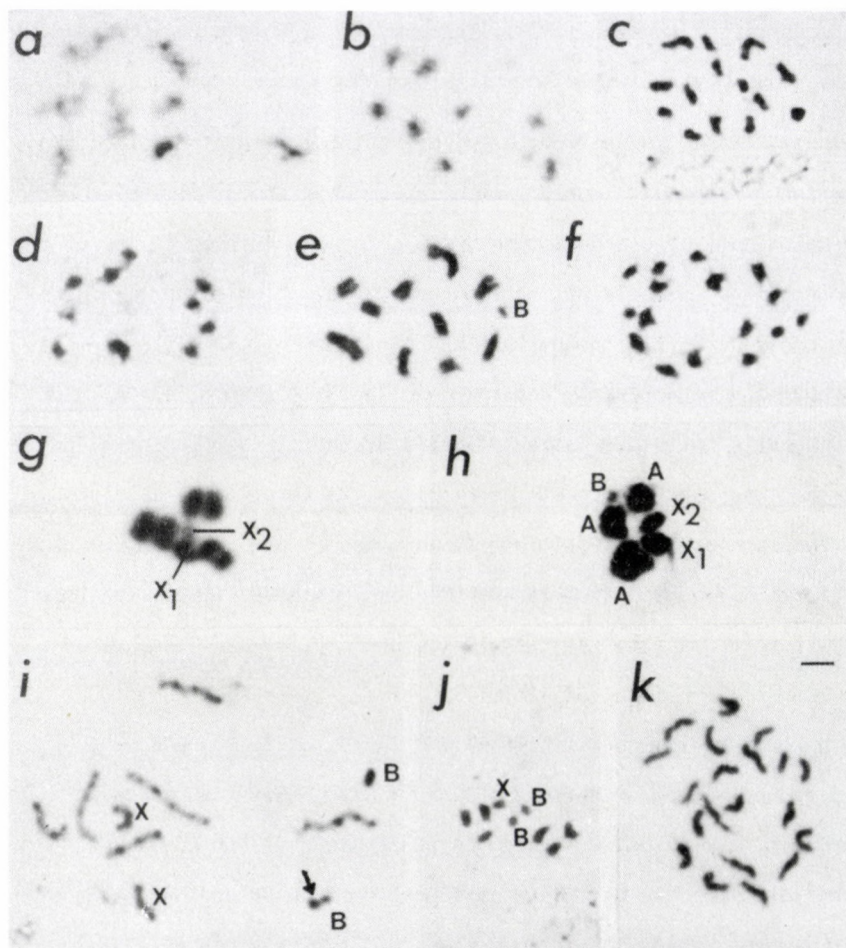
Figure 1.- a-b Somatic chromosomes of Stomaphis; **a,** S. quercus group (2n female=8); **b,** S. japonicus (2n=10); **c,** S. cupressi (2n=14). **d-f** Somatic chromosomes of Lachnus; **d,** L. roboris group from Castanea (2n=10); **e,** L. roboris group from Quercus robur (2n=10 + 1B); **f,** L. roboris group from Quercus ilex (2n=16). **g,** metaphase I of spermatogenesis in Stomaphis japonicus. **h,** metaphase I of spermatogenesis in L. roboris (2n=10 + 1B). **i,** C-banded somatic prophase of Maculolachnus submacula (2n female = 8 + 2B). **j,** male somatic metaphase of M. submacula (2n=7 + 2B). **k,** somatic metaphase of Tuberolachnus salignus (2n female = 20). Scale bar = 2 μm.

daughter nucleus that receives the X and the "B"s is viable and divides again (Fig. 21), and the resultant nuclei form spermatids (Fig. 2m).

This type of X chromosome/B chromosome system, with the "B"s being maintained in a constant number and inherited through the male, is like that found in Euceraphis (Blackman, 1988). It seems to be unique to Aphididae. The "B"s are possibly relics of a multiple X chromosome system.

Cinarinae   In Cinara, the karyotype is very stable; more than 70% of the species so far studied have 2n=10, which is probably the primitive number for the genus. Some of the deviations from this basic karyotype are of taxonomic interest. Members of the subgenus Cupressobium Börner all have karyotypes based on 2n=12, the permanently parthenogenetic C. fresai Blanchard having a structurally heterozygous 2n=13 (Blackman, 1980a). In subgenus Cinarella Hille Ris Lambers, aphids of the pinea group have 2n=8, 10, 11 or 14. The 2n=8 form seems to be pilosa Zetterstedt (= maculata Gmelin). Populations with 10, 11 and 14 chromosomes are found in the UK. The 2n=10 form is recorded from Canada (Sun and Robinson, 1966), and the 2n=14 form is recorded from the USSR (Rukavishnikov, 1979). Presumably these are hitherto unrecognised sibling species. Other species of Cinarella have 2n=14 (pergandei Wilson) and 2n=16 (maritimae Dufour). The pilicornis group (subgenus Cinaropsis Börner) also shows taxonomically useful karyotype variation; C. piceicola (Cholodkovsky) has 2n=8, and populations identified as C. pilicornis (Hartig) from UK and New Zealand have 2n=10, whereas 2n=14 is recorded from USSR (Rukavishnikov, 1972).

Spermatogenesis is relatively straightforward in Cinara (Fig. 2n-w). In C. pini (L.), sex determination is XX/XO, the X chromosomes being longer than any autosomes, and there are no "B"s (Fig. 2n). In anaphase I, the X chromosome is not stretched to the same extent as in Lachnini (Fig. 2p-s; cf. Fig 2d-k). During the short telophase between the meiosis I and II,
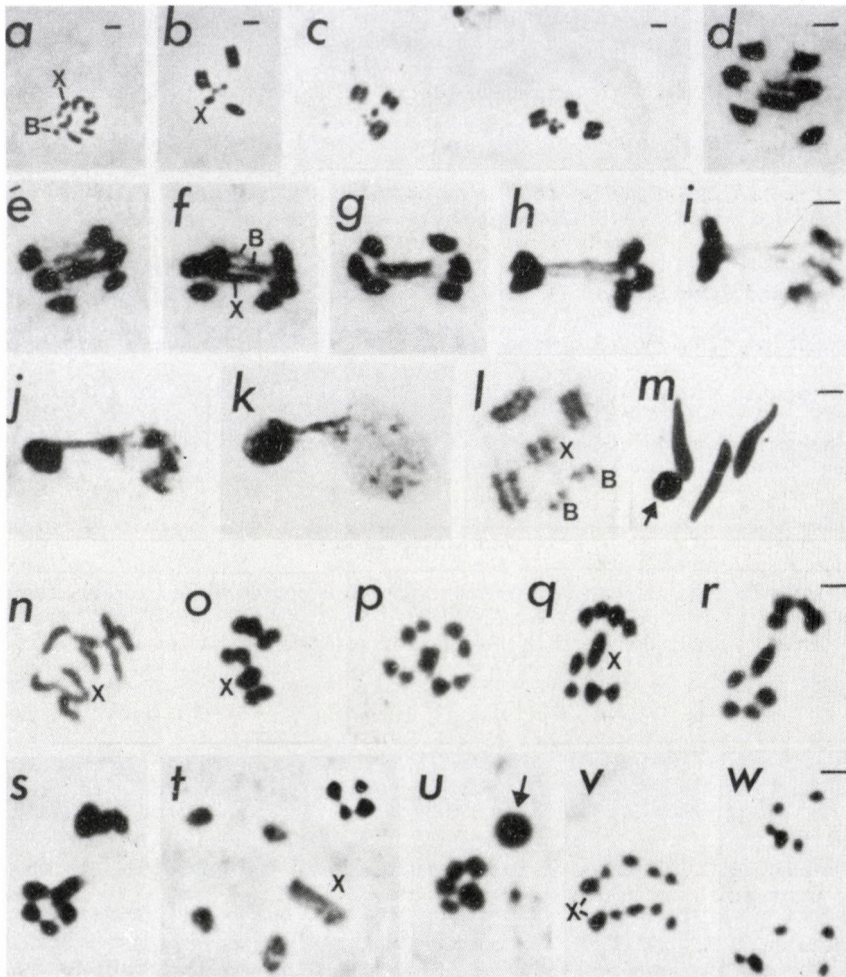
Figure 2.- **a–m** Spermatogenesis in <u>Maculolachnus</u> <u>submacula</u>; **a,** spermatogonial metaphase (2n=7 + 2B); **b,** prometaphase I; **c,** metaphase I; **d–k,** anaphase I (daughter nucleus destined to receive X and B chromosomes is to the right); **l,** metaphase II secondary spermatocyte, about to enter anaphase II: **m,** spermatids, start of elongate of sperm tails (round mass arrowed is a degenerating spermatocyte II without X or "B" chromosomes). **n–w** Spermatogenesis in <u>Cinara pini</u>; **n,** male somatic prophase, 2n=9; **o,** metaphase I; **p–s,** anaphase I; **t,** telophase (degenerating nucleus without X at top right); **u,** metaphase II (degenerating nucleus arrowed); **v–w;** anaphase II. Scale bars = 2 μm.

the chromosomes of the secondary spermatocyte with the X only partially decondense (Fig. 2t).

Traminae   No functional sexual phase is known in Traminae, and there are no identifiable X chromosomes. Protrama have many small chromosomes that are difficult to count accurately, whereas Trama and Neotrama have fewer, large chromosomes with extensive blocks of constitutive heterochromatin (Blackman 1980a). Some of this heterochromatin is located terminally or interstitially on predominantly euchromatic chromosomes, while the rest forms separate heterochromosomes. In Trama troglodytes von Heyden, the extent and distribution of heterochromatin varies greatly both within and between populations (Blackman, 1980b and Fig. 3), but there are always 10 euchromatic sections (which contain the coding sequences of DNA). Two of these are often joined via a block of heterochromatin (Fig. 3c,d,g,h).

LITERATURE

Blackman, R.L., (1980a) Chromosome numbers in the Aphididae and their taxonomic significance. Syst. Ent., **5.** 7-25.

Blackman, R.L., (1980b) Chromosomes and parthenogenesis in aphids. In Insect Cytogenetics (eds R.L. Blackman, G.M. Hewitt and M. Ashburner). Symp. R. ent. Soc. London, **10.** 133-148.

Blackman, R.L., (1985) Aphid cytology and genetics. In Evolution and Biosystematics of Aphids (ed. H. Szelegiewicz). Proc. Int. Aphid Symposium at Jablonna, 5-11 April 1981. Ossolineum, Wroclaw, 510 pp.

Blackman, R.L., (1988) Stability of a multiple X chromosome system and associated B chromosomes in birch aphids (Euceraphis spp.; Homoptera: Aphididae). Chromosoma (Berl.), **96.** 318-324.
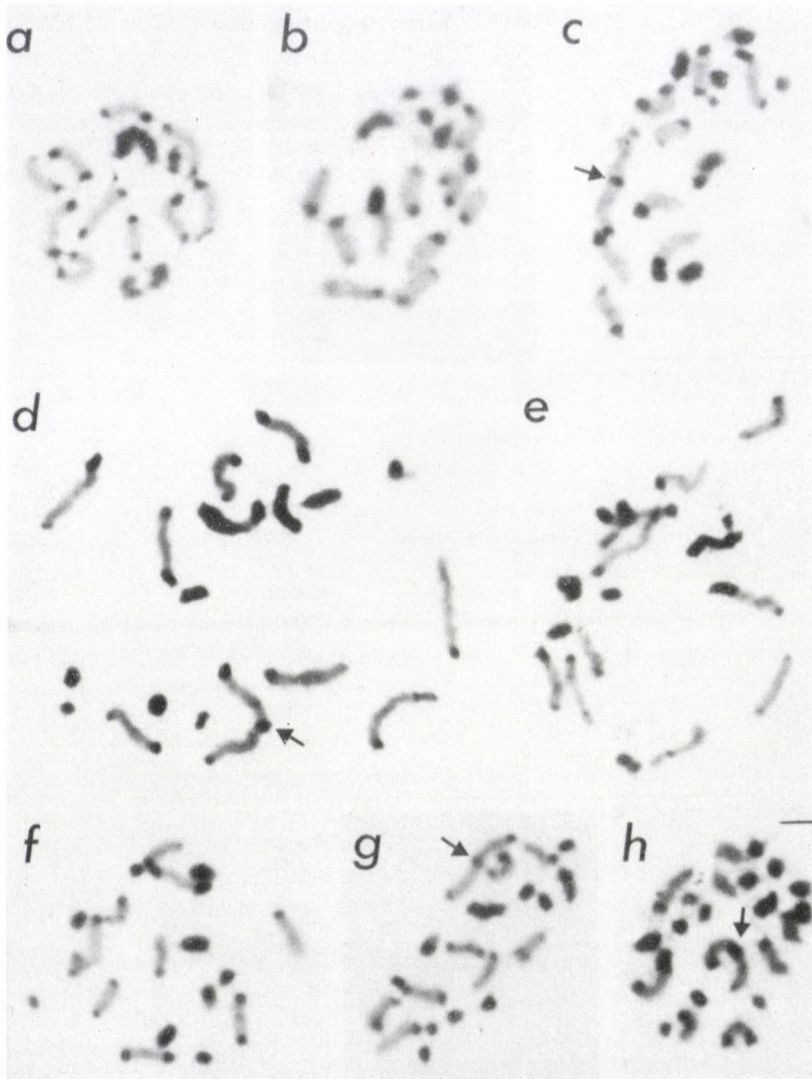
Figure 3. - Variable distribution of constitutive heterochromatin in Trama troglodytes in populations from S.E. England, revealed by C-banding. All karyotypes have 10 euchromatic sections, but in some two of these are joined by a block of heterochromatin (arrowed). **a**, 2n=14, from Artemisia vulgaris; **b**, 2n=16, from Sonchus oleraceus; **c**, 2n=16 (with fusion) from Cirsium arvense; **d**, 2n=18 (fusion), from C. arvense; **e**, 2n=17, from C. arvense; **f**, 2n=19, from Artemisia; **g**, 2n=20 (fusion), from C. arvense; **h**, 2n=22 (fusion) from Artemisia. Scale bar = 2 μm.

Honda, H., (1921) Spermatogenesis in aphids: the fate of the smaller
    secondary spermatocyte. Biol. Bull. Woods Hole, **40.** 349-369.

Rukavishnikov, Yu.M., (1972) [On the karyology of aphids with cyclical
    parthenogenesis.] In [Apomixis in plants and animals]. Sib. Otdel.
    Akad. Nauk. SSR, **1972.** 229-232.

Sun, R.-Y. and Robinson, A.G., (1966) Chromosome studies on 50 species of
    aphids. Can. J. Zool., **44.** 649-653.

GENETIC STUDIES OF *RHOPALOSIPHUM* IN AUSTRALIA

Dinah F. Hales and Rosemary Cowen

School of Biological Sciences, Macquarie University, N.S.W. 2109,

Australia.

ABSTRACT

As part of a larger study of cereal aphids in Australia, we have

examined samples of *Rhopalosiphum* Koch collected from grasses and cereals,

using chromosomal and electrophoretic methods. The samples included

Rhopalosiphum maidis (Fitch) with 2n=8 and 2n=9, *R. padi* (L.) with 2n=8,

R. insertum (Walker) with 2n=10, *R. rufiabdominalis* (Sasaki) with 2n=8, and a

form similar to *R. padi* with 2n=9. It was suggested on the basis of

morphology and chromosomes that the latter form may be a hybrid between

R. padi and *R. insertum*, but the electrophoretic patterns indicate that it

is unlikely to be a hybrid and represents a separate introduction of a

possibly undescribed species.

INTRODUCTION

We report here genetic studies of the genus *Rhopalosiphum* Koch on

grasses and cereals in Australia.

MATERIALS AND METHODS

Rhopalosiphum spp. were collected from grasses and cereals, usually on

the Macquarie University campus in Sydney but occasionally elsewhere as

noted. They were maintained as virus-free clonal cultures on barley

seedlings in an airconditioned room at about $20^{O}C$ and a photoperiod of 16h.

Air-dried chromosome preparations and electrophoresis were carried out as

described previously (Hales and Lardner 1988, Hales *et al*. in press).

RESULTS

Chromosome numbers

Rhopalosiphum maidis (Fitch) had 2n=8 and 2n=9; the karyotypes were similar to those reported by Brown and Blackman (1988) and were associated respectively with maize and with grasses, as also reported by those authors. *Rhopalosiphum padi* (L.) and *R. rufiabdominalis* (Sasaki) had 2n=8; *R. insertum* (Walker) had 2n=10, and other populations superficially resembling *R. padi* had 2n=9. This form could be considered on the basis of its chromosomes to be a possible hybrid of *R. padi* and *R. insertum*. Morphologically it also showed intermediate characteristics, particularly in antennal length and curling of the processus terminalis, and in the length and shape of hairs on the abdominal tergites in apterae.

Electrophoresis

Comparisons were made of 2n=8 and 2n=9 *R. maidis*, and of *R. padi*, *R. insertum* and the 2n=9 *R. padi*-like form.   For *R. maidis*, no consistent association of electrophoretic pattern with chromosome number could be found.   One 2n=8 clone had a faster-running homozygous glucose-phosphate isomerase, and two 2n=9 clones, both from southern Queensland, had a slower homozygous glucose-6-phosphate dehydrogenase.   Apart from possible adenylate kinase, aldolase and esterase differences (again not associated with karyotype), all other clones were identical for all loci tested (totals: 6 2n=9 clones, 3 2n=8 clones, 24 loci; additional clones tested for some loci).

For the *R. padi/R. insertum* group, however, electrophoretic differences between the three forms were consistent with karyotype.   The results for enzymes displaying differences are summarised in Table 1, with the mobilities expressed as normal, fast or slow in relation to *R. padi*.

Table 1   Summary of Electrophoretic Differences between *R. padi*,

"2n=9" and *R. insertum* (n=normal, s=slow, f=fast)

Enzyme	*R. padi*	"2n=9"	*R. insertum*	Comments
GPI	n	ns	n	2n=9 heterozygous
PGM	ns	nf	n	Possible sub-bands, not heterozygous
?GPD	n + faint s	faint n + f	f	" "
6PGD	n	s	s	
AAT$_C$	n	f	n	
AAT$_A$	ns	f	f	*R. padi* apparently heterozygous[*]
ENOL	n	f	n	
PGK	n	s	not tested	
PK	n	s	not tested	
GAPD	n	f	not tested	

[*]   A similar 3-banded pattern in *Schoutedenia lutea* (van der Goot) shows no segregation despite sexual reproduction (Hales, unpubl.), so this interpretation needs confirmation.

DISCUSSION

Our results have confirmed Brown and Blackman's contention (1988) that *R. maidis* with 2n=8 shows a preference for maize while the 2n=9 karyotype is associated with grasses. This clear biological difference, however, could not be related to electrophoretic patterns, as occasional clones of either karyotype showed homozygous differences in particular enzyme systems. The 2n=10 karyotype and heterozygous 2n=8 karyotype reported by Brown and Blackman (1988) have still not been recorded in Australia. A

mechanism for the origin of homozygous variants in this permanently parthenogenetic species has not been proposed.

The *R. padi*-like populations with 2n=9 continue to be of uncertain status, but represent a genetic entity quite distinct in morphology, karyotype and electrophoretic pattern from both *R. padi* and *R. insertum*. The hypothesis that the 2n=9 form might be a hybrid between *R. padi* and *R. insertum* is not well supported by the electrophoretic data. We do not see, for any enzyme, a heterozygous pattern of bands corresponding to those expected on the basis of the putative parent species. The only enzyme for which the 2n=9 form is heterozygous is glucose-phosphate isomerase; it has one allozyme of the same mobility as that in both *R. padi* and *R. insertum*, and one slower allozyme shown by neither of the "parent" species. Of course, the clones of *R. padi* and *R. insertum* present in Australia, and especially the small sub-sample tested, probably do not represent the level of genetic diversity of either of these species in Europe, where both can reproduce sexually. We cannot discount the possibility that the 2n=9 form might contain alleles represented in the European (or perhaps North American) populations of *R. padi* and *R. insertum*, but absent from our Australian samples. Loxdale and Brookes (1988), however, showed that even in Britain there was little genetic variability in *R. padi*, despite sexual reproduction in at least part of its range. We do not know of any previous genetic studies on *R. insertum*, but it has been found in Australia only recently (Ridland and Carver 1987) and the Australian population is likely to have been derived from one (or a few) clones. Therefore, while it is possible that the unique allozymes in the 2n=9 form could have been derived form overseas populations of *R. padi* or *R. insertum*, the lack of heterozygosity suggests that it is not a hybrid. The overall electrophoretic data imply a closer relationship to *R. insertum* than to

R. padi.

If the 2n=9 form is not a hybrid between *R. padi* and *R. insertum*, what is it? It may be a separate species, perhaps undescribed, introduced from Europe, North America or Asia. *Rhopalosiphum* is a difficult genus from the viewpoint of morphological taxonomy; Eastop and Hille Ris Lambers (1976) listed 16 current species and a myriad of synonyms. It has been suggested that *R. insertum* may be part of a species complex in North America (see Ridland and Carver 1987). In the circumstances it seems that the identity and origin of the 2n=9 form will be uncertain until the European and North American members of the *R. padi/R. insertum* complexes have been investigated by genetic methods.

In practical terms, the discovery of a separate genetic form of *Rhopalosiphum* means that future survey work on cereal aphids must distinguish this form from the superficially similar *R. padi*. Studies on the biology of the 2n=9 form are in progress and specimens have been deposited in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra.

REFERENCES

Brown, P.A. and Blackman, R.L. (1988). Karyotype variation in the corn leaf aphid, *Rhopalosiphum maidis* (Fitch) species complex (Hemiptera: Aphididae) in relation to host-plant and morphology. *Bull. ent. Res.*, **78**, 351–363.

Eastop, V.F. and Hille Ris Lambers, D. (1976). *Survey of the World's Aphids*. Dr. W. Junk, The Hague, 573 pp.

Hales, D.F., Chapman, R.L., Lardner, R.M., Cowen, R. and Turak, E. (in press). Aphids of the genus *Sitobion* occurring on grasses in southern Australia. *J. Aust. ent. Soc.*, **29**.

Hales, D.F. and Lardner, R.M. (1988). Genetic evidence for the occurrence of a new species of *Neophyllaphis* Takahashi in Australia (Homoptera: Aphididae). *J. Aust. ent. Soc.* **27**, 81-85.

Loxdale, H.D. and Brookes, C.P. (1988). Electrophoretic study of enzymes from cereal aphid populations. V. Spatial and temporal genetic similarity of holocyclic populations of the bird-cherry oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), in Britain. *Bull. ent. Res..*, **28**, 241-249.

Ridland, P. and Carver, M. (1987). *Rhopalosiphum insertum* (Walker) (Homoptera: Aphididae) newly recorded from Australia. *J. Aust. ent. Soc.*, **26**, 128.

GENE FLOW IN APHIDS

H.D. Loxdale

Entomology & Nematology Department, Rothamsted Experimental

Station, Harpenden, Herts, AL5 2JQ, UK.

ABSTRACT

This paper examines gene flow between field populations
of the cereal aphids *Sitobion avenae* (F.), *Sitobion fragariae*
(Walker) and *Rhopalosiphum padi* (L.) using a mathematical
simulation model (Slatkin's) and statistical analyses of
allozyme data (*F* statistics). The results obtained are
related to the flight behaviour of these aphids and to their
respective host plant abundances.

INTRODUCTION

Genetic markers can be employed to study gene flow
between natural populations, including aphids. Presently,
such markers are mainly allozymes (Slatkin, 1985b). DNA
markers are becoming increasingly popular, although some have
important drawbacks for demographic population studies (Lewin,
1989).

This paper outlines the use in aphidology of certain
recent theoretical approaches to the study of gene flow
between natural populations, especially Slatkin's (1981, 1985a
and b) simulation model and Nei & Chesser's (1983) estimation
of fixation indices and gene diversity based on Wright's
(1943, 1951) original statistics. Analyses are performed on

allozyme data for three species of cereal aphid:- *Sitobion avenae* (F.), *Sitobion fragariae* (Walker), and *Rhopalosiphum padi* (L.).

Slatkin's Simulation Model

Slatkin (1980, 1981, 1985a) described a model for assessing the amount of gene flow between natural populations from allozyme frequency data. He defined the *occupancy number of an allele* (i) to be the number of *demes** in which it is present (d), whilst the *conditional average frequency* ($\bar{p}(i)$) was its mean frequency in these demes. Using computer simulations, Slatkin (1981) found $\bar{p}(i)$ to be approximately independent of the selection intensity and mutation rates assumed ($\bar{p}(i)$ vs. i), although it did depend strongly on the overall level of gene flow. Because of this latter finding, $\bar{p}(i)$ was employed as a rough estimate of the amount of gene flow in a subdivided population of a species. He later plotted $\bar{p}(i)$ versus i for various rates of migration (m), holding the number of demes and deme size constant, and two models of dispersal - the 'island model', in which immigration from all populations is equally likely and the 'one-dimensional stepping stone model', in which immigration is more likely from adjacent populations. He found (Figs. 1a and b) that the basic pattern of results was similar for the two models, and that $\bar{p}(i)$ was dependent on the migration rate, but that the value of Nm rather than m alone determines the importance of gene flow (*cf.* Slatkin, 1980, 1981, 1985a and b for further details).

*deme = subpopulation

Slatkin (1985a) studied rare alleles in more detail as indicators of gene flow. Here he showed that the value of $\bar{p}(1)$, the average frequency of the alleles found only in one deme (private alleles) provided a quantitative estimate of the amount of interpopulation gene flow, something lacking in the previous purely qualitative graphical assessments. He plotted simulated values of Nm (effective population size* x migration rate = number of immigrants per generation) against $\bar{p}(1)$ for a sample size of 25 (N_{sam} = 25) and obtained an inverse straight line relationship which was approximately linear over a 1000 fold range between Nm 0.01 - 10 and nonlinear above and below these extreme values. The inverse relationship could be expressed by the equation:-

$$ln(\bar{p}(1)) = a \, ln(Nm) + b \qquad (1)$$

where a and b are constants (-0.505 and -2.44 respectively). Thus if values of $\bar{p}(1)$ are known for particular species, the value of Nm may be calculated, i.e.

$$Nm = e^{\frac{(ln(\bar{p}(1)) - b}{a}} \qquad (2)$$

$\bar{p}(1)$ is not sensitive to the number of demes in the sample. However, increasing the number of individuals sampled per deme (N_{sam}) increases the number of private alleles in the sample. Hence, the accuracy of estimates of Nm is increased, whilst the average frequency of private alleles in the sample is decreased. Differences in sample size may be approximately

*effective population size = number of individuals in a population contributing genetically to the next generation (cf. Parkin, 1979, for further details). In the case of aphids and for a given species population, the effective population size is determined by the severity of successive population bottle-necks and the survival of overwintering eggs (Blackman, 1981).

adjusted for by dividing the estimate of Nm by the ratio of the actual sample size to 25.

The amount of migration (m) can be derived from the formula:

$$I = \exp(-D) = m/(m + v) \tag{3}$$

where I and D are the average genetic identity and distance between populations over all loci sampled and v the mutation rate (Nei, 1975, p. 194). Hence, if average I values are known for particular species and assuming a mutation rate of 2 x 10^{-6} per gene per generation (Larson et $al.$, 1984), m may be calculated as follows:-

$$m = \frac{I \, v}{(1 - I)} \tag{4}$$

The value of N, the effective population number, can then be calculated by dividing Nm by m.

Application to aphid data

(1) $Sitobion$ $avenae$

Loxdale et $al.$ (1985) surveyed allozyme frequencies over a range of enzyme loci in four British $S.$ $avenae$ populations collected from wheat in 1981 and in six British and three Spanish populations collected from wheat in 1982 (sites minimally $\geq$ 16 km apart, maximally 2025 km). In Fig. 2, the British and Spanish allozyme frequency data is presented for both sampling years (1981 & 1982, 13 sites, closed circles) and 1982 only (9 sites, open circles). As may be seen, the graphs are essentially similar to one another. Compared to those presented by Slatkin (Fig. 1a & b), these graphs suggest that moderate to high gene flow has occurred between the

Fig. 1.
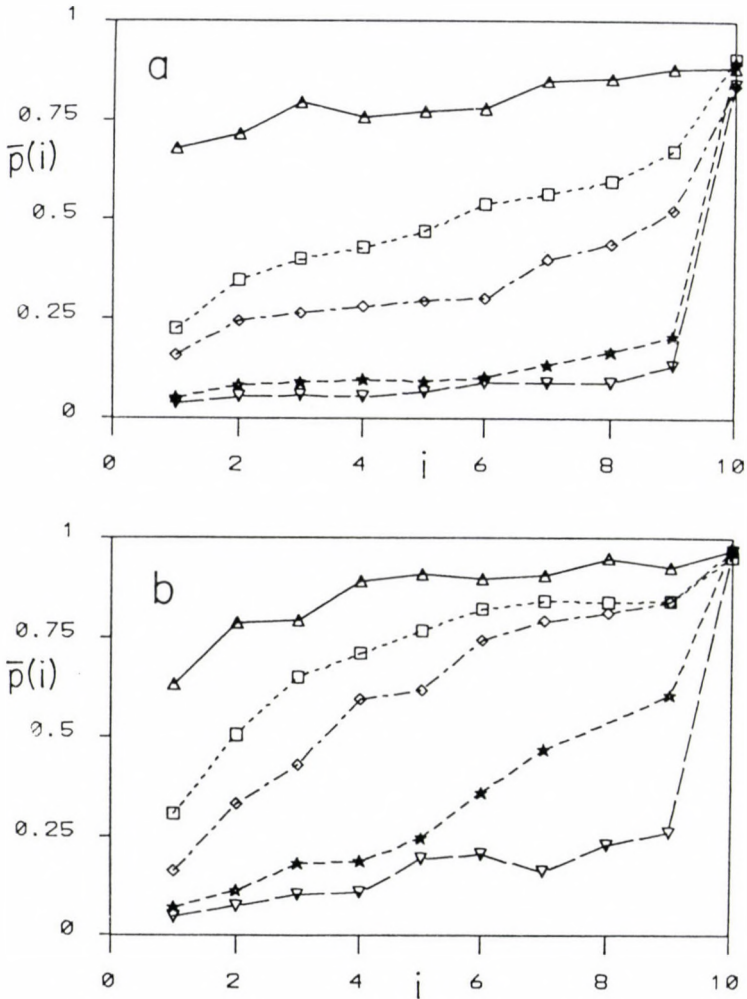
Legends to Figures

Figure 1. Conditional average frequency, $p(i)$, for neutral alleles. In both parts, μ (mutation rate) = 10^{-4}, d = 10 and N (deme size) = 25. $\triangle$——$\triangle$ m (migration rate) = 0.001, $\square$---$\square$ m = 0.005, $\diamondsuit$ — $\diamondsuit$ m = 0.01, $*$---$*$ m = 0.05, ∇ — ∇ m = 0.1. Part a: island model; part b: one-dimensional stepping stone model. (Reproduced from Slatkin, 1981 with permission).
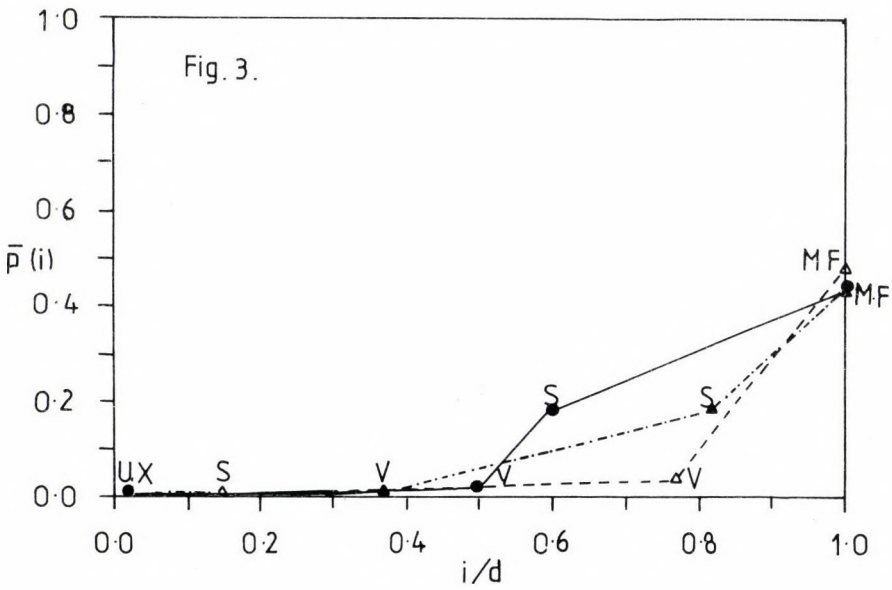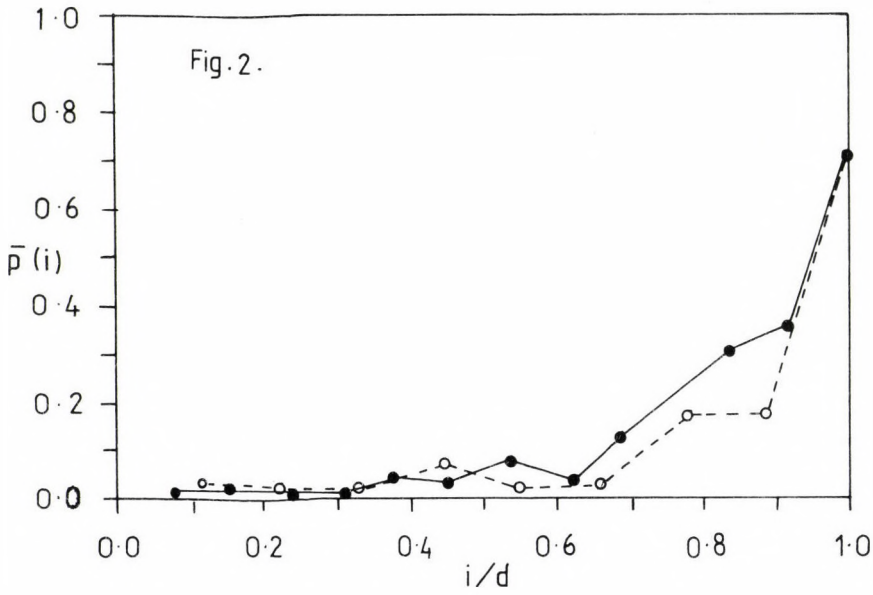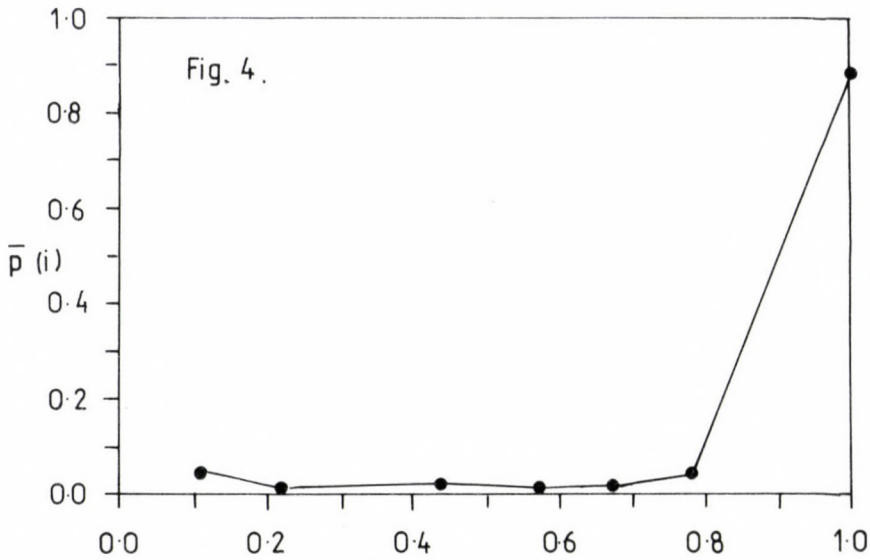
Fig. 2.

Fig. 3.

Fig . 2-4. Conditional average frequency, $\bar{p}(i)$, plotted as $\bar{p}(i)$ versus i/d (occupancy no./no. of demes). *Sitobion avenae* (Fig. 2); ●──● 1981–82 data (d_{sam} = 13), o---o 1982 data only (d_{sam} = 9), *Sitobion fragariae* (Fig. 3); ▲-·-▲ *samples from D. glomerata* (d_{sam} = 27), △──△ *samples from R. fruticosus* (d_{sam} = 13); ●──● samples from both hosts (d_{sam} = 40) and *Rhopalosiphum padi* (Fig. 4); 1985–86 data (d_{sam} = 7-9).

subpopulations sampled.

The $\bar{p}(1)$ values for the two data sets (9 and 13 sites) are 0.027 and 0.019 respectively. Using equation (2), these values give Nm values of 1.6 and 3.0. Thus the Nm for the $S.$ $avenae$ allozyme data collectively may be taken to be about 2.0.

The average genetic identity value obtained over all 13 loci examined by Loxdale et $al.$ (1985) was 0.896. Using equation (4), this gives the migration rate as $m = 2 \times 10^{-5}$, or two long distance migrant aphids (say > 20 km) per 100,000 population. By dividing $Nm = 2$ by m, the effective population number N is around 100,000, a very small value considering the large geographical area sampled.

Only with $S.$ $avenae$ is enough data available to calculate $Nm,$ m and $N.$ For the other species of aphid discussed, only qualitative assessments of gene flow are possible.

(2) $Sitobion$ $fragariae$

The biochemical polymorphism of this species has recently been studied by Loxdale & Brookes (1987, 1990a). Loxdale & Brookes concentrated, in particular, on examining genetic variability at the GOT (glutamate oxaloacetete transaminase) locus within and between local populations around Rothamsted. Spatial and temporal data were obtained over a number of years (1981, 1983-6). Six GOT alleles were detected in total (U, X, S, M, F & V), in four homozygous and seven heterozygous combinations.

In Fig. 3, the conditional allele frequency data for these alleles in which spatial and temporal data have been combined, is plotted as $\bar{p}(i)$ vs. i/d for aphids infesting

Rubus fruticosus, *Dactylis glomerata* and both hosts. The samples from the primary host give a pattern indicative of more gene flow than those from the secondary host. This agrees broadly with conclusions drawn from the raw gene frequency data, especially the comparatively greater spatial allelic homogeneity of populations infesting the primary rather than the secondary host (Loxdale & Brookes, 1990a). The combined data for aphids from both hosts gives a pattern indicative of moderate gene flow, less than *S. avenae* (Fig. 2), although more data is required to confirm this trend.

(3)   *Rhopalosiphum padi*

Loxdale & Brookes (1988) studied holocyclic populations of this species collected at various sites in Britain from the primary host *Prunus padus* in 1985 & 1986 (sites minimally 3 km apart, maximally ~ 400 km). The species was much less polymorphic than the two *Sitobion* species described, only having two polymorphic loci (GOT and SORDH, sorbitol dehydrogenase) out of 14 studied.

In Fig. 4, the combined data for both GOT and SORDH and both sampling years is presented. The pattern for *R. padi* from *P. padus* is indicative of high gene flow, again a conclusion which can also be drawn from the spatial and temporal similarity of the GOT and SORDH frequencies (Loxdale & Brookes, 1988).

Other approaches to studying gene flow

Allele frequency differences between natural populations can be assessed using coefficients of genetic identity and distance e.g. Nei's (cf. Nei, 1975; Slatkin, 1985b; Loxdale,

et al. 1985) or by using a genetic contingency chi-square test
i.e. that described by Workman & Niswander, 1970 (cf. also
Ferguson, 1980; Loxdale et al., 1985). Alternatively, the
heterozygosity of populations can be assessed using F
statistics (cf. Wright, 1965, 1978; Workman & Niswander, 1970;
Nei & Chesser, 1983). The most important statistic, F_{ST}, can
be defined as the "correlation between random gametes within
subpopulations relative to the gametic array of the total
population" (Workman & Niswander, 1970). It is described by
the ratio $F_{ST} = 1 - H_S/H_T$, where H_S and H_T represent the
expected heterozygosities under Hardy-Weinberg equilibrium or
gene diversities within subpopulations and in the total
population, respectively (Nei & Chesser, 1983). Another
statistic, F_{IS}, is described by the ratio $F_{IS} = 1 - H_O/H_S$,
where H_O is the observed frequency of all heterozygotes. In
brief, F_{ST} measures the allelic heterogeneity between local
populations, whereas F_{IS} is a measure of average deviation of
genotype proportions from Hardy-Weinberg expectations in
random mating subpopulations (panmictic populations). F_{ISi}
can be calculated for individual subpopulations (Nei &
Chesser, 1983). F statistics do not provide any more
information than χ^2 contingency assessment or normal
assessment of deviations of genotypic proportions from Hardy
Weinberg expectations using a χ^2 test (cf. Ferguson, 1980).
However, they do provide a quantitative index of diversity
(F_{ST}) and deviation from random mating (F_{IS}). F_{ST} is related
to χ_G^2, the χ^2 of the genetic contingency analysis by $F_{ST} =$
$\chi_G^2/2N_T$ or $\chi_G^2 = F_{ST}2N_T$, where N_T is the total population size

(Workman & Niswander, 1970). Hence, a significance value can
be assessed for F_{ST}.

Calculation of F_{ST} and F_{IS} for *Sitobion fragariae*
populations on *R. fruticosus* and *D. glomerata* are presented in
Table 1. The indices were calculated by the method described
by Nei & Chesser (1983) which takes into account differences
in the size of subsamples.

Table 1 F_{ST} and F_{IS} values for *Sitobion fragariae* populations
on primary and secondary hosts

	Host	
	R. fruticosus	*D. glomerata*
No. of subsamples	13	27
Total population size (N_T)	4041	8122
F_{IS}	$-0.07^{N.S.}$	0.245***
F_{ST}	0.066***	0.177***

N.S. = not significant at the 5% level of probability ($P=0.05$)
***, $P < 0.001$

The slightly negative F_{IS} value for aphids on *R.
fruticosus* is indicative of a slight heterozygote excess.
However, the total population does not significantly deviate
from Hardy-Weinberg expectations ($P = 0.05$) (F_{IS} would be zero
if observed genotype proportions were completely concordant
with Hardy-Weinberg expectations). The F_{ST} value 0.066
(approx. 6%), whilst significant at the 5% level, is small,
showing that the population of *S. fragariae* on *R. fruticosus*
to be fairly homogeneous at the GOT locus, both spatially and
temporally. The value is similar to that found at the malate
dehydrogenase (MDH) locus by Wöhrmann & Tomiuk (1988) for rose
aphids, *Macrosiphum rosae*, infesting roses in Europe ($F_{ST} =
0.03$ for populations from Tübingen, West Germany; 0.08 for all
European populations studied)

In contrast, the F_{IS} value for *S. fragariae* from *D. glomerata* (F_{IS} = 0.245) shows populations to deviate significantly from Hardy-Weinberg expectations and is indicative of a homozygote excess in these populations. The F_{ST} value of 0.177 (approx. 18%) shows the populations on the secondary host to be spatially and temporally fairly heterogeneous. The value may be compared to a value of F_{ST} = 0.27 for European populations of *M. rosae* examined at the phosphoglucomutase (PGM) locus by Wöhrmann & Tomiuk (1988).

The homozygote excess observed in the *S. fragariae* populations sampled stems from an excess of SS GOT homozygotes. The presence of the S bearing genotypes within populations tends to cause deviations from Hardy-Weinberg proportions (Loxdale & Brookes, 1990a). Since the S-bearing genotypes are rare on *R. fruticosus*, we proposed that such insects may be predominantly anholocyclic on the secondary host.

DISCUSSION

Because of dilution effects, direct methods are generally not applicable to the study of long distance migration of very small insects, including aphids. Yet such migration may be important in the population biology of the species in question, allowing re-stocking of depleted areas or re-colonization of areas previously inhabited or expansion into completely new regions. As stated in Slatkin (1985b), Wright (1931) showed theoretically that if a fraction, *m*, of a population is replaced by immigration, there will be no significant differentiation if $Nm > 1.0$, where N is the

effective population size. Wright suggested that *one*
immigrant every other generation is sufficient to prevent
differentiation due to genetic drift. In the case of aphids,
one long distant alate migrant could be very important,
perhaps, founding an entire population, especially if it
possesses an advantageous trait.

Because of the problems inherent in mark-release-recapture
as applied to long distance migration studies of aphids, (but
cf. Taimr & Kriz, 1978), inferences are best drawn from gene
frequency data, such as allozyme data, although some
researchers have succeeded in establishing the probable
migratory range of certain aphid species using aerial density
data obtained from suction sampling alone (e.g. Taylor *et al.*,
1979).

The analysis of the cereal aphid allele frequency data
using Slatkin's methods confirms the conclusions previously
drawn from other earlier analyses. Thus there is high gene
flow between subpopulations of *S. avenae* and *R. padi*, and a
more restricted level between local *S. fragariae*
subpopulations, especially when infesting *D. glomerata*
(Loxdale, *et al.*, 1985; Loxdale & Brookes, 1988, 1990a).

The *Nm* value for *S. avenae* ($Nm \gtrsim 2.0$) is smaller than might
be expected, although it is similar to that quoted by Slatkin
(1985a) as representative of high gene flow ($Nm > 1.0$). It is
considerably lower than values for all the various pest insect
species quoted by Daly (1989), with the exception of *Lymantria
dispar*, the gypsy moth ($Nm = 0.3$; George, 1984), which has
wingless females and hence might be expected to show a

restricted interpopulation gene flow.

The m value presently calculated for *S. avenae* (2×10^{-5})
is small. This result additionally suggests that the amount
of gene flow occurring between *S. avenae* subpopulations is
less than might be assumed from earlier analyses e.g. genetic
distance data (Loxdale *et al.*, 1985) or aerial density data
(Taylor *et al.*, 1982). Clearly, the level of migration is not
enough to prevent local heterogeneity of allele frequencies,
despite the small average D values noted between
subpopulations, even between populations separated by
geographical barriers (cf. Loxdale *et al.*, 1985). However,
that the effective population size is calculated to be small
(˜100,000) over a large geographical area is less surprising
and fits with the assumed predominantly anholocyclic life
cycle of this species (Loxdale *et al.*, 1985).

With the *S. fragariae* data, the F_{ST} value for aphids on
D. glomerata (*Table* 1) shows that populations on this host are
more heterogeneous than those on the primary host, a
conclusion drawn earlier from the allele frequency data.
Hence there may be less gene flow occurring between *S.
fragariae* populations on the secondary host compared to those
on the primary. The similarity of the F statistics derived
for *S. fragariae* on *R. fruticosus* (GOT, F_{ST} = 0.066) and
Macrosiphum rosae on roses (MDH, F_{ST} = 0.03) (Wöhrmann &
Tomiuk, 1988) (Tübingen data) may reflect the similar level of
population movement in these less migratory species.

It is of interest that the abundance and distribution of
the host plants of the various aphid species discussed above

may be largely responsible for the migratory behaviour of the insects in question, which in turn is reflected in their patterns of genetic diversity. In the case of *S. avenae*, a more migratory species, its major host wheat is ephemeral, being harvested annually. This may account for the need for mass migration, sometimes long distance, in this species.

In the case of *R. padi*, its aerial abundance and more migratory behaviour (Taylor *et al.*, 1982; Tatchell *et al.*, 1988) may stem from the fact that the primary host, whilst widely distributed in Britain and Europe, is relatively rare (Tatchell *et al.*, 1983). Hence, in the autumn especially, aphids seeking the primary host may have to fly long distances to find it. In contrast, both the primary and secondary hosts of *S.fragariae*, are common and widespread, which may mean that this aphid species has to fly relatively shorter distances, thus accounting for a reduced migratory behaviour, lower aerial abundance and levels of interpopulation gene flow.

In conclusion, this paper shows how Slatkin's simulation model and *F* statistics may be profitably employed to aphid allozyme frequency data, thereby revealing something about migratory behaviour of the insects concerned. Whilst neither provide any new insight into population biology than might be derived by other approaches (χ^2 contingency testing of allele frequency differences between subpopulations and deviations of genotype proportions from Hardy-Weinberg expectations assessed using direct χ^2 methods) they do give a quantitative estimate which may be valuable in comparative studies.

ACKNOWLEDGEMENTS

REFERENCES

Blackman, R.L. (1981). Species, sex and parthenogenesis in aphids. In "The evolving biosphere" (ed. P.L. Forey), pp. 75-85. Cambridge University Press, Cambridge. 311 pp.

Daly, Joanne, C. (1989). The use of electrophoretic data in a study of gene flow in the pest species *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). In "Electrophoretic studies on agricultural pests" (eds. H.D. Loxdale & J. Den Hollander), pp. 115-141. Systematics Association Special Vol. 39, Oxford University Press, Oxford. 486 pp.

Ferguson, A. (1980). Biochemical systematics and evolution. Blackie & Son Ltd., Glasgow. 194 pp.

George, C. (1984). Allozyme variation in natural populations of *Lymantria dispar* (Lepidoptera). Genet. Sel. Evol., 16, 1-14.

Larson, A., Wake, D.B., Yanev, Kay P. (1984). Measuring gene flow among populations having high levels of genetic fragmentation. Genetics, 106, 293-308.

Lewin, R. (1989). Limits to DNA fingerprinting. Science, 243, 1549-1551.

Loxdale, H.D., Tarr, I.J., Weber, C.P., Brookes, C.P., Digby, P.G.N. & Castanera, P. (1985). Electrophoretic study of enzymes from cereal aphid populations. III. Spatial and temporal genetic variation of populations of *Sitobion avenae* (F.) (Hemiptera: Aphididae). Bull. ent. Res., 75, 121-141.

Loxdale, H.D. & Brookes, C.P. (1987). Use of electrophoretic markers to study the spatial and temporal genetic structure of populations of a holocyclic aphid species - *Sitobion fragariae* (Walker) (Hemiptera: Aphididae). In "Population structure, genetics and taxonomy of aphids and Thysanoptera" (eds. J. Holman, J. Pelikan, A.F.G. Dixon & L. Weismann), pp. 100-110. SPB Academic Publishing, The Hague.

Loxdale, H.D. & Brookes, C.P. (1988). Electrophoretic study
    of enzymes from cereal aphid populations. V. Spatial and
    temporal genetic similarity between holocyclic populations
    of the bird-cherry oat aphid *Rhopalosiphum padi* (L.)
    (Hemiptera: Aphididae) in Britain. Bull. ent. Res., **78**,
    241-249.

Loxdale, H.D. & Brookes, C.P. (1990a). Electrophoretic study
    of enzymes from cereal aphid populations. VI. Spatial and
    temporal allozyme variation at the GOT-locus in local
    populations of the blackberry-grain aphid *Sitobion fragariae*
    (Walker) (Hemiptera: Aphididae) in south-east England. J.
    Anim. Ecol., (submitted).

Loxdale, H.D. & Brookes, C.P. (1990b). Prevalence of *Sitobion
    fragariae* (Wlk.) over *Sitobion avenae* (F.) on wild Cocksfoot
    grass (*Dactylis glomerata*) in south-east England. Bull.
    ent. Res. (in press).

Nei, M. (1975). Molecular population genetics and evolution.
    North Holland Publishing Co., Amsterdam. 288 pp.

Nei, M. & Chesser, R.K. (1983). Estimation of fixation
    indices and gene diversities. Ann. Hum. Genet., **47**, 253-259.

Parkin, D.T. (1979). An introduction to evolutionary
    genetics. Edward Arnold, London. 223 pp.

Slatkin, M. (1980). The distribution of mutant alleles in a
    subdivided population. Genetics, 95, 503-524.

Slatkin, M. (1981). Estimating levels of gene flow in natural
    populations. Genetics, **99**, 323-335.

Slatkin, M. (1985a). Rare alleles as indicators of gene
    flow. Evolution, 39, 53-65.

Slatkin, M. (1985b). Gene flow in natural populations. Ann.
    Rev. Ecol. Syst., 16, 393-430.

Taimr, L. & Kříž, J. (1978). Stratiform drift of the hop
    aphid (*Phorodon humuli* Schrank). Z. ang. Ent., 86, 71-79.

Tatchell, G.M., Parker, S.J. & Woiwod, I.P. (1983). Synoptic
    monitoring of migrant insect pests in Great Britain and
    western Europe. IV. Host plants and their distribution for
    pest aphids in Great Britain. Report (1982) for Rothamsted
    Experimental Station, Harpenden, Herts., U.K. Part 2, pp.
    45-159.

Tatchell, G.M., Plumb, R.T. & Carter, N. (1988). Migration of
    alate morphs of the bird cherry aphid (*Rhopalosiphum padi*)
    and implications for the epidemiology of barley yellow dwarf
    virus. Ann. appl. Biol., **112**, 1-11.

Taylor, L.R., Woiwod, I.P. & Taylor, R.A.J. (1979). The
    migratory ambit of the hop aphid and its significance in
    aphid population dynamics. J. Anim. Ecol., 48, 955-972.

Taylor, L.R., Woiwod, I.P., Tatchell, G.M., Dupuch, M.J. &
    Nicklen, J. (1982). Synoptic monitoring for migrant insect
    pests in Great Britain and western Europe. III. The
    seasonal distribution of pest aphids and the annual aphid
    aerofauna over Great Britain 1975-80. Report (1981) for
    Rothamsted Experimental Station, Harpenden, Herts., U.K.
    Part 2. pp. 23-121.

Wöhrmann, K. & Tomiuk, J. (1988). Life cycle strategies and
    genotypic variability in populations of aphids. J. Genet.,
    67, 43-52.

Workman, P.L. & Niswander, J.D. (1970). Population studies on
    southwestern Indian tribes. II. Local genetic
    differentiation in the Papago. Am. J. hum. Genet., 22,
    24-49.

Wright, S. (1931). Evolution in Mendelian populations.
    Genetics, 16, 97-159.

Wright, S. (1943). Isolation by distance. Genetics, 28,
    114-138.

Wright, S. (1951). The genetical structure of populations.
    Ann. Eugen., 15, 323-354.

Wright, S. (1965). The interpretation of population structure
    by F-statistics with special regard to systems of mating.
    Evolution, 19, 395-420.

Wright, S. (1978). Evolution and the genetics of
    populations. Vol. IV. Variability within and among natural
    populations. The University of Chicago Press, Chicago. 580
    pp.

SITOBION: GENETICS AND THE ENVIRONMENT

Eren Turak and Dinah F. Hales,

School of Biological Sciences, Macquarie University, N.S.W. 2109 Australia.

ABSTRACT

There are at least three genetically different forms of Sitobion on cereal crops in southern Australia. These forms are morphologically similar but can be distinguished by protein electrophoresis. We believe that two species are represented: a species near S. fragariae (Walker), with a diploid chromosome number of 18, and two chromosomal races of S. miscanthi (Takahashi), one with 2n=17 and the other with 2n=18. These three forms are common in the field at different times of the year. Experiments were carried out to determine whether this seasonal difference between the three genetic forms reflected different environmental tolerances. Growth rate, reproductive rate and offspring weight were used as parameters of performance under different temperature regimes. The results showed that the observed seasonal differences reflect different temperature tolerances.

INTRODUCTION

The taxonomy of Sitobion in Australia is confused. The two species that occur on grasses in Australia are Sitobion miscanthi (Takahashi) and a species near S. fragariae (Walker) (Carver, pers. comm.). Previous observations had shown that "S. miscanthi" populations had at least two chromosome numbers, 2n=18 and 2n=17 (Hales unpublished). These two forms are referred to in this paper as "S. miscanthi" and "2n=17" respectively. Protein electrophoresis is used to determine whether these forms are conspecific or represent separate species.

It was observed that S. nr fragariae, "S. miscanthi" and "2n=17" were different from one another in their seasonal distribution. S. nr fragariae was found in the field from winter to early summer, "S. miscanthi" only in summer and "2n=17" in autumn and winter and then in summer. These observations suggest that the three genetic forms of Sitobion have different temperature tolerances and experiments were therefore designed to test this hypothesis. Growth rate, reproductive rate and offspring weight were chosen as parameters of performance. These parameters in aphids are dependent on two extrinsic factors, temperature and food quality, and two intrinsic factors, birth weight and whether the aphid is winged or wingless (Dixon 1987). By using wingless aphids from high quality host plants, the important factors affecting these parameters are reduced to temperature and birth weight.

MATERIALS AND METHODS

Aphids were obtained from uncrowded, virus free clones of Sitobion established on barley seedlings and maintained at $20^{o}C$ and 16 hour photoperiod.

Karyotyping was carried out as described previously (Hales and Lardner 1988). Cellulose acetate electrophoresis was also described previously (Hales et al. in press).

Performance experiments were carried out in controlled temperature rooms at Macquarie University. Four different temperature regimes were used : $12^{o}C$, $15^{o}C$, $20^{o}C$, $25^{o}C$. First large numbers of newborn aphids of each genotype were placed on plants at the experimental temperature. After they started reproducing, their offspring were weighed within 4 hours of birth and placed separately on plants. These aphids were numbered and checked the day after their transfer. 20 were selected as experimental animals and observed daily. They were weighed within 10 hours of their adult moult. Their 1st, 2nd or 3rd

offspring were weighed within 4 hours of birth. The 2nd or 3rd offspring were weighed only when the 1st one was thought to have been born more than 4 hours before the time of observation. The number of offspring was recorded daily for each aphid until death.

As host plant quality is an important factor influencing performance in aphids (Dixon 1987), efforts were made to standardize this parameter. The individual aphids were transferred on to plants of the same age. All experiments were carried out under a 16 hour photoperiod.

RESULTS

The cellulose acetate electrophoresis for glucose-phosphate isomerase (GPI) and hexokinase (HK), showed these enzymes to have different mobilities in the three forms. For PGI, S. nr fragariae was the slowest, and "2n=17" the fastest. For HK the order was the reverse. The results from the 25 loci tested (Table 1), show clearly that the two forms of "S. miscanthi" are much more similar to each other than they are to S. nr fragariae.

Chromosome preparations (Fig. 1) showed as expected, that both S. fragariae and S. miscanthi had diploid chromosome numbers of 18 with the two presumed X chromosomes much longer than all the autosomes. In the "2n=17", however, one of the autosomes is longer than the sex chromosomes.

Pair	Variant loci	
	Number	%
S. nr fragariae- "S. miscanthi"	9	36
S. nr fragariae-"2n=17"	9	36
"S. miscanthi"- "2n=17"	2	8

Table 1   Summary of loci showing electrophoretic differences (total 25 loci). All differences were homozygous.
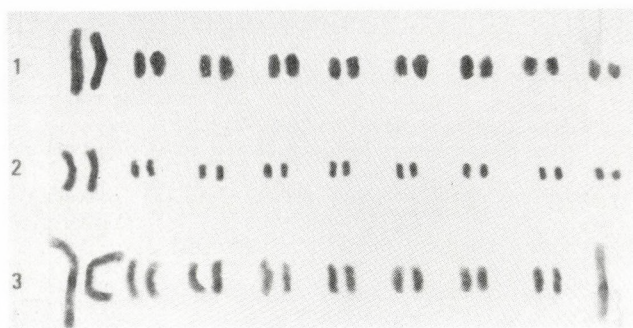
Fig. 1.   Chromosomes of the three forms. 1-<u>S</u>. nr <u>fragariae</u>, 2-"<u>S</u>. <u>miscanthi</u>", 3- "2n=17".
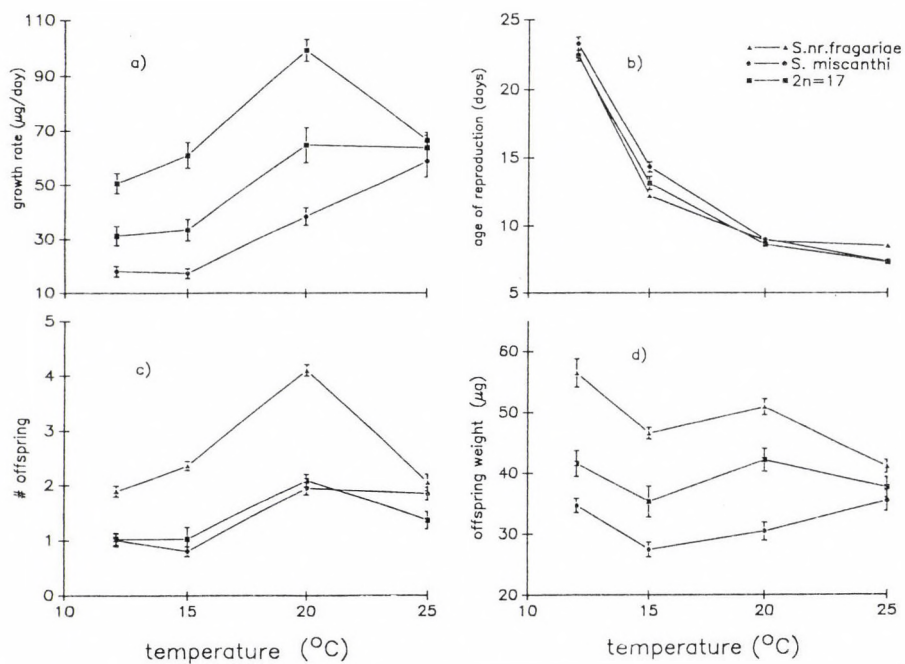
Fig. 2. a)   Growth rates from birth to adult moult.
        b)   Age at birth of the first offspring.
        c)   Daily average number of offspring within the
             first 7 days of reproduction.
        d)   Offspring weight. (Means +- 1 S.E.).
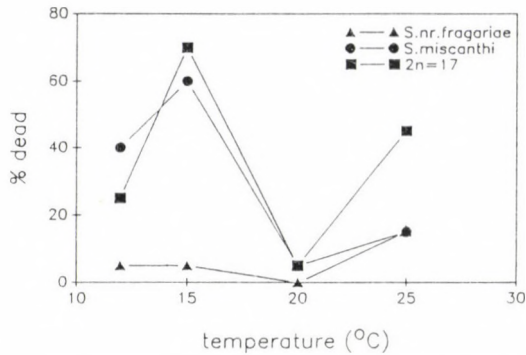
Fig.3. Percentage of aphids which died before 7 days of reproduction.

Within the temperature range of the experiments the three forms show different patterns with regard to their growth rates, number of offspring produced and offspring weight (Fig.2 a, c and d).

The most obvious distinction between the three forms can be seen in the growth rates. Sitobion nr fragariae increases rapidly until $20^{o}C$ and declines at $25^{o}C$. The "2n=17" has very similar growth rates at $20^{o}C$ and at $25^{o}C$ but appears to have peaked at $20^{o}C$, whereas S. miscanthi grows at steadily increasing rates up till $25^{o}C$. The three forms are affected by temperature in a similar way to one another with regard to the age at which they commence reproduction (Fig.2 b).

The offspring weight results (Fig.2 d) show a considerable drop at $15^{o}C$ which is unexpected. This drop and the very high mortality at this temperature (Fig.3) was probably caused by a factor other than temperature in the room used for the $15^{o}C$ experiment.

DISCUSSION

The extent of electrophoretic differences between S. nr fragariae and "S. miscanthi" (Table 1) is indicative that these two are separate species. "2n=17" however, differs from "S. miscanthi" at only 8 % of the tested loci and we regard this as insufficient evidence for assigning them to two species. We regard "2n=17" to be a chromosomal race of S. miscanthi. Karyotypes of the three forms (Fig.1) show that it is likely that the long autosome of "2n=17" is a result of the fusion of two autosomes. Thus it is probable that such a fusion occurred in the 2n=18 form of S. miscanthi giving rise to the 2n=17 form. The homozygous electrophoretic differences, however, suggest that the fusion may have occurred prior to the arrival of the aphids in Australia, i.e. in their Asian country of origin where sexual reproduction can occur. The relative abundance of "2n=17" in comparison with "S. miscanthi", its performance and the fact that it has been collected almost throughout the year, is indicative of adaptive advantages conferred on the 2n=17 form as a result of the genetic changes associated with the chromosomal fusion.

ACKNOWLEDGEMENTS

REFERENCES

Dixon, A.F.G. (1987) Parthenogenetic Reproduction and the Rate of increase of Aphids. In Minks A. K. and Harrewijn P.(editors) Aphids, Their Biology, Natural Enemies and Control Vol.2A pp. 269-287. Elsevier, Amsterdam.

Hales, D.F., Chapman, R.L., Lardner, R.M., Cowen R., Turak, E. (In press). Aphids of the genus Sitobion occurring on grasses in southern Australia. Journal of the Australian Entomological Society 29.

Hales, D.F. and Lardner, R.M. (1988). Genetic evidence for the occurrence of a new species of Neophyllaphis Takahashi in Australia (Homoptera: Aphididae). Journal of the Australian Entomological Society 27: 81-85.

KARYOTYPE VARIATION IN RELATION TO ESTERASE ACTIVITY AND
INSECTICIDE RESISTANCE IN MYZUS NICOTIANAE BLACKMAN

Yehia A. I. Abdel-Aal

Plant Protection Department, College of Agriculture,
Assiut University, Assiut 71516, EGYPT

Emmett P. Lampert; R. Michael Roe and Christopher D. Harlow

Department of Entomology, North Carolina State University,
Raleigh, NC 27695-7613, U.S.A.

ABSTRACT

The tobacco aphid, Myzus nicotianae Blackman has evolved
insecticide resistance, particularly, against organophospha-
tes. Resistance to malathion was always associated with chro-
mosome translocation and high hydrolytic activity towards
4-nitrophenolic and 1-naphtholic esters. A wide range
electrofocusing resulted in at least 12 esterase bands.
Esterase 3 (pI $\simeq$ 4.85) seemed to be a resistance associated
enzyme since it was not apparent in the susceptible aphids
which possessed normal chromosome configuration.

INTRODUCTION

The intensive chemical control of aphids, as well as the
breeding of aphid resistant crop plants has resulted in
several aphid species in the spread of adapted biotypes
(Weber, 1985). Recent recognition of the tobacco aphid, Myzus
nicotianae Blackman (1987) as a species separate from the

green peach aphid, M. persicae (Sulzer), could be a phenomenal example of the effect of host-plant affinity. Myzus nicotianae is presumably isolated from M. persicae by being a permanently parthenogenetic, tobacco-adapted form with its own morphometric characteristics. Although the usual color of M. nicotianae is green, a new red form started to appear in North Carolina (USA). Correlated with the appearance of this red form were increasing reports of insecticide failure.

Although resistance of aphid species to insecticides has become a world-wide problem, only in M. persicae its biochemical basis (Devonshire and Moores, 1982) and the molecular events responsible for this resistance (Field et al. 1989) have been identified. The aim of this study is to demonstrate the extent of esterase and karyotype variations in resistant and susceptible clones of M. nicotianae.

MATERIALS AND METHODS

Aphids

When the red form of the tobacco aphid was observed in North Carolina (USA), red and green specimens were collected from several locations and laboratory colonies were established. A total of eight cultures were established plus a reference green culture established in 1983, before the appearance of insecticide resistance. These nine cultures were maintained as separate clones.

Specimens from the above cultures were karyotyped and found to have 2n=12 and were frequently heterozygous for autosomal translocation (Blackman, 1987).

Bioassay

A slide-dip technique was used in which aphids were stuck by means of a double side adhesive tape to a microscope slide (15 apterae/slide). The slides were dipped in aqueous dilutions of commercial formulation of malathion for 30 seconds, and mortality was observed 24 hours later. At least five malathion concentrations and 3-4 replicates were used to generate the toxicity line from which the LC_{50} value was computed.

Esterase assay

Acetates and propionates of 4-nitrophenol and 1-naphthol were synthesized from the corresponding acid anhydride and phenol in the presence of sulfuric acid as a catalyst. 1-naphthyl acetate was used as a substrate to screen for the general carboxylesterase activity in the nine standard cultures using Fast Blue B salt as a dye coupler. The detailed procedure was described by Devonshire (1975).

For the comparison between Clayton (old) and Duplin red and green, esterase activity towards 4-nitrophenolic and 1-naphtholic esters was assayed at 30° by monitoring the release of 4-nitrophenol and 1-naphthol at 400 and 307.6 nm, respectively.

Electrofocusing

Thirty apterous adults from each clone were homogenized in distilled water containing 0.1% Triton X-100. The homogenate was centrifuged at 5,000 g for 2 min. and the supernatant was applied at 10 µl/lane of LKB Ampholine IEF PAGPLATE® (pH range

3.5-9.5). After focusing for 1.5 hours, the gel was stained for esterase bands using 0.13% (W/V) Fast Blue B salt and 0.02% (w/v) 1-naphthyl acetate in 0.2 M phosphate buffer, pH 6.0.

RESULTS

Interclonal variation and resistance associated esterases

Resistance ratios and carboxylesterase activity were correlated with aphid body color and chromosome rearrangement in the nine standard cultures (Table 1). From this table there appears to be a clear cut association between resistance to malathion, high esterase activity and chromosome transloca-tion, independent of the body color. This finding was also obtained from testing 22 additional field cultures (Harlow and Lampert, unpublished data).

Table 1   Esterase activity, resistance to malathion, and karyotype variation in M. nicotianae.

Collection site	Color/karyotype[a]	Activity[b]	R.R.[c]
Clayton (old)	G/N	0.18	1.00
Carteret	G/N	0.21	0.98
	R/T	0.50	4.33
Clayton	G/N	0.19	1.17
	R/T	0.52	3.96
Duplin	G/T	0.52	3.51
	R/T	0.51	3.83
Halifax	R/T	0.49	3.61
Lenoir	R/T	0.51	3.34

[a] G=Green, R=Red, N=Normal, T=Translocated. [b] umol 1-naphthyl acetate hydrolyzed/min·mg protein. [c] Resistance ratio based on a 24 ppm LC_{50} value for the first clone.

General esterase activity

The data obtained from testing the esterase activity towards the nitrophenolic and naphtholic esters in three representative clones are shown in Table (2). From this table, attention is called to the following points: (a) the phenolic esters were more reactive than the naphtholic esters; (b) the propionates were more ractive than the acetates; (c) Duplin red showed higher activity than Duplin green towards the naphtholic esters, while, the reverse held true towards the nitrophenolic esters; (d) 1-naphthyl acetate emphasized the interclonal esterase variation. The data in this table confirm the association between resistance and high esterase activity.

Table 2   Carboxylesterase activity towards 4-nitrophenolic (A) and 1-naphtholic (B) esters ($-O\overset{O}{\overset{\cdot\cdot}{C}}-R$).

Clone	Activity[a] (A), R =		(B), R =	
	CH_3	C_2H_5	CH_3	C_2H_5
Clayton (old)	1.92	2.57	0.12	0.50
Duplin (Red)	2.65	3.52	0.56	1.61
Duplin (Green)	3.07	3.69	0.36	0.96

[a] Specific activity in μMol substrate hydrolyzed/min·mg protein.

Resolved esterase activity

The esterase bands as resolved by electrofocusing are shown in Fig. 1. The pattern was almost identical for all but one esterase (E3). E3 seems to be a population marker since

it was not detected in the susceptible aphids. The same finding was also confirmed when all the standard cultures were examined (data not shown).

Figure 1. Tobacco aphid esterases, separated by electrofocusing, from Duplin red (lane 1); Duplin green (lane 2) and Clayton old (lane 3). E3 is a resistance associated esterase with pI of ≃ 4.85.
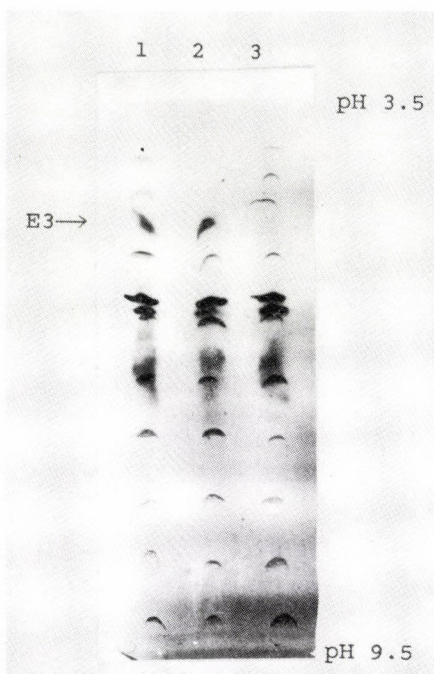
DISCUSSION

The incidence of resistance in M. nicotianae to insecticidal esters has been increasing. In this species and its presumed taxonomic origin, M. persicae, there is an association between insecticide resistance and general esterase activity and resistance associated esterase(s). Unlike M. persicae, however, loss of the sexual phase in the tobacco aphid makes it impossible to apply principles of population genetics to understand the role of insecticidal selective

pressure in the development of resistant biotypes. Structure rearrangement is common in aphid chromosomes (Brown and Blackman, 1988) particularly in those species which reproduce entirely by parthenogenesis. This may be followed by or associated with phenotypic plasticity and biochemical adaptation. Evidence available at present suggests that chromomome rearrangement itself is somehow involved in the increase of esterase activity and resistance beyond that found in cytologically normal clones of M. persicae (Blackman and Devonshire, 1978).

The elevated activity of total esterases and E3 in M. nicotianae is likely to have a causal implication in resistance. In support, DEF was found to synergize malathion toxicity against the resistant aphids (Harlow and Lampert, unpublished data). The data suggest that E3 and its related informational macromolecules form the foundation for improved detection of resistance (Brown and Brogdon 1987) and for unravelling the phyllogenetic relationship of M. nicotianae to other species of the genus Myzus.

322   ABDEL-AAL ET AL.

LITERATURE

Blackman, R.L., (1987) Morphological discrimination of a
    tobacco-feeding form from Myzus persicae (Sulzer)
    (Hemiptera: Aphididae), and a key to New World Myzus
    (Nectarosiphon) species. Bull. ent. Res. 77, 713-30.

Blackman, R.L. and Devonshire, A.L., (1978) Further studies
    on the genetics of the carboxylesterase regulatory system
    involved in resistance to organophosphorus insecticides in
    Myzus persicae (Sulzer). Pestic. Sci. 9, 517-21.

Brown, P.A. and Blackman, R.L., (1988) Karyotype variation in
    the corn leaf aphid, Rhopalosiphum maidis (Fitch), species
    complex (Hemiptera: Aphididae) in relation to host-plant
    and morphology. Bull. ent. Res. 78, 351-63.

Brown, T.M. and Brogdon, W.G., (1987) Improved detection of
    insecticide resistance through conventional and molecular
    techniques. Ann. Rev. Entomol. 32, 145-62.

Devonshire, A.L., (1975) Studies of the carboxylesterases of
    Myzus persicae resistant and susceptible to orga-
    nophosphorus insecticides, in "Proc. 8th British Insectic.
    Fungic. Conf.", Vol. 1, 67-73.

Devonshire, A.L. and Moores, G.D., (1982) A carboxylesterase
    with broad substrate specificity causes organophosphorus,
    carbamate and pyrethroid resistance in peach-potato aphids
    (Myzus persicae). Pestic. Biochem. Physiol. 18, 235-46.

Field L.M., Devonshire, A.L., Ffrench-Constant, R.H. and
    Forde, B.G., (1989) Changes in DNA methylation are asso-
    ciated with loss of insecticide resistance in the peach-
    potato aphid Myzus persicae (Sulz.). FEBS Letters, 243,
    323-7.

Weber, G., (1985) Population genetics of insecticide
    resistance in the green peach aphid, Myzus persicae
    (Sulz.) (Homoptera, Aphididae). Z. ang. Ent. 99, 408-21.

POLYPHENISM AND HOST-PLANT PREFERENCE IN THE BLACK BEAN, *APHIS FABAE* SCOP.

Jim Hardie and Jane Glascodine,

Agricultural and Food Research Council Link Research Group in Aphid Biology,

Department of Pure and Applied Biology, Imperial College at Silwood Park,

Ascot, Berks SL5 7PY, U.K.

ABSTRACT

Field-collected and laboratory-reared aphids were offered the choice of larvipositing (parthenogenetic adults) or settling (oviparae and males) on either a detached, mature spindle leaf (*Euonymus europaeus*) or a germinating tick bean (*Vicia faba*). Alate fundatrigeniae showed no distinct preference for bean or spindle while the majority of other adult females (fundatrices, apterous fundatrigeniae, apterous and alate exules) larviposited on bean. Gynoparae showed a marked preference for larviposition on spindle, oviparae preferred to settle on spindle while males proved restless and preference could not be judged.

Host-plant selection for larviposition could be modified hormonally. During their first, second and fourth stadia, gynoparae were reared on beans treated with juvenile hormone I or the juvenile hormone mimic, kinoprene. The resulting adults, which were devoid of any overt larval characters, showed differences in host-plant preference from untreated and solvent-treated controls. This finding suggests that juvenile hormone may have a role in alternative polyphenism associated with heteroecy i.e. the differences in host plant preference shown by alate exules and gynoparae.

INTRODUCTION

The dual-discrimination theory of host selection by aphids proposes that chemosensory stimuli are detected as both plant species-specific, flavour cues as well as nutritional cues which indicate the physiological condition of the plant (Kennedy and Booth, 1951; 1954). The extent to which either of these

cues are utilized by heteroecious aphids in selecting summer or winter hosts
may differ with species (Dixon, 1985) and the associated studies have,
necessarily, been mainly concerned with migrating forms. There have been no
systematic investigations of alternative-host preference for each of the
various morphs occurring in the heteroecious life cycle, indeed information on
other forms is extremely limited (e.g. Marrkula and Myllymaki, 1963). In
previous reports a simple primary versus a secondary host-plant preference
test revealed differences between the summer and autumn migrants of *Aphis
fabae* (Hardie, 1980; 1981). The present paper extends these tests to other
clonal morphs and to some field-collected forms.

　　Significant changes in host selection were shown to occur when autumn
migrants of *A. fabae* were treated topically with juvenile hormone (Hardie,
1981). Treated gynoparae found the secondary host to be a more acceptable
site for larviposition than did control aphids. As in other insects, juvenile
hormone controls metamorphosis and the "adult" aphids tested after treatment,
although capable of parturition, retained some larval characters. Since the
same study showed that larval gynoparae displayed a preference for the summer
host, it was possible that the hormone-induced change in "adult" gynoparae was
due to an effect on successive (i.e. larval-adult) rather than on alternative
(i.e. adult or single stadium) polyphenism. The present paper attempts to
reveal an effect of juvenile hormone on alternative polyphenism which could
offer a physiological explanation of the differences between summer and autumn
migrant host preferences.

MATERIALS AND METHODS

Insects:- Fundatrices and apterous and alate fundatrigeniae were collected
from spindle trees (*Euonymus europaeus*) at Silwood Park. These aphids could
be distinguished from *Aphis euonymi* but could only be initially identified as
belonging to the *A. fabae* group (see discussion). The clone of *A. fabae* sensu
stricto had been cultured in the laboratory since 1946 (Kennedy and Booth,
1951). Apterous and alate exules were reared in isolated or crowded, long-day
(LD 16:8) conditions at 15 C. Gynoparae, males and oviparae were induced by

short days (LD 12:12). All morphs were reared on tick beans (*Vicia faba*)
except one series of oviparae which were fed on detached spindle leaves.

Host preference experiments:- The experimental technique has been described
previously (Hardie, 1980; 1981). Single, adult aphids or groups of ten
oviparae were placed in a gauze-topped glass tube which was inverted over a
germinating tick bean and a detached, mature spindle leaf with its petiole
buried in damp sand. Although neonatal larvae are relatively sessile, the
spindle leaf and bean were separated to restrict any larval movement from one
to the other. Larviposition preference was judged when five or more progeny
had been deposited and the mother was recorded as having produced the majority
of this first-born batch of progeny on spindle or bean. Settling preference
of the sexual forms was scored after 48 h. The age of field-caught adults was
unknown but laboratory-reared insects were tested on the second day after
final moult.

Hormone treatment:- Germinating tick bean stipules (growing points removed)
were dipped into solutions of 0.0001% juvenile hormone I (Calbiochem),
0.0001%, 0.001% or 0.01% kinoprene (2-propynyl(E,E)-3,7,11-trimethyl-2,4-
dodecadienoate; Zoecon Corporation) or 1% aqueous acetone as a control. The
stipules were allowed to dry before two adult, gynopara-producing females were
placed on them. After 24 h these adults were removed and any larvae
(presumptive gynoparae) deposited were left on the treated stipules. The
aphids were transferred to newly treated bean stipules every two or three days
except during their third stadium when they were placed on clean beans. The
third stadium is most sensitive to the juvenilizing effects of juvenile
hormone and juvenile hormone mimics (see Hardie, 1984). Young adults, which
were morphologically identical to untreated gynoparae (i.e. showed no external
signs of juvenilization or apterization) were tested for larviposition
preference.

RESULTS

The percentage of the different morphs larvipositing or settling on either bean or spindle are shown in Figure 1. A distinct preference for bean is seen in fundatrices, apterous fundatrigeniae and apterous and alate exules while gynoparae preferred to larviposit on spindle. The field-collected alate fundatrigeniae did not show a preference but oviparae, reared on bean or spindle, preferred to settle on spindle although some were not on either plant. Significant differences were found between the larviposition site of the following groups {fundatrices, apterous fundatrigeniae, apterous exules, alate exules} {alate fundatrigeniae} {gynoparae} (p<0.05, Chi-squared test). Males did not settle for any length of time so it was impossible to discern their host preference.
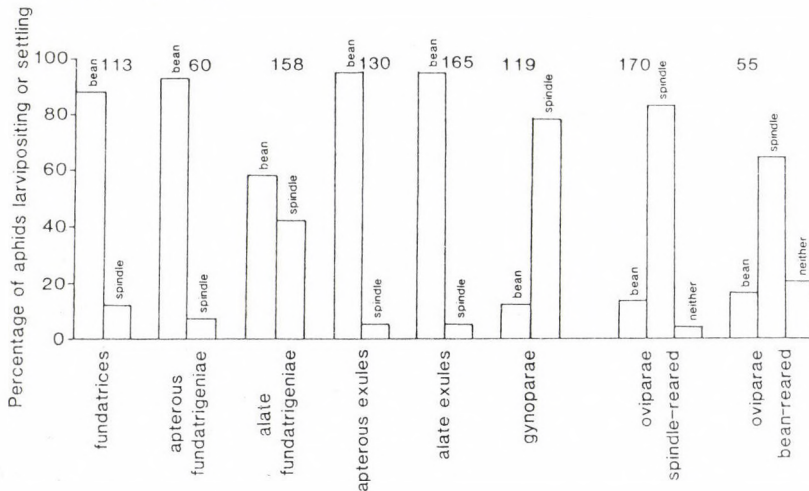
FIGURE 1. Larviposition and settling (oviparae) preferences of the female morphs shown as percentages of aphids producing either the majority of their first-born progeny, or settling after 48 h, on bean or spindle. Numbers indicate insects tested.

The effect of juvenile hormone I and kinoprene treatment on larviposition site selected by gynoparae is shown in Figure 2. Solvent-treated controls behaved similarly to untreated insects (cf. Figure 1). Juvenile hormone I and the lowest concentration of kinoprene showed an apparent increase in the acceptability of bean as a larviposition site but these results were not

significantly different from the acetone controls. However, the two higher
concentrations of kinoprene showed significant increases in the numbers
larvipositing on bean (p<0.05, Chi-squared test).
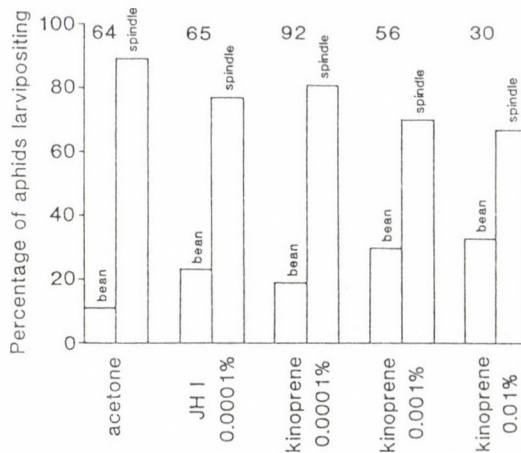
FIGURE 2.   Larviposition selection by control and juvenile hormone or
kinoprene treated gynoparae.   Numbers indicate insects tested.

DISCUSSION

The newly germinating tick bean and the detached spindle leaf offer plant
material of different physiological condition but if detachment induces
premature scenescence both would be expected to be acceptable to aphids
(Kennedy and Booth, 1954).   The surface area of the plant tissue also differs
but the fact that the summer and autumn migrants show opposite preferences
demonstrates that this factor is not important in determining insect choice
(see Hardie, 1981).

Three sub-species of morphologically similar, heteroecious, black aphids
are included in the A. fabae species-complex found on spindle trees in the
spring (Muller, 1982).   As these sub-species can only be separated by their
secondary host-plant preferences (Muller, 1982; 1986; Theime, 1987) it was
only possible to identify the spindle-caught aphids used in this study as A.
fabae s. str. if they larviposited on bean.   By far the majority of aphids
overwintering on spindle at Silwood Park are A. fabae s. str. (M.E. Cammell

pers. comm.; and see Cammell et al., 1989). This statement is supported by the observations that only a few fundatrices and apterous fundatrigeniae deposited young on spindle (in a similar proportion to the laboratory-reared exules). The alate fundatrigeniae were taken from the same population of aphids but spindle and bean provided equally suitable sites for larviposition. In the field, these migrants have been seen to recolonize spindle (Kennedy et al., 1950).

The results further indicate that although the first two apterous generations occur on the primary host in the field they are not only capable of reproducing on the secondary host but show a preference for it. This finding is in contradiction to the reported behaviour of spring generations of *Rhopalosiphum insertum* and *R. padi* where fundatrices refused or were reluctant to reproduce on oats (Orlob and Arny, 1960; Orlob, 1961, Markkula and Myllymaki, 1963). In addition, the finding does not appear to lend support to the fundatrix-specialization hypothesis for the evolution of heteroecy. This theory hinges on the primary host being an obligatory part of the life cycle because the fundatrix is evolutionarily constrained to the ancestral, woody host (see Moran, 1988). The larval fundatrix is certainly constrained to the natal plant by her mother's choice of larviposition site and, as an adult, by her apterous morphology although apterous *A. fabae* (probably fundatrigeniae and later generations) are known to move from spindle to nearby secondary hosts in spring (Kennedy et al., 1950). However, the current work does not include observations on feeding preferences for larval fundatrices. Although *A. fabae* oviparae could be reared on primary or secondary host material, the results would support an ovipara-specialization theory as adult, virgin females prefered to settle on spindle irrespective of larval nutrition. It is generally accepted that present day aphids are descended from sexual ancestors and in *A. fabae* gynoparae are the obligatory link between secondary and primary hosts with the spring migration to secondary hosts appearing more facultative.

The other parthenogenetic morphs used in the present study were clonal. They indicate that the autumn migration to the primary host is achieved by a

distinct change in host preference and that this preference is due more to plant flavour than nutrient composition. Similar observations were made for *R. padi* (Dixon, 1971) although previous work on the same clone of *A. fabae* had indicated a large nutrient contribution (Kennedy and Booth, 1951; 1954). This contradiction may arise because the latter authors used sugar beet as the secondary host choice, beet appears to be less attractive than bean (see Hardie, 1980).

Continuous treatment of gynoparae with kinoprene resulted in bean becoming significantly more attractive as a larviposition site while not interfering with metamorphosis, at least at the morphological level. This result suggests that the hormone mimic is affecting the behavioural phenotype associated with alternative rather than successive polyphenism. Juvenile hormones and their mimics are known to have a variety of effects on photoperiodically controlled polyphenism in *A. fabae* including sexual/asexual and alate/apterous morph determination (Hardie, 1984). The present results extend these findings and indicate that juvenile hormone may also play a role in controlling the expression of host-plant preference associated with heteroecy.

REFERENCES

Cammell, M.E., Tatchell, G.M. and Woiwod, I.P. (1989) The pattern of abundance of the black bean aphid, *Aphis fabae* Scop., in Britain. J.appl. Ecol. In press.

Dixon, A.F.G., (1971) The life-cycle and host preferences of the bird cherry-oat aphid, *Rhopalosiphum padi*, L., and their bearing on theories of host alternation in aphids. Ann. appl. Biol., 68, 135-147.

Dixon, A.F.G., (1985) Aphid Ecology. Blackie Publ., Glasgow, 157 pp.

Hardie, J., (1980) Reproductive, morphological and behavioural affinities between the alate gynopara and virginopara of the aphid, *Aphis fabae*. Physiol. Ent., 5, 385-396.

Hardie, J., (1981) The effect of juvenile hormone on host-plant preference in the black bean aphid, *Aphis fabae*. Physiol. Ent., 6, 369-374.

Hardie, J., (1984) A hormonal basis for the photoperiodic control of polymorphism in aphids. In Photoperiodic Regulation of Insect and Molluscan Hormones. Ciba Foundation Symposium 104. Pitman Press Publ., Bath. pp.240-252.

Kennedy, J.S. and Booth, C.O., (1951) Host alternation in *Aphis fabae* Scop. I. Feeding preferences and fecundity in relation to age and kind of leaves. Ann. appl. Biol., 38, 25-64.

Kennedy, J.S. and Booth, C.O., (1954) Host alternation in *Aphis fabae* Scop. II. Changes in the aphids. Ann. appl. Biol., 41, 88-106.

Kennedy, J.S., Ibbotson, A. and Booth, C.O., (1950) The distribution of aphid infestation in relation to leaf age I *Myzus persicae* (Sulz.) and *Aphis fabae* Scop. on spindle trees and sugar-beet plants. Ann. appl. Biol., 37, 651-679.

Markkula, M. and Myllymaki, S., (1963) Biological studies on cereal aphids, *Rhopalosiphum padi* (L.), *Macrosiphum avenae* (F.), and *Acyrthosiphum dirhodum* (Wlk.) (Hom.,Aphididae). Ann. agric. Fenn., 2, 33-43.

Moran, N.A., (1988) The evolution of host-plant alternation in aphids: Evidence for specialization as a dead end. Am. Nat. 132, 681-706.

Muller, F.P., (1982) Das problem *Aphis fabae*. Z. angew. Ent., 94, 432-446.

Muller, F.P., (1986) The role of subspecies in aphids for affairs of applied entomology. J. appl. Ent., 101, 295-303.

Orlob, G.B., (1961) Biology and taxonomy of cereal and grass aphids in New Brunswick (Homoptera: Aphididae). Can. J. Zool., 39, 495-502.

Orlob, G.B. and Arny, D.C., (1960) Transmission of barley yellow dwarf virus by different forms of the apple grain aphid, *Rhopalosiphum fitchii* (Sand.). Virology, 10, 273-274.

Theime, T., (1987) Members of the complex of *Aphis fabae* Scop. and their host plants. In Population Structure, Genetics and Taxonomy of Aphids and Thysanoptera. SPB Academic Publishing, The Hague, pp. 314-323.

ROLE OF FARNESENE ISOMERS AND OTHER TERPENOIDS IN THE DEVELOP-

MENT OF DIFFERENT MORPHS AND FORMS OF THE APHIDS APHIS FABAE

AND MYZUS PERSICAE

Adriaan M. van Oosten[r], Jirí Gut[r], Paul Harrewijn[*], Paul G.M.
Piron[*]

[r] TNO Division of Technology for Society, P.O. Box 217, 2600 AE
Delft, the Netherlands
[*] Research Institute for Plant Protection, P.O. Box 9060, 6700 GW
Wageningen, the Netherlands

ABSTRACT

Different forms of the aphid Myzus persicae contain differ-
ent amounts and ratios of (E)-ß-farnesene and α-farnesene iso-
mers.

This focussed our attention on the role of farnesene isomers
in morph and form determination in aphids. External application
of 100 ng of (E)-ß-farnesene, a quantity not exceeding the
amount naturally occurring in a mature aphid can cause thanato-
sis or kill aphids immediately. This is probably caused by
stimulation of neurotransmission. Aphid populations are always
exposed to certain doses of farnesenes dependent on population
density, e.g. released by crowded aphids. This raised the ques-
tion whether sublethal doses of (E)-ß-farnesene or other farne-
sene isomers could affect developmental processes in aphids.
Although these compounds are not supposed to be precursors of
juvenile hormone, they are synthesized via the mevalonic acid
pathway and are present especially in symbionts and embryos of
the aphid M. persicae in sublethal quantities. This opens up the
possibility of feed-back systems governing production of inter-
nal messengers including JH III. An example is the inhibition of
growth and development of Aphis fabae and M. persicae after
external application of (E,E)-α-farnesene (less than 100 ng).
This isomer is characteristic for gynoparae and males of these
aphid species.

Already in 1963 Von Dehn found an inhibition of wing produc-

tion in <u>A</u>. <u>fabae</u> after external application of farnesol, also produced via the mevalonic acid pathway, which probably is a precursor of juvenile hormone III.

In repeating these experiments we found an extremely high mortality even with greatly diluted solutions of farnesol in acetone or isopropylalcohol, which was not mentioned by Von Dehn. This effect may be attributed to the fact that commercially available farnesol consists of a mixture of farnesol isomers, of which (E,E)-farnesol is only one out of four components and the only one that can be transformed to JH III.

The effects of mevalonic acid metabolites on morph-related differentiation are in concordance with chromatographic determination of farnesene isomers in different forms of <u>M</u>. <u>persicae</u>.

INDTRODUCTION

Both the amounts present and the ratio of isomers of (E)-ß-farnesene, the alarm pheromone of aphids, are related to morphs and forms of aphids (Gut and Van Oosten, 1985). External application of sublethal doses of (E)-ß-farnesene resulted in reduced wing production, growth and reproduction of <u>Myzus</u> <u>persicae</u> (Sulzer) (Gut et al., 1987). The reports quoted above provide evidence that (E)-ß-farnesene can evoke hormonal effects in aphids and possibly also in other insects. This was confirmed by the work of Mauchamp and Pickett in 1987.

Prolonged exposure of <u>Aphis</u> <u>fabae</u> Scopoli to vapour of technical (E)-ß-farnesene induced inhibition of development and reproduction.

Farnesenes are synthesized via the mevalonic acid pathway. They are not supposed to be precursors of Juvenile hormone, which, however, does not exclude the possibility of feed-back regulation of the hormonal system of aphids with farnesenes, either externally applied or produced in the aphids as a by-product of cholesterol synthesis. Already in 1963 Von Dehn found an inhibition of wing production in <u>A</u>. <u>fabae</u> after external application of farnesol, also produced via the mevalonic acid pathway, which is probably a precursor of juvenile hormone III.

This focussed our attention on a comparison of the effects of farnesenes and farnesols on aphids that had been reared under short-day and long-day conditions. As substantial amounts of farnesene isomers such as (E,E)-α-farnesene are found in sexual forms we included treatments with synthetic farnesenes mainly consisting of (E,E)-α-farnesene. A number of terpenoid end products may be synthesized via the mevalonic acid pathway. Some of these may have a function in a possible multivalent feed-back regulation of messengers and hormones in aphids and the effects of a few purified isoprenoids upon developmental processes in two biotypes of the aphid <u>M</u>. <u>persicae</u> were investigated.

MATERIALS AND METHODS

Aphids

Stock cultures of <u>M</u>. <u>persicae</u> and <u>A</u>. <u>fabae</u> were maintained on chinese cabbage and broad bean plants in a climatic room, with long-day (16 h photoperiod, $20 \pm 1°$ C) and short-day (10 h photoperiod, $17/14 \pm 1°$ C) conditions, rH was between 60 and 70%.

Artificial diets

Chemically defined diets were prepared for <u>M</u>. <u>persicae</u> as reported earlier (Harrewijn, 1983). Growth and development on these diets equals that on their optimal host plants. Aphids on diet sachets were kept in cabinets with the same long-day and short-day conditions as mentioned above.

Origin of synthetic compounds

Technical (E)-ß-farnesene was synthesized according to the method of Dawson et al. (1982) and after redistillation was 95% pure. Technical (E,E)-α-farnesene (containing at least 49% of this compound) was synthesized according to the same method but modified with respect to the catalyst and temperature. Purified (E,E)-α-farnesene was obtained from apples cv. Granny Smith according to the method of Murray (1969). Farnesol was obtained from Aldrich Company (F20-3 mixture). Dolichol and squalene were obtained from Sigma (resp. nrs D 4511 and S 3626).

Determination of farnesene isomers

If necessary the composition of the alarm-pheromone of un-treated and treated aphids was estimated as previously reported (Gut and Van Oosten, 1985).

Topical application of farnesenes and farnesol

0.1% and 1.0% solutions of (E)-ß-farnesene, (E,E)-α-farne-sene and farnesol were made in acetone and in isopropylalcohol. 0.01 µl of these solutions were applied with a very fine paint-brush to the dorsum of L_1-stage offspring of winged virginoparae.

Treatments with squalene and dolichol

Pre-apterae and pre-alatae of M. persicae biotype M_2 and M_3 were confined to artificial diets with and without squalene in groups of 10 aphids per cage of 16 mm diameter with a diet sachet on top. 10 mg of squalene was mixed with 20 mg Tween-20 and subsequently homogenized in 5 ml of artificial diet. Blanks were made by dissolving 20 mg of Tween-20 in 5 ml of diet. Sachets containing 0.3 ml diet were replaced every third day.

Dolichol was dried with pure N_2-gas, redissolved in acetone (500 mg in 0.5 ml) and dorsally applied to pre-apterae of M. persicae with a micro-pipette. To that end the aphids were fixed in a small vacuum-operated table that can be orientated under a stereomicroscope and was cooled by perfusion of an ethanol/water mixture to +5° C. After treatment the aphids were kept on the artificial diet 148 in groups of 3 or 4 per cage.

RESULTS

Application of pure (E)-ß-farnesene and technical preparations of (E,E)-α-farnesene

Farnesenes are strongly hydrophobic compounds and need to be dissolved in organic media prior to external application. Alt-hough the lowest mortality is induced by either acetone or iso-propylic alcohol, both cause 10-20% mortality in the blanks. In short-term experiments (E)-ß-farnesene stimulates development in A. fabae (Table 1). In untreated aphids maturation took at least 8 days at 20° C, whereas a single application of (E)-ß-farnesene

resulted in adult and reproducing apterae within 7 days. α-far-
nesene, however, exerted a different effect. First instar larvae
of A. fabae treated with isopropylic alcohol only developed
normally to apterae, depending on the crowding conditions.
Development of larvae, treated with (E,E)-α-farnesene, however,
was profoundly affected both under long-day and short-day condi-
tions. About 50% of the long-day larvae reached maturity, alt-
hough only 5% produced one or a few offspring. None of the
short-day larvae reached adulthood, and eventually died between

Table 1   Daily offspring production of A. fabae treated with
          (E)-ß-farnesene.

Days after birth	double blank	isopropylic alcohol	(E)-ß-farnesene
7	0	0.2	1.3
8	4.0	1.7	3.8
9	4.6	1.6	4.4

8 and 10 days after birth in their second or third larval stage.
These moribund larvae showed a reddish colouration, typical for
larvae developing into gynoparae. Whatever significance this may
have, one should realize that production of gynoparae normally
only occurs after two generations of short-day conditions.

    Treatments of adult individuals with (E,E)-α-farnesene
strongly reduced reproduction. Even under crowded conditions, no
larvae of treated mothers developed into alatae. The number of
offspring produced by the F_1 generation amounted to only one
third of the untreated aphids, resulting in a 65% reduction in
numbers of individuals in the F_2 generation.

Treatments with farnesol

    In contrast to the experiments of Von Dehn (1963), farnesol
did not completely inhibit wing formation in A. fabae. As Table
2 shows, however, mortality of farnesol-treated larvae is as
high as 87% after one week that is before the termination of
their normal development.

    Summarizing: sesquiterpenoids related to (E)-ß-farnesene can
cause a high mortality among larvae of both A. fabae and M.

persicae. The action of (E,E)-α-farnesene is slower than that of farnesol: usually α-farnesene-treated larvae will go through three or more moults before they eventually die.

Table 2   % mortality (after one week) of long-day-reared $\underline{A}$. $\underline{fabae}$ treated with farnesol and (E)-β-farnesene.

Morphs	Treatment		
	isopropyl-alcohol	farnesol	(E)-β-farne-sene
L_1 stage from untreated virginoparous apterae	0	87	
L_1 stage from untreated virginoparous alatae	0	75	64
desc. of treated vir-ginoparous apterae	0	0	
desc. of treated vir-ginoparous alatae	0	0	43

Terpenoid end products of mevalonate metabolism

In this experiment pre-apterae and pre-alatae of two bio-types of $\underline{M}$. persicae were given access to diets in which the terpenoid end-product squalene was incorporated. As the aphids were not yet adult, reproduction usually did not start until 24 h after the treatments had begun (batch 1). As Table 3 shows, 2000 μg squalene per ml of artificial diet, which is biochemi-cally (although not necessarily physiologically) equivalent to 500 ng of the sesquiterpenoid end products, did not inhibit maturation and reproduction in biotype M_2. In apterae however, it reduced the production of winged morphs and the survival of the offspring. This effect is much more pronounced in M_3, where only 6% of the offspring reached adulthood. Most larvae remained for several days in the second or third stage until they eventually died. Some individuals developed into intermediate morphs. Al-though the pre-alatae of this biotype completed their wing dev-elopment, none of them started reproduction. The inhibition of the production of winged morphs is also seen in maternal treat-ment of short-day M_3 biotype. The remaining 24% of winged morphs may be gynoparae and males, but their small size also resulting

Table 3   Daily offspring and course of development of Myzus
          persicae treated with mevalonate metabolites. B =
          blank, tr = treatment

Batch no.	Biotype M₂						
	squalene (diet)				dolichol appl.		
	pre-apterae long day		pre-alatae long day		pre-apterae long day		
	B	tr	B	tr		B	tr
1	0.5	0.8	0.7	0.2		3.0	2.9
2	2.9	1.5	2.0	1.4		4.3	3.2
3	1.7	1.9	1.1	0.8		2.6	2.0
4	1.6	2.0	1.3	1.2		2.3	1.0
average reproduction	1.7	1.6	1.3	0.9		3.5	2.5
% survival (average)	100	71	98	100		100	100
average % of winged morphs	30	15	8	6		4	28

Batch no.	Biotype M₃						
	squalene (diet)				mothers squalene diet, offspring basic diet		
	pre-apterae long day		pre-alatae long day		pre-apterae short day		
	B	tr	B	tr		B	tr
1	0.8	0.8	–	–		3.2	–
2	3.3	0.6	–	–		3.4	2.6
3	1.0	0.0	–	–		2.8	1.8
4	2.2	0.5	2.6	–		3.0	3.0
average reproduction	1.8	0.5	2.6	0.0*		3.1	2.1
% survival (average)	88	6	100	0		93	82
average % of winged morphs	79	0	0	–		84	24

* all dead

from squalene treatment renders morph establishment difficult
unless the chromosomes are examined, which is now under way.

Dolichol with its C_{90} configuration was topically applied at
a dose of 3 µg/aphid of 250 µg. After treatment the individuals
were kept under low crowding conditions. All aphids survived and

the proportion of winged morphs among the dolichol-treated
aphids was much higher than in the blanks.

Table 4   Presence of farnesene isomers in offspring of apterous
          M. persicae treated with squalene (ng/aphid of 250 µg)

Biotype	farnesene isomer	Haemolymph		Homogenized (after rinsing)	
		basic diet	squalene diet	basic diet	squalene diet
M$_2$	(E)-ß-farnesene	8.3	2.6	5.4	11.5
	(Z,E)-α-farnesene	0.2	0.09	0.2	0.4
M$_3$	(E)-ß-farnesene	5.5	2.0	6.9	7.5
	(Z,E)-α-farnesene	0.2	0.1	0.3	0.3

Table 4 demonstrates that the amount of (E)-ß-farnesene
present in haemolymph excreted by the siphunculi is much lower
in squalene-treated adult offspring (F$_1$ generation) from aptrous
mothers, suggesting that the proportion of endogenously circula-
ting farnesenes is reduced. This obviously does not hold for the
next (F$_2$) generation, as homogenised individuals (including all
the embryos) showed an even higher amount of farnesene in squa-
lene-treated individuals. It may be noted, that we previously
found a lower proportion of (E)-ß-farnesene in haemolymph of
apterae-producers (such as winged virginoparae) than in alatae-
producers, and a higher amount of this compound in apterous vir-
ginoparae that give birth to a high pro-portion of alatae, sug-
gesting that squalene interferes with the regulatory mechanism
of the activity of internal farnesenes.

DISCUSSION

Our results demonstrate that related sesquiterpenoids may
exert different effects upon aphids. Although low doses of (E)-
ß-farnesene (vapour or application) may affect the neurophysio-
logical system, as in a behavioural reaction to the alarm pher-
omone, the effects of higher doses could be based upon feed-back
reactions (Gut et al., 1987). High doses of (E,E)-α-farnesene
evoke effects that probably go beyond any regulation present in

nature. Still, some of the moribund larvae showed characteristics of sexuals, and we previously demonstrated that winged males and gynoparae always contain relatively high amounts of (E,E)-α-farnesene.

At first, we could not easily explain the high mortality after farnesol treatment, or why our results differed from those of Von Dehn (1963). Moreover, farnesol application did not completely inhibit wing formation in virginoparae. It should be noted, however, that the farnesol we used consisted of four isomers, of which mainly the (E,E)- and the (Z,E)-isomer were present. The (E,E)-isomer is a precursor of JH III. A hormonal effect of the (Z,E)-isomer on insects has been reported, but the (Z,Z)- and (E,Z)-isomers did not have such activity (Yamamoto and Jacobson, 1962). In addition, aphid biotype and conditions of Von Dehn's experiments may have been different from ours.

Farnesol can be transformed into JH III. Although their mode of action can partly be based upon a feed-back regulation in mevalonic acid metabolism, the excess of farnesol is probably transformed into JH III. Farnesenes cannot be transformed into JH III, although they may affect the activity of the endocrine system by interfering with key enzymes of the mevalonic acid pathways or exert an effect upon the target of JH III or messengers involved in the production of apterae.

Both (E,E)-α-farnesene and the isoprenoid end product squalene retarded development and inhibited moulting, though α-farnesene exerted its effect mainly under short-day regimes. (E,E)-α-farnesene seems to be related with the origin of sexual forms in <u>M</u>. <u>persicae</u> and <u>A</u>. <u>fabae</u> (Gut et al., 1987). Winged males and gynoparae always contain relatively high amounts of (E,E)-α-farnesene. At this moment we cannot say whether exogenous α-farnesene reduces production or activity of endogenous α-farnesene, or whether it affects the presence of (E)-ß-farnesene or activates JH III (Poulter, 1975).

An explanation of the effect of squalene could be an end product inhibition of a rate-limiting step in mevalonate metabolism (see Fig. 1, and Brown and Goldstein, 1980). Inhibition of HMG CoA reductase would result in a reduced JH III production

VAN OOSTEN et al.

and the occurrence of sexuals. Dolichol, also an product of prenyl transferase, may exert such an effect, whereas squalene seems to inactivate at least one site of farnesene production in casu the one from which farnesenes are released into the haemolymph, simulating a fast acting endocrine system. When steroids and farnesenes are both produced by symbionts (Gut et al., 1987) squalene treatment may prevent moulting by inhibition of sterole (and ecdysone) production.

Figure 1. The biosynthetic pathways of isoprenoid end products of the mevalonate metabolism with possible feedback interactions in aphids
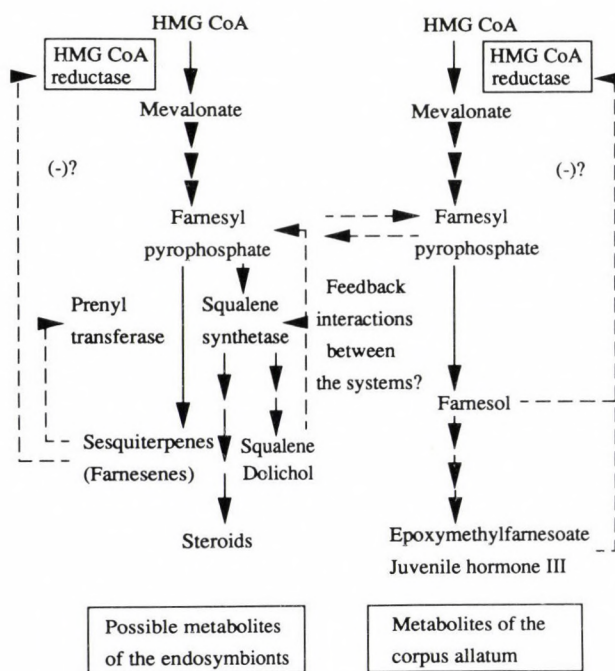
It is intriguing that α-farnesene affects development of short-day individuals, which have a supposed reduced JH III production by the corpus allatum. Aphids under this condition are already deprived of part of their production of mevalonate

metabolites, and the targets left that can produce farnesenes and steroids (symbionts oenocytes?) may thus be more valuable. However, a direct interference with the target of internal messengers should not be overlooked.

There are several reports of the regulation of the endocrine activity in insects via feed-back systems (Edwards et al., 1983). Although farnesenes are not mentioned in this study, comparable feed-back systems exist in the regulation of choles-terol production of mammalial cell systems (Brown and Goldstein, 1980; Zakharová, 1988). Evidence has been provided, however, on the regulation of related terpenoids in plant cell systems. Ex-amples may be the regulation of the biosynthesis of α-farnesene in apples (Huelin and Coggiola, 1970), the regulation of chloro-phyll biosynthesis in plants (Rüdiger and Benz, 1984) and the regulation of carotenoid biosynthesis (Bramley, 1985).

Experiments with ^{14}C-labeled mevalonic acid and admini-stration of intermediate substrates are now under way to esta-blish the site of synthesis of farnesenes and other isoprenoid end products and their mode of action.

REFERENCES

Bramley, P.M., (1985). The <u>in</u> <u>vitro</u> biosynthesis of carotenoids. Adv. Lipid Res., 21, 268.

Brown, M.S. and Goldstein, J.L., (1980). Multivalent feedback regulation of HMG CoA reductase, a control mechanism coordi-nating isoprenoid synthesis and cell growth. J. of Lipid Res. 21, 505-517.

Edwards, J.P., Bergot, B.J. and Staal, G.B., (1983). Effects of three compounds with anti-juvenile hormone activity and a juvenile hormone analogue on endogenous juvenile hormone levels in the tobacco hornworm, <u>Manduca</u> <u>sexta</u>. J. Insect Physiol. 29(1), 83-89.

Gut, J. and Van Oosten, A.M., (1985). Functional significance of the alarm pheromone composition in various morphs of the green peach aphid, <u>Myzus</u> <u>persicae</u>. Entomol. exp. & appl. 37, 199-204.

Gut, J., Harrewijn, P., Van Oosten, A.M. and Van Rheenen, B., (1987). Additional function of alarm pheromones in devel-opmental processes of aphids. Med. Fac. Landbouww. Rijks-univ. Gent 52(2a), 371-378.

Huelin, F.E. and Coggiola, J.M., (1970). Superficial scald, a functional disorder of stored apples. VII - Effect of ap-plied α-farnesene, temperature and diphenylamine on scald

and the concentration and oxidation of α-farnesene in the fruit. J. Scient. Food Agric. 21, 584-590.

Mauchamp, B. and Pickett, J.A., (1987). Juvenile hormone-like activity of (E)-ß-farnesene derivatives. Agronomie 7(7), 523-529.

Murray, K.E., (1969). α-Farnesene: isolation from the natural coating of apples. Aust. J. Chem. 22, 197-204.

Poulter, C.D., Satterwhite, D.M. and Rilling, H.C., (1975). Prenyltransferase. The mechanism of the reaction. J. Amer. Chem. Soc. 98(11), 3376-3377.

Rüdiger, W. and Benz, J., (1984). Synthesis of chloroplast pigments in chloroplast biogenesis. Ellis, R.J. (ed.), Elsevier, Amsterdam, p. 225-244.

Von Dehn, M., (1963). Hemmung der Flügelbildung durch farnesol bei der schwarzen Bohnenlaus, _Doralis_ _fabae_ Scop. Naturwissenschaften 17, 578.

Yamamoto, R.T. and Jacobsen, M., (1962). Juvenile hormone activity of isomers of farnesol. Nature 195, 908-909.

Zakharová, O.S., (1988). Mevalonic acid and isoprenoids as regulators of proliferation in mammalian cells. (in Russian). Usp. Sovrem. Bio. 106, 442-453.

ENDEMISM IN THE APHIDOIDEA FAUNA OF THE INDIAN REGION

A. K. Ghosh,

Zoological Survey of India, 27 Jawaharlal Nehru Road,

Calcutta 700 016, India

ABSTRACT

Out of a total of 214 genera and 801 species, about 23% of
the genera and 53.6% of aphidoid taxa are recorded as endemic to
the Indian region. The nature of endemism, evolution and distribu-
tion of endemic taxa is discussed.

INTRODUCTION

The Indian Region can be classified following Udvardy (1975)
into two major Realms, 13 biogeographic Provinces and 5 Biomes
(Table 1). The diversity of terrestrial ecosystem in the region
has long been known to contribute to the unique biota. Aphidoids
have been recorded in the region from wide variety of host plants
(Raychaudhuri ed. 1983, Agarwala and Ghosh, M.R. 1985). The fauna
of the region is known to be made up of elements from the Oriental,
Ethiopean, Malayan, Palaearctic and Nearctic regions plus a high
percentage of endemic elements. In the present paper, the endemism
of the aphid fauna of the Indian region is discussed.

TABLE 1

Biogeographical Classification of Indian Region

Realm	Biomes	Provinces
1. PALAEARCTIC	1. Mixed Mountain and Highland system	1. Himalayan Highlands
2. INDOMALAYAN	1. Tropical Humid Forest	1. Malabar Rain Forest
	2. Tropical Dry or Deciduous Forest	2. Ceylonese Rain Forest
	3. Warm Deserts or Semi Desert	3. Bengalian Rain Forest
	4. Mixed Island System	4. Indus Ganges Monsoon
		5. Burma Monsoon Forest
		6. Mahanadian
		7. Coramandal
		8. Ceylonese Monsoon Forest
		9. Decan Thorn Forest
		10. Thar Desert
		11. Laccadive Islands
		12. Andaman Nicobar Island

ENDEMISM IN THE APHIDOIDEA OF THE INDIAN REGION

Endemism and rarity have been interpreted by biologists in more than one way. Endemic taxa need not necessarily be rare. In the case of higher plants, a high degree of endemism has been correlated with the age and isolation of an area and with the diversification of its habitats. These factors may play key roles

both in evolution leading to new endemics and the survival of relic
endemics (Cain, 1944; Kruckeberg and Rabinowitz, 1985).
One can also consider the taxon cycle dealing with faunal groups
(ants, birds) which is interpreted as a modern version of the
idea that insular species have an evolutionary progression of
stages (Ricklefs and Cox, 1978, Kruckeberg and Rabinowitz, 1985).

The aphidoid fauna of Indian region consists of 214 genera
and 801 species (based on published record up to 1988); of these
51 genera (23%) and 429 species (53%) appear to be endemic. Most
of these endemic taxa are regional or local; this association
however, needs testing by collecting in all regions, especially
those area with similar host-plants.

Some distinctive feature, however, tend to emerge. At the
generic level, the subfamily Anoeciinae, Pterocommatinae and
Chaitophorinae do not exhibit any endemism (Agarwala and M.R.
Ghosh, 1985 mentioned one endemic genus in the Anoceiinae by
error), but 75 and 78% of the species in the subfamilies
Anoeciinae and Chaitophorinae are endemic. The largest number
of endemic genera occurs in the Aphidinae (27 of 106), followed
by Drepanosiphinae (10 of 31), Hormaphidinae (6 to 24), Pemphi-
ginae (4 of 20), Lachninae (3 of 14) and Greenideinae (1 of 10).
Although the subfamily Greenideinae is known to have largely
evolved in South-East Asia (as have the Anoeciinae and the
Hormaphidinae) the level of endemism at the generic level remains
surprisingly low; at the species-level, however, the same high
level (78%) of endemism (as noted in the Anoeciinae and the
Chaitophorinae) is present (Table 2).

TABLE 2

Number of genera, species and percentage of endemism

in the Aphidoidea of the Indian region

(Up to - 1988)

	Total number of genera	Endemic number	%	Total number of species	Endemic number	%
I. Family						
APHIDIDAE						
ANOECIINAE	2	0	0	16	12	75
APHIDINAE	106	27	25	467	195	41
LACHNINAE	14	3	21	37	25	66
PTEROCOMMATINAE	1	0	0	1	0	0
CHAITOPHORINAE	4	0	0	27	21	78
DREPANOSIPHINAE	31	10	32	57	43	74
GREENIDEINAE	10	1	10	81	64	78
HORMAPHIDINAE	24	6	25	48	28	58
PEMPHIGINAE	20	4	20	61	40	66
TOTAL	212	51	23	795	428	53
II. Family						
ADELGIDAE						
PINENI	1	0	0	3	0	0
ADELGINI	1	0	0	3	2	66
TOTAL	2	0	0	6	2	66
GRAND TOTAL	214	51	23	801	430	53,6

EVOLUTION AND DISTRIBUTION OF ENDEMIC TAXA

The level of engemism is said to depend on three factors, viz. geographic area, ecological breadth and isolation. Although Carlguist (1974) propounded this theory on the basis of endemism in Island ecosystems, the same theory seems to hold far other terrestrial systems. It is also noteworthy that the provinces of the island biome in Indian region do not have any endemic aphids perhaps due to their proimity to the continent. Perhaps, one can apply to aphids the theory proposed by Stebbins (1980) to account for endemism in plants; the primary cause of localized or endemic distribution patterns is an adaptation to a combination of ecological factors that are themselves localized. Next to climate and edaphic factors, the gene pool of a population is of critical importance.

The geographical distribution of endemic taxa in the Indian region, appears to be determined by ecological factors (sensu Stebbins, 1980). The differences, in both microclimate and macroclimate appear to play a significant role in the distribution of flora and consequently of the aphid taxa; even within apparently similar ecological situations, differences of microclimate arrayed from the forest floors to the upper canopy in the tropics are known to promote microhabitat variation that is exploited by distinct biota(Kruckeberg and Rabinowitz 1985). This is evident from the fact that the great plains of India (Indo Gangetic plains and Indus Plain) offer little ecological variation and hot, humid or semi aric conditions, and that this vast mass is characterised by an aphid fauna that is largely eurythermic

and cosmopolitan (Agarwala and M.R.Ghosh, 1985), with almost
no endemic species. On the other hand the phenomenon of endemism
is noted to be highly positively correlated with the total number
of species found in Northeastern India, Northwestern India and the
Peninsular region (r: on a level of 0.9 or 0.8); the differences
between the Himalayan Highland, representing typical features of
the Palaearctic Realm and the old stable part of the Peninsular
India representing the ancient Gondowna land, are otherwise well
known.

Outside the political boundary of India, Nepal, Bangladesh
and Sri Lanka, Pakistan, which is predominantly made up of Warm
Deserts or Semi Desert Biomes, exhibits interesting elements of
endemism at the generic level; out of 51 endemic genera known
from the region, at least seven have Pakistan, as the type locality,
but almost all of these taxa have been recorded from the mountain
ranges that are geographically contiguous with the Northwestern
Himalayas. With further exploration, most of these taxa may turn
out to be only regional endemics.

The endemic genera in the _Aphidoidea_ of the Indian region
also exhibit of a high percentage of monotypic taxa (80%). This
feature however is not correlated with the occurrence of typical
endemic plant groups.

LITERATURE

Agarwala, B.K. and Ghosh, M.R. (1985). Biogeographical Conside-
    rations of Indian Aphididae (Homoptera). Ins.matsum.,**31**:81-96.

Cain,S.A.(1944). Foundations of Plant Geography. Harper.New York.

Carlquist, S./1974) Island Biology. New York.Columbia University
    Press.

Kruckeberg, A.R.and Rabinowitz, D.(1985). Biological espects of
    endemism in higher plants. Ann.Rev.Ecol.Syst., **16**:447-479.

Raychaudhuri, D.N. (1983). Food Plant Cataloque of Indian Aphididae.
    Aphidological Society of India, Calcutta.

Ricklets, S.E. and Cox, G.W. (1978). Tages of taxon cycle, habitat
    distribution and population density in the avifauna of West
    Indies. Ann.Nat. **112**:875-895.

Stebbins, G.L. (1980). Rarity of plant species; a synthetic view
    point. Rhodora, **82** (829):72-86.

Udvardy, M.D.F. (1975). A classification of the biogeographical
    provinces of the world. International Union for Conservation
    of Nature and Natural Resources. Gland, Switzerland.

EASTERN ELEMENTS IN THE SWISS APHID FAUNA
(XEROTHERMOPHILOUS STEPPE INHABITANTS)

Erwin Jörg and Gerolf Lampel

Entomological Department, Zoological Institute,
CH-1700 Fribourg, Switzerland

ABSTRACT

After some general remarks on the inner Alpine dry valleys
we review their xerothermophilous aphid fauna with special
emphasis on the Valais (Switzerland). A survey of the collected
aphid species is given in form of a table, which contains their
areas of origin (geoelements) and general distribution. The most
interesting species are discussed in detail.

THE DRY VALLEYS OF THE ALPS

At first sight, the Alps seem to be a uniform mountain-
chain. But crossing them from north to south one passes through
three completely different floristic and climatic regions:

1. north of the Alps a belt of deciduous forest with a rela-
   tively humid Central European-Atlantic climate,
2. the inner Alpine belt of conifers with a hot and dry sub-
   continental climate, and
3. a belt of deciduous forest or sweet chestnut with a mild,
   more or less Mediterranean climate south of the Alps (BRAUN-
   BLANQUET, 1961).

Shielded against rain by mighty mountains, a great number of plants of the inner Alpine valleys belong to the typical xerothermophilous steppe vegetation, which probably immigrated from the eastern and southern prairies during the warmer period after the last glacial epoch. These hot and dry valleys can be found across the Alps, from south-west to north-east. BRAUN-BLANQUET (1961) mentions the following different regions:

1. catchment area of the Durance (France = F)
2. upper Romanche Valley (F)
3. Maurienne and Tarentaise (F)
4. catchment area of the Dora Riparia and the uppermost part of the Val Chisone (Italy = I)
5. Valley of Aosta (I)
6. Valais (Switzerland = CH)
7. Rhine area of the North- and Central-Grisons (CH)
8. Lower Engadine (CH) and the upper Tyrolese Inn Valley (Austria = A)
9. upper Adda Valley (I)
10. South Tyrol (Val Venosta) (I)
11. central region of the River Adige and the Eisack Valley (I)
12. Puster Valley and the basin of Lienz (A)
13. Möll Valley, central Gurk and Metnitz Valley together with the adjacent Murgau (A).

The extremely dry regions are mostly located in the western part of the Alps with exception of the South Tyrol, which is located in the eastern part (cf. Fig. 1).

We carried out our investigations mainly in the Valais and less intensively in the Valley of Aosta, the Lower Engadine and South Tyrol. The climatic, floristic and faunistic conditions of these four different regions are discussed in detail by JÖRG & LAMPEL (1988).

Fig. 1. Dry regions in the inner Alpine valleys (according to BRAUN-BLANQUET, 1961).

Species	Host-plant	Origin	Collection sites	Further distribution
Chaetosiphella stipae HRL., 1947	*Stipa capillata* L.	PM	Martigny, Saillon, Mont d'Orge, Sion, Raron, (CH); Gressan, Laatsch (I)	P, E, F, D, CS, H, SU, Mongolia
Therioaphis trifolii ventro-maculata F.P.MÜLLER, 1968	*Astragalus onobrychis* L.	SP	Sion (CH)	A, CS, PL
Aphis calaminthae (CB., 1952)	*Acinos arvensis* (LAM.) DANDY *Hyssopus officinalis* L.	PM	Saillon (CH); Aymavilles (I)	I, D, A, CS, PL, H
Aphis gerardianae MORDV., 1929	*Euphorbia seguierana* NECKER	PM	Saillon, Mont d'Orge, Sion (CH)	F, CS, R, H, SU
Aphis montanicola HRL., 1950	*Pulsatilla montana* (HOPPE) RCHB.	PM	Zeneggen (CH)	SU
Aphis stachydis MORDV., 1929	*Stachys recta* L.	SP	Saillon, Sion (CH); Schlanders, Tartsch (I)	F, D, DDR, CS, R, H, SU
Xerobion eriosomatinum NEVS., 1929	*Kochia prostrata* (L.) SCHRADER	T	Nus, Gressan (I)	BG, SU
Acaudinum longisetosum HOLM., 1970	*Centaurea scabiosa tenuifolia* (SCHLEICHER ex GAUDIN) ARC.	?	Zeneggen (CH)	I, CS, R, SU
Brachycaudus mimeuri REMAUD., 1952	*Odontites lutea* (L.) CLAIRV.	PM	Saillon (CH)	E, F, I, DK, CS, H PL
Brachycorynella asparagi (MORDV., 1929)	*Asparagus officinalis* L.	P	Charrat-Vison, Saillon (CH)	I, D, DDR, CS, PL, BG, SU, USA
Coloradoa achilleae HRL., 1939	*Achillea millefolium* L.	?	Saillon (CH)	E, F, I, Germany, NL, GB, S, DK, SF, CS, PL, R, H, BG, TR, SU
Coloradoa campestris CB., 1939	*Artemisia campestris* L.	?	Saillon (CH)	F, Germany, GB, S, SF, DK, A, CS, PL, H, BG, R, SU
Macrosiphoniella linariae (KOCH, 1855)	*Aster linosyris* (L.) BERNH.	PM	Branson, Saillon, Mont d'Orge, Raron (CH)	F, I, D, DDR, CS, R, H
Macrosiphoniella staegeri HRL., 1947	*Centaurea vallesiaca* (DC.) JORD.	PM	Sion, Zeneggen (CH)	E, F, GR, DDR, CS, PL, R, BG, H, TR, SU
Macrosiphoniella subaequalis CB., 1942	*Artemisia campestris* L.	PM	Branson, Ardez (CH)	F, DDR, A, CS, PL, H, SU
Macrosiphoniella vallesiacae JÖRG & LAMPEL, 1988	*Artemisia vallesiaca* ALL. = *A. maritima vallesiaca* GAMS	T	Saillon, Raron (CH); Gressan (I)	?
Staegeriella asperulae BOSHKO, 1959	*Asperula aristata* L.f.	PM	Sion (CH); Apt (F)	SU
Titanosiphon artemisiae (KOCH, 1855)	*Artemisia campestris* L.	PM	Martigny, Branson, Sion, Zeneggen (CH); St-Marcel, Tartsch (I)	E, F, I, D, CS, PL, R, BG, H, SU, USA?
Uroleucon chondrillae (NEVS., 1929)	*Chondrilla juncea* L.	PM	Villefranche (I)	P, E, F, CH, GR, D, DDR, YU, CS, R, BG, H, PL, TR, SU

Tab. 1: Survey of the aphids collected in the inner Alpine valleys.

Like all the other inner Alpine valleys, the Valais was covered during the last glacial period (Würm) by a mighty ice-shield. So the immigration of plants and animals could take place only during the warmer period after the glacial epoch. Since the tree limit was at that time about 400 m higher than nowadays, it was possible for the organisms to traverse several passes to get into these valleys. To reach the Valais the eastern and southern elements probably had to cross the Little and Great Saint Bernard, the Theodul or the Simplon Pass. Some Mediterranean organisms came directly through the Rhone Valley, some eastern elements had the possibility to immigrate across the regions free from ice between the Alps and Scandinavia (cf. JÖRG & LAMPEL, 1988).

THE APHID MATERIAL: RESULTS AND REMARKS

A survey of the aphids, host-plants and localities is given in Tab. 1. In addition the recent distribution and the areas of origin are mentioned there. The latter correspond to the geoelements as they are defined by WALTER & STRAKA (1970). Therefore the abbreviations used in the table signify the following geographic regions: T = Turanian, P = Pontic, SP = Sub-Pontic and PM = Pontic-Mediterranean geoelement (more details in JÖRG & LAMPEL, 1988).

The Valais is one of the most interesting regions of Switzerland in regard to aphids. The first one who collected aphids there (between 1946 and 1948) was the late Swiss entomologist and botanist Dr. Robert Stäger. Unfortunately his material cannot be found in any Swiss collection, because it was given for determination to Dr. Hille Ris Lambers, who incorporated it into his own collection. Nevertheless he published three articles on this material (HILLE RIS LAMBERS, 1946-1947a,b, 1950), and also Stäger himself wrote a very short paper (STÄGER,

1957). Recently Stäger's work was shortly reported by MEIER
(1985).
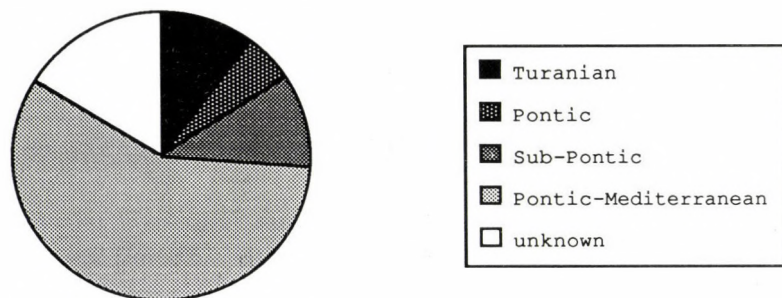
Fig. 2. The areas of origin of the aphid species collected.

From 1974 to 1989 the senior author (LAMPEL) and collabo-
rators gathered 334 samples of aphids from the Valais, and the
junior author (JÖRG) specially looked for xerothermophilous
relicts of eastern origin. The collection sites of the latter
are shown in Fig. 3. As it can be seen, these sites are all
located in the Valaisan main valley, because the insolation is
there much more intensive than in the other regions.

Finally we established a list of 17 species and one
subspecies which may be regarded as strictly xerothermophilous
elements of the Swiss aphid fauna, originated in the East-
European and West-Asian steppe and semi-desert zones. Of these,
six species (*Chaetosiphella stipae*, *Aphis montanicola*, *Aphis
stachydis*, *Macrosiphoniella staegeri*, *Titanosiphon artemisiae*,
and *Uroleucon chondrillae*) had already been detected by Stäger
and were refound by us. A seventh species, *Acaudinum longi-
setosum*, had (after MEIER, 1985) "been collected by Hille Ris
Lambers on April 29, 1950 near Visp" (Zeneggen?). Also the
presence of this species was confirmed by us. Of the remaining
species, ten are new for Switzerland (thereof one even new for

science) or Western Europe (*Xerobion eriosomatinum*, not found in Switzerland but nearby in the Valley of Aosta, Italy).

Below are some historical or other additional remarks on some of the established xerothermophilous aphids:

The material of Stäger enabled Hille Ris Lambers to erect many new taxa. *Chaetosiphella stipae*, *Aphis montanicola* and *Macrosiphoniella staegeri* were new for science.

- *Chaetosiphella stipae* was erected by Hille Ris Lambers as a subspecies of *C. tshernavini* (MORDV., 1921) and later on raised to the species level (see e.g. EASTOP & HILLE RIS LAMBERS, 1976). Hille Ris Lambers, who apparently had not seen specimens of *C. tshernavini* s. str., states that the Swiss material differs from the latter by "the remarkably forked or sawed dorsal hairs" (HILLE RIS LAMBERS, 1946-1947a). In reality also the dorsal hairs of *C. tshernavini* are sawed, but they are much shorter than in *C. stipae* and fan-shaped (SZELEGIEWICZ, 1985). As a second representative of the Siphinae in the Valais, which is very similar to *C. stipae*, exists *Atheroides hirtellus* HAL., 1839 (LAMPEL, 1983). It differs from *C. stipae* (*Atheroides stipae* in BÖRNER, 1950 !) in that the apical segment of the rostrum is shorter than the third antennal segment (HEIE, 1982). The distribution of *C. stipae* from Mongolia to Portugal can bee seen in JÖRG & LAMPEL (1988, Fig. 3).

- *Aphis montanicola* seemed to be restricted to Switzerland and to one locality (Zeneggen, Valais), but meanwhile it was discovered also in the Moldavian SSR (VERESHZHAGIN et al., 1985). The Moldavian SSR lies in the distribution zone of *Pulsatilla montana*. The existence of *A. montanicola* in Western Siberia (IVANOVSKAYA, 1977) however must be called into question (JÖRG & LAMPEL, 1988; HOLMAN, 1966).

- For *Macrosiphoniella staegeri* the authors together with Dr. A. Rupais as guest from Riga could establish on May 1, 1989 a third locality of its occurrence in the Valais: Sion, Tourbillon-Hill. It is of historical interest, that already

Fig. 3. Map of the collection sites in the Valais (Switzerland).

STÄGER (1957) supposed a Pontic origin for this "relict of a warmer period".

- Erroneously HILLE RIS LAMBERS (1950) described *"Dactynotus margarithae"* as a species new to science. It is now regarded as a synonym of *Uroleucon chondrillae*. *U. chondrillae* is widespread between Soviet Middle Asia and Portugal (see map in JÖRG & LAMPEL, 1988) and up to the Baltic Sea. F.P. MÜLLER (1987) records it from the GDR from dry and sandy ruderal places near the sea shore and mentions its "West-Asiatic origin".

Of those species not previously known from Switzerland, the most interesting are those that as a rule do not go farther westward and are relics of a warmer climate that prevailed after the last glacial period. The nearest occurrence of them is now in the eastern steppes far from Switzerland. We can mention here the following species and subspecies: *Therioaphis trifolii* ssp. *ventromaculata*, *Aphis gerardianae*, and *Xerobion eriosomatinum*, though the latter exists only in the Valley of Aosta (Italy) and - like its host-plant - has not succeeded in surmounting the Alps to Switzerland.

- *Therioaphis trifolii* ssp. *ventromaculata* was found only once in Switzerland in 1980 (LAMPEL, 1983). It is sure, that the aphid, like its host-plant *Astragalus onobrychis*, is of eastern origin. The nearest other place where the aphid can be found is in the region of the Lake of Neusiedl in Austria (near the Hungarian frontier). Though *Astragalus onobrychis* exists also in Eastern Switzerland (Lower Engadine), the aphid has not been found there (LAMPEL, 1988). The general distribution known today can be seen from Fig. 4 (CH,A,CS,PL). In Poland *T. trifolii* ssp. *ventromaculata* settles *Astragalus arenarius* L. and goes relatively far to the north. Therefore we believe it to be a Sub-Pontic element.
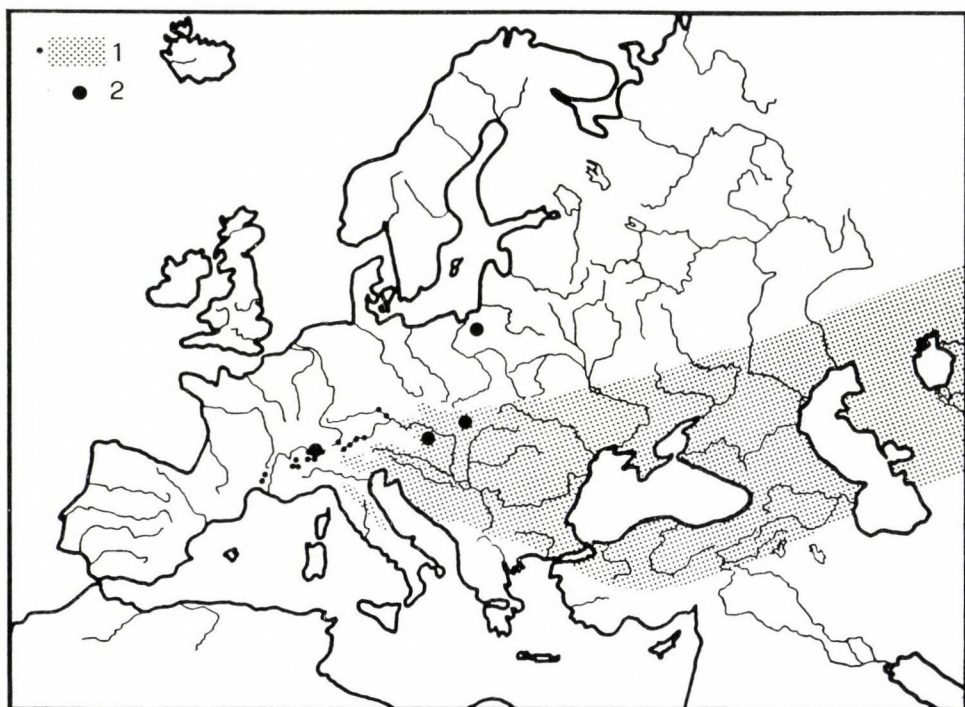
Fig. 4. Distribution map of *Astragalus onobrychis* and *Therioaphis trifolii* ssp. *ventromaculata*. 1 *A. onobrychis* (according to HESS, LANDOLT & HIRZEL, 1977); 2 *T. trifolii* ssp. *ventromaculata* (according to HOLMAN & PINTERA, 1977; HUCULAK, 1967; LAMPEL, 1983; F.P. MÜLLER, 1968; SZELEGIEWICZ, 1968, 1978).

– *Aphis gerardianae* is a black aphid living on *Euphorbia seguierana* (formerly *E. gerardiana*) in dry places in the Rhone Valley (Valais). The determination was possible only with the aid of Russian literature, which we do think was not available to HILLE RIS LAMBERS when he, in 1946-1947(a), identified the aphid collected by Stäger from *E. seguierana* at Raron (VS) as *Aphis euphorbiae* KALT., 1843. *Aphis gerardianae* can be distinguished from the latter by its much shorter siphunculi (LAMPEL, 1983). As can be seen from Fig. 5 in JÖRG & LAMPEL (1988), the nearest eastern locations of *A. gerardianae* are in Czechoslovakia and Hungary. According to LECLANT (1978) it exists also in Southern France.

- A very interesting finding is an aphid of Turanian origin, *Xerobion eriosomatinum*, found in Italy near the Swiss frontier in the Valley of Aosta for the first time in Western Europe. Its nearest other location is Bulgaria; all other findings have been made in the European and South-West Asian Soviet Union (see Fig. 9 in JÖRG & LAMPEL, 1988; this map shows, that even the host-plant distribution is discontinuous).

- Probably also of Turanian origin is the new species *Macrosiphoniella vallesiacae* from the Valais and the Valley of Aosta living on *Artemisia vallesiaca* ALL. = *A. maritima* ssp. *vallesiaca* GAMS. The typically Turanian distribution of the host-plant (see Fig. 19 in JÖRG & LAMPEL, 1988) with two very disjunct western areas (Western Alps, Illyrian Coast) indicates, that the aphid must be of Turanian origin; but in the eastern literature we cannot find any reference to an aphid on *Artemisia vallesiaca*. Therefore we would be very interested to hear, if eastern colleagues are able to detect our species also in the main area of distribution of its host-plant.

For some other aphids found by us, Switzerland is also on the western edge of their distribution, but these species show a continuity in the eastern direction (see distribution maps in JÖRG & LAMPEL, 1988).

- *Aphis calaminthae* and *Macrosiphoniella linariae* are typical Pontic-Mediterranean species which do not exist in the USSR, but go southward as far as Italy and (*M. linariae*) Southern France.

- *Aphis stachydis* does not exist in the south and seems to be a Sub-Pontic element, which has expanded not only westward, but also eastward. It was found by Stäger in the Ticino, and we have found it in the Valais and in South Tyrol.

- For *Brachycorynella asparagi* BÖRNER wrote in 1952: "So far known only from the East-Mediterranean region and Eastern Europe." But he expected it to occur sporadically also in Central Europe. Meanwhile beside our Swiss findings there are now records from the FRG, GDR and Northern Italy (JÖRG & LAMPEL,

1988; F.P. MÜLLER, 1961; COCEANO, 1989). As the host-plant
Asparagus officinalis is now widely cultivated in Europe, it may
be expected, that the aphid will in the future be found also in
West- and Southwest-Europe.

REFERENCES

BÖRNER, C. (1950): Neue europäische Blattlausarten. Selbstverlag,
    Naumburg/Saale, 19 pp.
BÖRNER, C. (1952): Europae centralis Aphides. Schrift. Thüring.
    Landesarbeitsgemeinschaft Heilpflanzenkde. u. -beschaffung,
    4, und Mitt. Thüring. Bot. Ges., Beiheft 3, Weimar, 488 pp.
BRAUN-BLANQUET, J. (1961): Die inneralpine Trockenvegetation.
    Geobotanica selecta 1. Fischer, Stuttgart, 273 pp.
COCEANO, P.G. (1989): Un nuovo pericolo per l'asparagicoltura
    italiana. L'Informatore Agrario, 45 (24), 73-74.
EASTOP, V.F. & HILLE RIS LAMBERS, D. (1976): Survey of the world's
    aphids. Junk, The Hague, 573 pp.
HEIE, O.E. (1982): The Aphidoidea (Hemiptera) of Fennoscandia and
    Denmark. II. Scandinavian Science Press, Klampenborg, 176 pp.
HESS, H.E., LANDOLT, E. & HIRZEL, R. (1977): Flora der Schweiz 2.
    Birkhäuser, Basel & Stuttgart, 956 pp.
HILLE RIS LAMBERS, D. (1946-1947a): Neue Blattläuse aus der
    Schweiz (Homopt., Aphidae). Mitt. Schweiz. Entomol. Ges., 20,
    323-331.
HILLE RIS LAMBERS, D. (1946-1947b): Neue Blattläuse aus der
    Schweiz II (Homopt. Aphidae). Mitt. Schweiz. Entomol. Ges.,
    20, 649-660.
HILLE RIS LAMBERS, D. (1950): Neue Blattläuse aus der Schweiz
    (III) (Homopt., Aphidae). Mitt. Schweiz. Entomol. Ges., 23,
    37-46.
HOLMAN, J. (1966): Contributions to the taxonomy of the genus
    Aphis (Homoptera, Aphididae) - II. Acta entomol. bohemoslov.,
    63, 91-110.
HOLMAN, J. & PINTERA, A. (1977): Aphidodea. Acta Faunistica Ent.
    Mus. Nat. Pragae, Suppl. 4, 101-116.
HUCULAK, S. (1967): Mszyce (Homoptera, Aphidodea) Pojezierza
    Mazurskiego III. Fragm. faunistica (Warszawa), 14, 93-131.
IVANOVSKAYA, O.I. (1977): Tli sapadnoj Sibiri II (Semejstvo
    Aphididae). Isd. "Nauka", Sib. Otdel., Novosibirsk, 328 pp.
JÖRG, E. & LAMPEL, G. (1988): Xerothermophile Aphiden der Schweiz
    und angrenzender Gebiete mit besonderer Berücksichtigung des
    Kantons Wallis (Homoptera, Aphidina). Mitt. Schweiz. Entomol.
    Ges., 61, 43-88. - See also : Aphids of hot, dry habitats in
    Switzerland. Aphidologists Newsletter, 24, 1, 15-17 (1989).
LAMPEL, G. (1983): Für die Schweiz neue Blattlaus-Arten
    (Homoptera, Aphidina) 3. Mitt. Schweiz. Entomol. Ges., 56,
    125-162.

LAMPEL, G. (1988): Ökologische Untersuchungen im Unterengadin : Blattläuse (Sternorrhyncha, Aphidina). Ergebn. wiss. Unters. Schweiz. Nationalpark, 12, 13.Lfg., D301–D330. – See also : Ecology of aphids in the Lower Engadine area. Aphidologists Newsletter, 24, 1, 17–20 (1989).

LECLANT, F. (1978): Étude bioécologique des aphides de la région méditerranéenne. Thèse Univ. Sci. Techn. Languedoc, Montpellier, 318 pp.

MEIER, W. (1985): Aphid species from East and West with some additions to the aphid fauna of Switzerland and with descriptions of a new species (Additions to the aphid fauna of Switzerland III). Proc. Internat. Aphidol. Symp. Jablonna 1981, 431–446.

MÜLLER, F.P. (1961): Ergänzungen zur Blattlausfauna von Mitteleuropa. Mitt. Dtsch. Entomol. Ges., 20, 69–70.

MÜLLER, F.P. (1968): Eine neue Subspecies zu *Therioaphis trifolii* (MONELL 1882) (Homoptera, Aphidina). Reichenbachia, 10, 261–265.

MÜLLER, F.P. (1987): Einfluss von Biotop und Biotopveränderungen auf die Aphidenfauna (Homoptera : Aphididae) im Küstenstreifen der DDR. Wiss. Z. Univ. Rostock, 36, Naturw. Reihe, Heft 2, 81–83.

STÄGER, R. (1957): Beitrag zur Kenntnis der Aphiden-Fauna der Walliser Steppenheide. Mitt. Schweiz. Entomol. Ges., 30, 99–101.

SZELEGIEWICZ, H. (1968): Mszyce, Aphidodea. Katalog fauny Polski 21,4. Pánstwowe Wydawnictwo Naukowe, Warszawa, 316 pp.

SZELEGIEWICZ, H. (1978): Przeglad systematyczny mszyc Polski (A check list of the aphids of Poland). Pánstwowe Wydawnictwo Naukowe, Warszawa, 40 pp.

SZELEGIEWICZ, H. (1985): Klucze do oznaczania owadów Polski XVII, 5b: Mszyce – Aphidodea Chaitophoridae. Pánstwowe Wydawnictwo Naukowe, Warszawa-Wroclaw, 58 pp.

VERESHZHAGIN, B.V., ANDREEV, A.V. & VERESHZHAGINA, A.B. (1985): Tli Moldavii. Shtiinza, Kishinev, 160 pp.

WALTER, H. & STRAKA, H. (1970): Arealkunde, 2. Aufl. Ulmer, Stuttgart, 478 pp.

NEWLY RECORDED APHID SPECIES IN THE PHYTOGEOGRAPHIC PROVINCE OROCANTABRIAN OF SPAIN

J. M. Nieto Nafría*, G. Remaudière** and M. P. Mier Durante*

* Departamento de Biología Animal, Facultad de Biología, Universidad de León, 24071 León, Spain.

** Service de Lutte biologique contre les Insectes, Institut Pasteur, 75724 Paris, France.

ABSTRACT

The Phytogeographic Province Orocantabrian is part of the Eurosiberian Region. It is characteristic of the western part of the Cantabrian Mountain Range in northern Spain.

We have collected aphids in this Province and have identified more than 240 species, about 50% of the total number of aphid species known in Spain. Most of the species collected are Euroatlantic or Eurosiberian species.

Of these species 1 Pemphiginae, 2 Phyllaphidinae, 1 Saltusaphidinae, and 11 Aphidinae Aphidini are recorded for the first time in Spain.

These results indicate the diversity of aphids in the Cantabrian Mountain Range.

INTRODUCTION

Most of the Iberian Peninsula (Fig. 1) forms part of the Phytogeographic Mediterranean Region, but the 50 to 100 km wide stretch only

in the north is part of the Phytogeographic Eurosiberian Region (Rivas
Martínez, 1987).

The Euroatlantic stretch in the Iberian Peninsula is attributed
(Rivas Martínez et al., 1984) to three Phytogeographic Provinces:
Pyrenean, Atlantic-Cantabrian (which stretches from Portugal to Brittany
in France) and Orocantabrian, which is limited to a part of the Cantabrian
Mountain Range. According to these authors the Orocantabrian Province
is well defined by its floral composition and by its vegetation.

Fig. 1. Position of the Phytogeographic Province Orocantabrian.

RESULTS

In 1986 and 1987 from May to July and in October and November,
designated areas in the Province were sampled. More than 240 species
and subspecies have been identified from the material collected. This

number may increased by 10 more species once the study of certain
complex groups, e. g., Aphis on Labiatae, has been completed. There
are also 4 new species yet to be described in various genera.

Of the 240 species and subspecies identified, the following 15
are reported for the first in Spain.

Patchiella reaumuri (Kaltenbach, 1843) (Pemphiginae)

Tilia cordata: Asturias: Poncebos, 7.VII.86; Tielve, 21.VI and
l.VII.87.

In the spring, this aphid causes a typical twisting of the young
shoots of Tilia and later migrated to the roots of Araceae. The fundatri-
genia has the following characteristics: media of fore wings with
2 branches, pterostigma wide and black, long body and antennal hairs
and short spinal bands on the abdomen. It is rather common in Europe.

Appendiseta robiniae (Gillette, 1907) (Phyllaphidinae)

Robinia pseudacacia: Asturias: Arenas de Cabrales,7.VII.86; Buelles(1)
5.VII.86; Cangas de Onís (1), 7.VII.86. Cantabria: Cosgaya, 3.VII.86;
Santander (1), VII.86. León: Beberino, l.VII.86; Cabañas Raras (2),
28.VI.86; La Robla (2), l.VII.86, 12.X.87 (sexuales); León (2), l.VII.86
and many other dates; Vegas del Condado (2), 8.XI.86 (oviparae); Villablino
29.VI.86. Vagrant: La Hermida (Cantabria), 9.XI. 86.

The localities marked are outside the Orocantabric Province and
indicated the following: (1) the Atlantic-Cantabrian Province and
(2) the Mediterranean Region, although in the majority of cases close
to its limits.

This species is North American in origin and is found in Canada
and the United States (USA), where it lives on Robinia pseudacacia,

although Forbes and Chao-kai Chan (1978) have also recorded it on
Sophora japonica. In 1979 Micieli de Biase and Calambuca reported
this species in Italy. Later, it was recorded by Lampel (1983) in
Corsica and Switzerland; and we have seen it in France and Wurzburg
(GFR).

In this part of Spain and in France, this aphid seems to be widespread.
Its population was very high in 1986, dropped considerably in 1987
and 1988, and increased again in 1989.

Ctenocallis setosus (Kaltenbach, 1846) (Phyllaphidinae)

Cytisus scoparius: Playa de Vega (Asturias) - in the Atlantic-Canta_
brian Province -, 6.VII.86. Vagrant: Puerto de la Magdalena (León),
3.VII.87.

Small, uncommon species living on the upperside of leaflets of
Sarothamnus scoparius, characterized by long tapering processes (2
pairs per segment) and by a pair of dark bands per segment. Recorded
from Great Britain, Holland, Germany, Denmark, Poland, France, Italy,
and some parts of the USA and Canada in North America. It is the second
species of the genus found in Spain; the first being C. israelicus.
The only other species in this genus, C. dobrovljnskyi Klodnitsky,
reported on Cytisus, has yet to be found in Spain.

Subsaltusaphis rossneri (Börner, 1940) (Saltusaphidinae)

Cyperaceae: Puerto de Leitariegos (León), 6.XI.86.

An elongate aphid densely covered with rather coarse nodules
and fine black intersegmental stripes. Its hosts are tall species
of Carex.

Recorded in Germany, Great Britain, Poland, Denmark, Sweden,

Norway, Finland, Czechoslovakia, and it has been observed in France.

Aphis (A.) coronillae Ferrari, 1872 (Aphidinae Aphidini)

Lathyrus pratensis: Murias de Paredes (León), 29.VI.86.

Stroyan (1984) regards this as a widely distributed species in Europe. The number of countries it is found in leads us to believe that it is Euroatlantic. Its identification is not very difficult (Stroyan, 1984 and Heie, 1986) although the first author recognizes two subspecies: A. coronillae coronillae and A. coronillae arenaria. Some of the specimens collected have chracters similar to those of both subspecies. Therefore, we cannot give a definitive subspecific name. L. pratensis is not the normal host plan reported for this species.

Aphis (A.) frangulae beccabungae Koch, 1855 (Aphidinae Aphidini)

Veronica sp.: Oseja de Sajambre (León), 9.VII.86.

The difficulty in identification of this subspecies makes its distribution difficult to establish exactly; however, it seems certain that it is Euroatlantic.

Aphis (A.) grossulariae Kaltenbach, 1843 (Aphidinae Aphidini)

Epilobium hirsutum: Vejo (Cantabria), 3.VII.86.

Recorded from various parts of Europe, Asia (Siberia and some Soviet Central Asian Republics), and USA.

Aphis (A.) helianthemi Ferrari, 1872 (Aphidinae Aphidini)

Helianthemum numularium subsp. urrialense: Sotres (Asturias) and Tresviso (Cantabria), 4.VII.86.

Remaudière and Leclant (1972) included this species in the Aphis spp. group that lives on Cistaceae. This host plant is endemic in the Peaks of Europe. It is reported from a large number of European

countries. It is not reported, however, from Portugal, Greece, Rumania or Bulgaria.

Aphis (A.) mammulata Gimingham et Hille Ris Lambers, 1949 (Aphidinae Aphidini)

Rhamnus alpina: Valporquero (León), 30.VI.86.

This species is easy to identify because of its very long frontal, antennal, and leg hairs and the large number and size of its marginal abdominal tubercles.

According to Heie (1986), it has been recorded in Austria, Czechoslovakia, Germany, Great Britain, Poland and Sweden on Rhamnus catharticus.

Aphis (A.) plantaginis Goeze, 1778 (Aphidinae Aphidini)

Plantago sp.: Amieva (Asturias), 11.VII.87.

These aphids are typically found at ground level and on the upper roots of Plantago spp.

It has been recorded in most of Europe, primarily in the Eurosiberian areas as well as Turkey and Siberia and in northern USA.

Aphis (A.) schneideri (Börner, 1940) (Aphidinae Aphidini)

Ribes petraeum: Burón (León), 2.VII.86; Ribes uva-crispa: Valporquero (León), 2.XI.86.

It is recognized by a large number of marginal abdominal tubercles, secondary hairs on the ultimate rostral segment and long antennal and leg hairs.

It is widespread in Europe on Ribes spp.

Aphis (A.) subnitida (Börner, 1940) (Aphidinae Aphidini)

Pimpinella villosa: La Magdalena (León) -in the Mediterranean Phytogeographic Region, although very close to the Euroatlantic area-,

29.VI.86.

As with the previously mentioned species, this species is not difficult to identify. It is typical of Pimpinellaspp.

Recorded from USSR (even Siberia), Finland, Sweden, Denmark, Poland, Austria and Germany. It is extending its range.

Aphis (A.) tripolii Laing, 1920 (Aphidinae Aphidini)

Aster tripolium: Ribadesella (Asturias) -in the Atlantic-Cantabrian Province, although very near its demarcation line-, 6.VII.86.

The Spanish material agrees with the measurements cited by Stroyan (1984) to separate this species from A. nasturtii and A. umbrella. It is a monophagous aphid.

It has been recorded only rarely in Sweden, Norway, Great Britain, Germany, France and Italy.

Aphis (A.) ulmariae Schrank, 1801 (Aphidinae Aphidini)

Filipendula ulmaria: Morgovejo and Prioro (León), 10.VII.86; Carmona (Cantabria), 8.VIII.86; Beberino (León), 5.VII.87.

A well-known species in central and northern Europe on this same plant (see Stroyan, 1984, for a more precise distribution). Carmona is in the Atlantic-Cantabrian Region. The specimens of the sample collected in this area, in mid-summer and in large numbers, were of two types: small yellow ones and large green, or dark green ones. Apart from living in the hollows of the wrinkled leaves, they can be found up to the tops of the plant.

Aphis (Protaphis) striata Hille Ris Lambers, 1967 (Aphidinae Aphidini)

Erigeron acer (roots). Aralla (León), 1.VII.86.

This is one of the few species of the subgenus that is easily

NIETO NAFRIA, REMAUDIERE, MIER DURANTE

recognizable. The other species are badly defined and their identifications are very difficult (Hille Ris Lambers, 1967; Stroyan, 1979). This species has been recorded on Hypochoeris glabra, H. radicata, Leontodon hispidus, L. taraxacoidis, and Picris hieracioides. This is the first time it has been recorded on a species of Erigeron.

It is known in Czechoslovakia, Denmark, Great Britain, Italy, Poland, and Rumania; and it has been observed in France.

CONCLUSIONS

The reported presence of approximately 240 species in the study area indicates the aphidological diversity of the Cantabrian Mountain Range and in particular the Orocantabrian Phytogeographic Province. The report of 15 new records in Spain (with an additional 10 yet to be reported) reflects a substantial increase in the total previously reported. Continued study in the Euro-Atlantic strip is indicated in order to increase our knowledge of the Spanish aphid-fauna.

ACKNOWLEDGEMENTS

REFERENCES

Forbes, A.R. and Chao-Kai Chan (1978). The aphids (Hom. Aphididae) of British Columbia, 6. Further additions. Jour. Entom. Soc. Brit.

Col, 75: 47-52.

Heie, O.E. (1986). The Aphidoidea of Fennoscandia and Denmark. III. Family Aphididae, subfamily Pterocommatinae and tribe Aphidini of subfamily Aphidinae. Fauna Ent. Scandinavica, 17:313 pp.

Hille Ris Lambers, D. (1967). New and little known members of the aphid fauna of Italy. Bol. Zoo. agr. Bachi., 2 (8): 1-32.

Lampel, G. (1983). Fur die Schweiz neue blattlaus-Arten (Hom. Aphidina), 3. Mitt. Schweiz Ent. Ges., 56: 125-162.

Micieli de Biase, L. and Calambuca, E. (1979). L'Appendiseta robiniae (Gillette), nuova specie per l'Italia su Robinia pseudacacia L. Inf. fitopatol., 11, 12: 31-33.

Remaudière, G. et Leclant, F. (1972). Nouveaux Drepanosiphoniella, Macrosiphoniella et Aphis du basin méditerranéen et du massif alpin (Hom. Aphididae). Ann. Soc. Ent. Fr. (N.S.), 8 (1): 73-103.

Rivas-Martínez, S. (1987). Memoria del Mapa de las series de vegetación de España. 1: 400.000. I.C.O.N.A. . Madrid: 268 pp.

Rivas-Martínez, S., Díaz-González, T.E., Fernández Prieto, J.A., Loidi, J. y Penas, A. (1984). La vegetación de la alta montaña cantábrica: Los Picos de Europa. Ediciones Leonesas. León. 295 pp.

Stroyan, H.L.G. (1979). Additions to the British aphid fauna (Hom. Aphidoidea). Zool. Jour. Linn. Soc., 65 (1): 1-54.

Stroyan, H.L.G. (1984). Aphids. Pterocommatinae and Aphidinae (Aphidini). Homoptera, Aphididae. Handbk. Ident. Br. Insects, 2 (6): 234 pp.

MYZUS PERSICAE (SULZER) AND ITS NATURAL

ENEMIES IN POTATO FIELDS

Abdel-Wahab M. Ali, S.A. Ahmed, F.M. Khalil, A.M.Salman
Department of Plant Protection, Faculty of Agriculture,
University of Assiut, Egypt.

ABSTRACT

Field trials were undertaken to determine the relative
abundance of *Myzus persicae* (Sulzer) and its natural enemies
on potatoes in Upper Egypt. The green peach aphid appeared
in both winter and summer plantations. The population
densities of aphids were significantly higher during summer
growing seasons than that of the winter. Number of predators
associated with the aphid in summer plantations also was
higher than that in the winter plantations. *C. undecimpun-
ctata* was the predominant predator making up more than 33%
of the total predator complex.

INTRODUCTION

The green peach aphid, *Myzus persicae* (Sulzer), is
among the most destructive of the insect pests of potato bec-
ause of its direct damage and its action in transmitting
plant viruses. Occurrence of this aphid species on potato
was found to be affected by some ecological factors such as
neighbouring crops and interplanting (Staniland, 1943),
potato varieties (Xia and Tingey, 1986) and temperature
(Pozarowska, 1987). However, *M. persicae* was recorded as
much more abundant on potato during the summer months (El-
Sayed, 1983 and Soliman, 1987).

Little information is available on the population dyn-
amics of the green peach aphid in the studied area,

particularly, the impact of the natural enemies on its
population.

The present study was conducted to determine the rel-
ative and seasonal abundance of the green peach aphid and
its natural enemies in potato fields in Upper Egypt.

MATERIALS AND METHODS

The present study was carried out at Assiut University
Experimental Station during the period from 1984 to 1986.

An area of about one feddan (4200 m^2) was cultivated
with potato variety Alpha. Normal agriculture practices
were performed and no insecticidal treatments were applied
during the study period. Potatoes were planted at two
planting dates. Winter plantations (nili plantations) in
which potatoes are usually planted during late September
(Local tubers) and summer plantations, in which potatoes
are planted during middle February (imported tubers). Samp-
les were based on plots (6x7 m). Each plot consisted of
ten rows (7 m length and 60 cm width) and each row contained
twenty potato plants. From sprouting until the ripenning
of the crop samples were taken weekly from twenty randomly
selected plots. Five leaves were taken from nonadjacent
plants from each plot forming a total of 100 leaves in each
sample. Each leaf was caged carefully and sealed separa-
tely in a polyethylene bag. Samples were then examined in
the laboratory under a stereomicroscope and numbers of
green peach aphids and associated natural enemies were
recorded.

RESULTS AND DISCUSSION

1- Abundance of M. *persicae*
1.1. Winter plantations

Data illustrated in Fig. 1 show the abundance of M.
persicae on potatoes during the winter growing seasons of
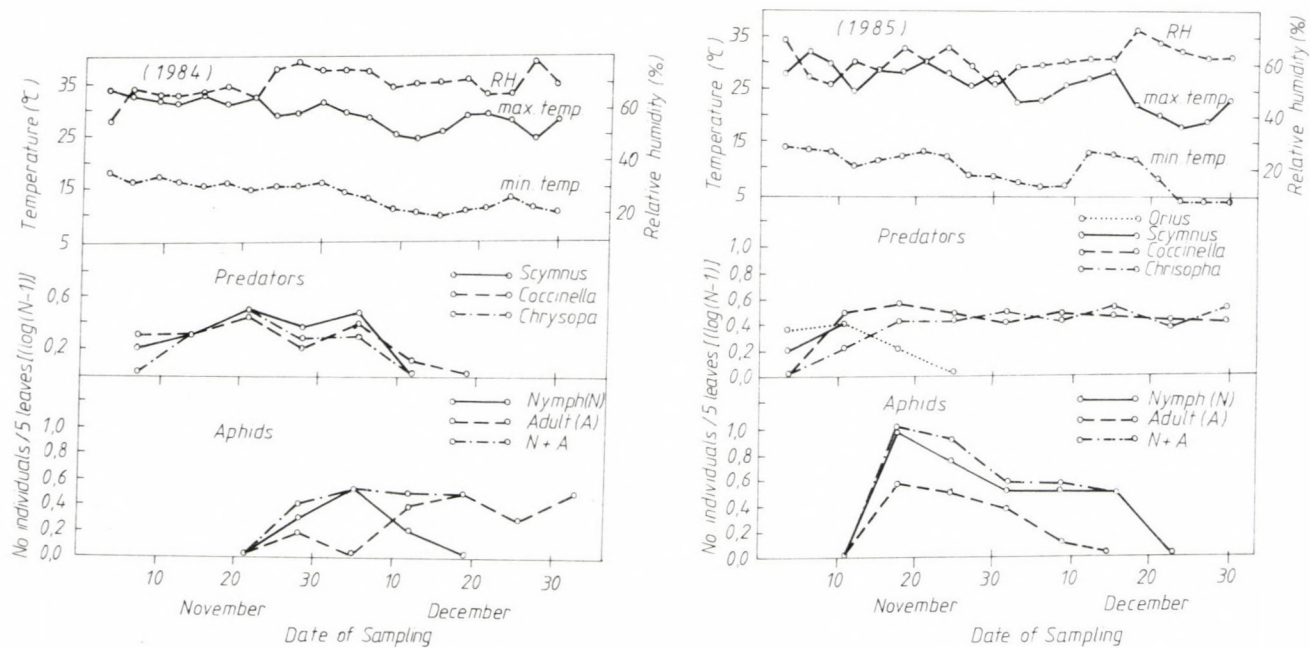
Fig. (1): Seasonal abundance of *M. persicae* and the associated predators on potato plants during the nili plantaion, Assiut (1984 and 1985).

Above: Weather records.

1984 and 1985. It is clear that the general trend of the populations of aphid more or less follows the same trend in the two seasons of investigation but in varying levels. The population was firstly detected during the second half of November and continued until the end of December. The number of aphids in 1984 was lower than in 1985. Total number of aphids collected in 1985 was nearly double that in 1984.

1.2. Summer plantations.

Data in Fig. 2 indicate the population trend of *M. per-sicae* in the summer plantations of 1985 and 1986.

It appears that the trend of populations of *M. persicae* tended to follow a similar pattern in each of the growing seasons. The initial infestation with the green peach aphid was recorded during the third week of March when the plants were about 4 weeks old. The population increased to reach the maximal level toward the end of March and disappeared from the plants during the first week of April.

The forementioned results indicate that the population densities of aphids in summer plantations were markedly higher than in winter plantations. Temperature during March appeared to be suitable for the development and multiplication of aphids and cold winter temperature presumably suppressed its reproductive potential. Previously, Harakly (1974); Marzouk (1975); El-Saadany and Abdel-Fattah (1976) suggested that *M. persicae* was the most predominant aphid species on potato plants in Egypt.

2- Abundance of Predators:

The common predator species collected from potato plants during the present study were *Coccinella undecimpunctata* L., *Scymnus interruptus* Goeze, *Orius albidipennis* Reuter, *Orius laevigatus* Fabricus and *Chrysopa carnea* Steph. .
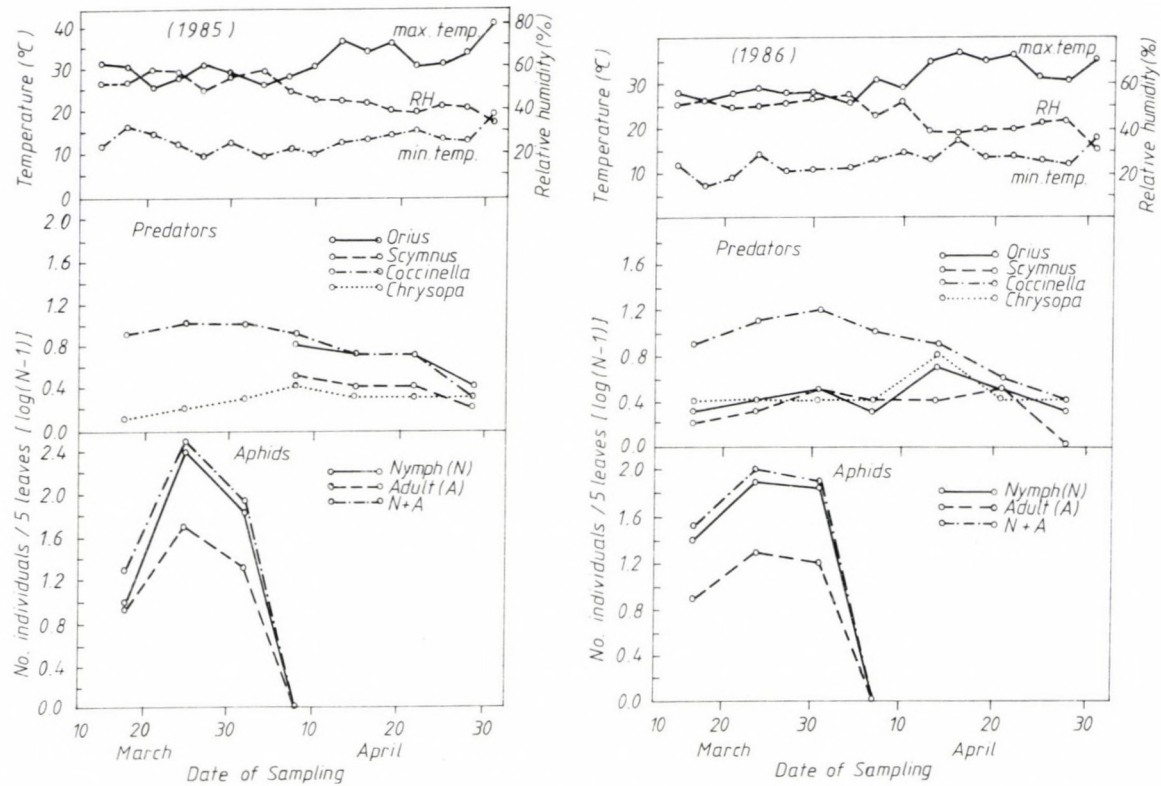
Fig. (2): Seasonal abundance of *M. persicae* and the associated predators on potato plants the Summer plantaion, Assiut (1985 and 1986).

Above: Weather records.

2.1- Winter plantations

Data in Fig. 1 show the seasonal abundance of the
common predators in the winter plantations of 1984 and
1985.

It is clear that *C. undecimpunctata* and *C. carnea*
were the predominant predators constituting about 40 and
34% of the species collected during the two growing
seasons, respectively. *Scymnus interruptus* followed the
former species and was collected in relatively low number
comparising 22% of the total. *Orius* spp. were scarce and
very few individuals were collected. The results also
show that considerable numbers of abundant predators were
observed during the first three weeks of November.

2.2- Summer plantations

Data in Fig. 2 show the abundance of the recovered
predator species from potatoes in the summer plantations
of 1985 and 1986.

Generally, predators appeared on potatoes from middle
March until the end of April. *Coccinella undecimpunctata*
was the predominant predator species during the summer
growing seasons comprising about 62% of the total predator
complex. *Orius* spp., *C. carnea* and *S. interruptus* were
recorded in relatively low numbers constituting about 18,
12, 9% of the total beneficial species, respectively. It
is clear, however, that *C. undecimpunctata* peaked earlier
than other predators species and generally coincided with
the population of the aphid. The late appearance of the
predators species other than *C. undecimpunctata* may be due
to their association with pests other than *M. persicae*.
These predators are known as important biocontrol agents
of other potato pests such as thrips, spider mites, and
lepidoptera as egg and/or early-instar stages   (Mack and

Smilowitz, 1979; and Garegory et al. 1984). This late
appearance of these predators and their low population den-
sities reduce their role in regulating M. *persicae* popul-
ation on potatoes.

The present results indicate that the population den-
sities of predators were markedly higher in summer plant-
ation than in winter ones. High density of predators in
summer may be due to the presence of abundant prey and/or
to favourable weather during this season. In addition,
high population density of C. *undecimpunctata* among all
predators and its association with the population of aphids
indicate that this species is well established in the stud-
ied agroecocsystem and it may contribute significantly to
the bio-control of aphids in potato field in the area
under study.

REFERENCES

El-Saadany, G. and Abdel-Fattah, M.I. (1976): Fluctuations
        of population densities of three Homopterous pests,
        Myzus persicae (Sulzer), *Aphid gossypii* (Glover)
        and *Empoasca decipiers* (Paoli), attacking potato
        plants in Egypt. Bull. Soc. Entomol., Egypte,
        60: 389-394.

El-Sayed, F.A.A. (1983). Studies on certain insects attack-
        ing potato in Egypt. Ph.D. Thesis, Fac. Agric.,
        Cairo Univ.

Garegory, P.W.; Lowell, R.N. and Donald, E.S. (1984):
        Natural mortality factors acting on potato aphid
        (*Macrosiphum euphorbia*) populations in processing
        tomato fields in Ohio. Environ. Entomol., 13:
        724-32.

Harakly, F.A. (1974): Preliminary survey of pests infes-
        ting solanaceous truck crops in Egypt. Bull. Sco.
        Entomol. Egypte, 58: 133-140.

Mack, T.P. and Smilowitz, Z. (1979): Diel activity of
        green peach aphid predators as indexed by sticky
        traps. Environ. Entomol., 8: 799-801.

Marzouk, I.A.A. (1975): Biological and ecological studies
        on some insects attacking potato plants. M.Sc.
        Thesis, Fac. Agric., Ain Shams Univ.

Pozarowska, P.J. (1987): Studies on low temperature surv-
        ival, reproduction and development in Scottish
        clones of *Myzus persicae* (Sulzer) and *Aulacorthum
        solani* (Kaltenbach) (Hemiptera:Aphididae) suscept-
        ible and resistant to organophosphates. Bull.
        Entomol. Res., 77: 123-134.

Soliman, M.M. (1987): Biological and ecological studies
        on certain potato pests. M.Sc. Thesis, Fac. Agric.
        Assiut Univ.

Staniland, L.N. (1943): A survey of potato aphids in the
        south-western agricultural advisory province. Ann
        Appl. Biol., 30: 32-42.

Xia, J.K. and Tingey, W.M. (1986): Green peach aphid
        (Homoptera:Aphididae): development and reproductive
        biology on *Solanum tuberosum* x S. *berthaultii*
        hybrid potato. J. Econ. Entomol., 79: 71-75.

APHIDS COLONIZING PEPPERS IN HUNGARY

AND THEIR IMPORTANCE AS VIRUS VECTORS

Z. Basky[1] and B. Raccah[2],

[1]Institute of Crop Protection and Soil Conservation Service

P.O. Box 250, H-5001 Szolnok, Hungary

[2]Agricultural Research Organization, The Volcani Center,

Institute of Plant Protection, Department of Virology,

P.O. Box 6, Bet Degan 50 250, Israel

ABSTRACT

In a two-year study, *Myzus persicae* (Sulzer) and *Aphis nasturtii* (Kaltenbach) proved to be the predominant species of aphids colonizing peppers in Hungary. Apart from these major species, *Aphis gossypii* Glover, *Aulacorthum solani* (Kaltenbach), *Acyrthosiphon pisum* (Harris) and *Hayhurstia atriplicis* (L.) also formed small colonies on peppers.

On the basis of individually tested aphids, *Aphis craccivora* Koch, *Aphis fabae* Scopoli, *Aphis nasturtii*, *Aulacorthum solani*, *Brachycaudus helichrysi* (Kaltenbach), *Capitophorus elaeagni* del Guercio, *Myzus persicae* and *Phorodon cannabis* (Passerini) proved to be vectors of CMV. Both CMV and PVY were transmitted by *Acyrthosiphon pisum*, *Hayhurstia atriplicis*, *Rhopalosiphum padi* (L.) and *Schizaphis graminum* (Rondani).

INTRODUCTION

Paprika is the most important spice and also an important vegetable in Hungary. However, little is known about the species of

aphids that colonize this crop. Although aphids are recorded as

important virus vectors of peppers in the field, the direct damage they

cause seldom justifies insecticide treatment. Kuroli (1971) reported

two species on peppers, *Myzus persicae* (Sulzer) and *Aphis nasturtii*

(Kaltenbach). In addition, smaller numbers of *Aphis craccivora* Koch,

Aulacorthum solani (Kaltenbach), and *Macrosiphum euphorbiae* (Thomas)

were also collected.

The present study describes the seasonal colonization of peppers

by aphids and reports on the virus transmitting potential of live-

trapped, alate aphids.

MATERIALS AND METHODS

Three thousand pepper plants were transplanted into 30 rows with

100 plants in each row. Flights of alate aphids were detected by means

of a yellow pan trap placed in the middle of the plot. In 1987 aphids

were collected twice weekly during July, once in August and three times

weekly from the middle row (A) and at the same time from another row (B)

from the 1st to the 23rd rows.

Alive, alate aphids were collected on weekdays between 7 and 10 am

from the yellow pan traps filled with water. Immediately after landing

in the trap, each alate aphid was transferred with a fine brush to a

pepper plant at the cotyledon stage and confined there for three hours.

At the end of this period, the aphids were placed individually into

serially numbered vials containing 70% alcohol. The same serial number

was given to the plant and the aphid. Whether the plants were infected

with virus was determined 4-6 weeks later by visual evaluation and by

the ELISA test (Clark & Adams, 1977). Antisera against CMV and PVY were

prepared in the Volcani Center, Bet Dagan, Israel as described by

Loebenstein et al. (1977) and Carlebach et al. (1982). Each plant was
tested for CMV and PVY.

RESULTS

Little activity of alate aphids was recorded in 1987 and 1988. In
1987, 1,665 alate aphids were caught from 22 June until 5 October. The
most frequently collected species were *M. persicae, Hayhurstia
atriplicis* (L.) and *Acyrthosiphon pisum* (Harris) and made up 25.9%,
22.2% and 17.7%, respectively, of the total number of aphids caught.

Among the aphids colonizing pepper, *M. persicae* proved to be the
most abundantly collected species; and *A. nasturtii* was the second most
commonly collected species. The number of *M. persicae* collected was
3,264 and *A. nasturtii* was 2,905 (Fig. 1).

On 7 July, eight apterous individuals of *H. atriplicis,* one
apterous *A. pisum* and four *A. pisum* nymphs were collected from peppers.
Aphis gossypii also formed small colonies in the middle of August, but
only alate *Macrosiphum euphorbiae* (Thomas) were present on peppers.

In 1988, of the 383 alatae caught from 26 May until 8 September,
A. pisum and *M. persicae* were the most abundant species. These species
comprized 26% and 12.3% of the total catch, respectively.

Myzus persicae was also the most abundant aphid in 1988. The 15th
row (collected twice weekly) yielded 1,086 individuals. Over the
growing period, when aphids were also collected from other rows, 3,712
aphids were collected (Fig. 2 a,b). In 1988, *A. nasturtii* again proved
to be the second most abundant species with 456 individuals collected
from the 15th row and 3,036 individuals from rows 1-23 (Fig. 2 a,b).
Small colonies of *A. gossypii* and *A. solani* were found both in the 15th
row and in the 1st to 23rd rows.
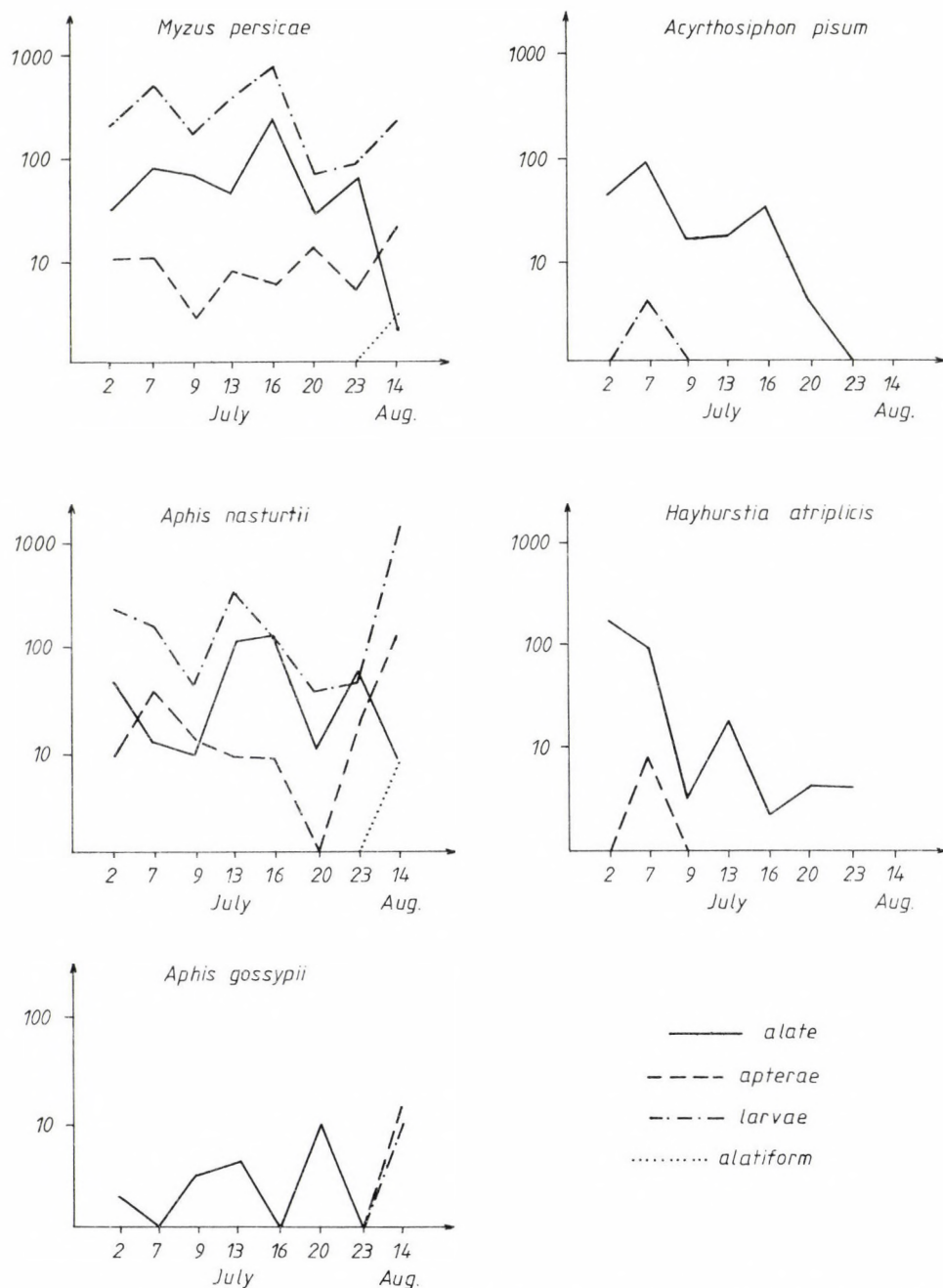
Fig. 1. Form composition and seasonal distribution of aphids collected at intervals from the same 100 pepper plants   Kecskemét, 1987
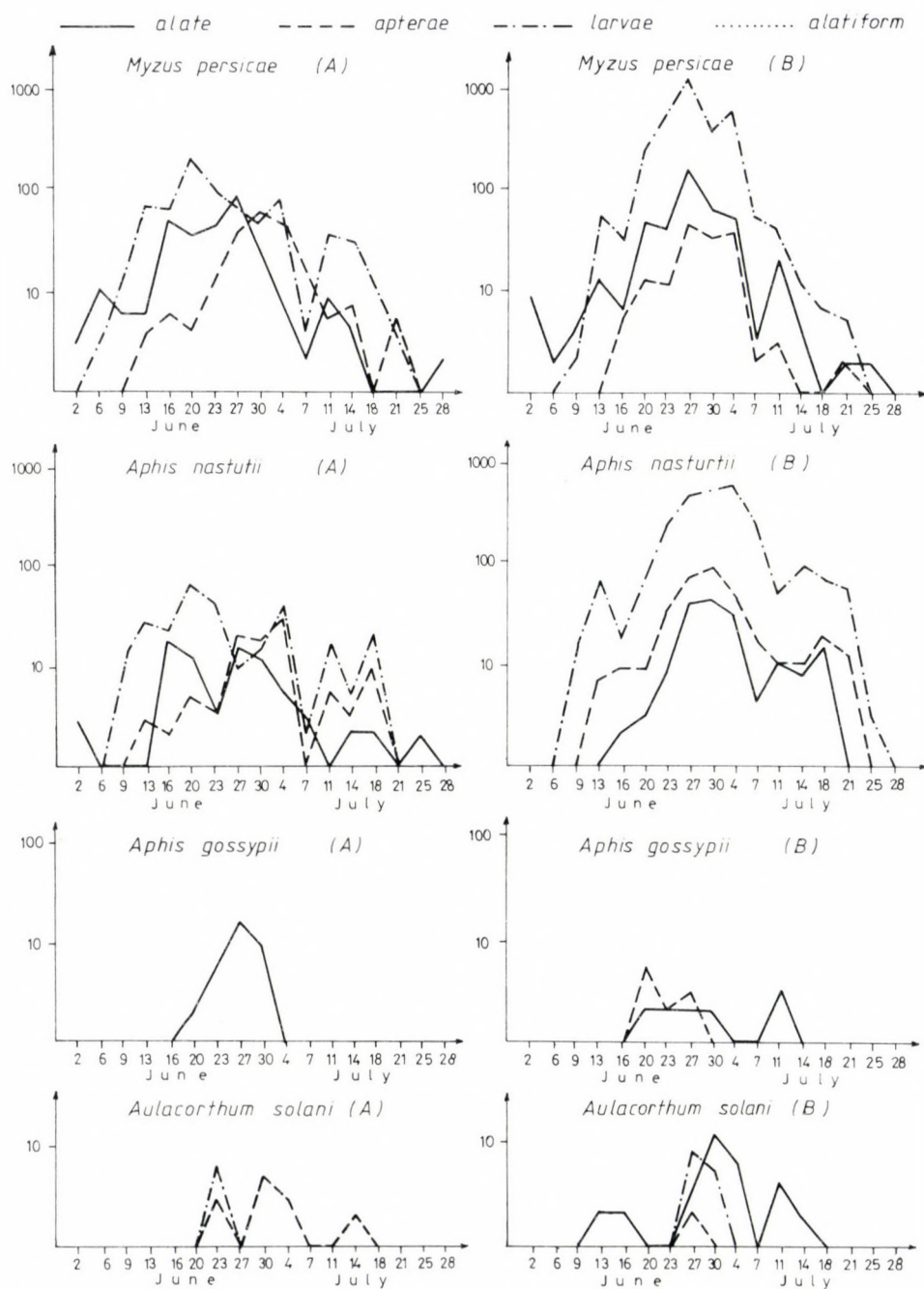
Fig. 2. Species and form composition of aphids collected twice weekly from 100 pepper plants. Kecskemét, 1988

BASKY AND RACCAH

In 1987, of 322 alate individuals caught alive and tested for virus, 25 individuals of 8 species were found to be positive for CMV or PVY or for both viruses (Table 1).

Table 1   Number of aphids tested, and the number and percentage that proved to be virus vectors.

Species	Number of alatae tested		Number found to be vectors				Percentage found to be vectors			
			PVY		CMV		PVY		CMV	
	1987	1988	1987	1988	1987	1988	1987	1988	1987	1988
Acyrthosiphon pisum	5	34		2	1	1		5.9	20	1.9
Aphis craccivora	-	2	-	1	-			50	-	
Aphis fabae	6	7			1				16.7	
Aphis nasturtii	8	1			2				25	
Aulacorthum solani	-	2	-	1				50		
Brachycaudus helichrysi	4	-			1				25	
Capitophorus elaeagni	4	-			1				25	
Hayhurstia atriplicis	51	-	1		3		2.0		5.9	
Myzus persicae	90	16			7	1			7.8	6.2
Phorodon cannabis	1	-			1				100	
Rhopalosiphum padi	28	4	1		1		3.6		3.6	
Schizaphis graminum	65	1	4		1		6.1		1.5	

Acyrthosiphon pisum, *Aphis fabae* (Scopoli), *A. nasturtii*, *Brachycaudus helichrysi* (Kaltenbach), *Capitophorus elaeagni* del Guercio and *Phorodon cannabis* (Passerini) carried CMV. Both CMV and PVY were carried by *H. atriplicis, Rhopalosiphum padi* (L.) and *Schizaphis graminum*.

In 1988, of 123 individuals tested for virus, *M. persicae* was positive for CMV, *Aphis craccivora* Koch and *A. solani* were positive for PVY and *A. pisum* was positive for both CMV and PVY (Table 1).

DISCUSSION

Apart from *M. persicae* and *A. nasturtii* that frequently colonized peppers, *A. gossypii, A. solani, A. pisum* and *H. atriplicis* also infested this crop.

All the aphid colonies were found on senescent leaves. Aphids are known to favour young and old leaves. One possible explanation for the preference for older leaves is the presence of soluble metabolites which are produced during senescence. High levels of soluble amino aphids are known to be preferred by aphids (Dadd and Krieger, 1968). Other explanations suggest the low level of secondary plant substances may be more important.

Secondary plant metabolites often act as barriers and protect plants against colonization by polyphagous aphids (Dixon, 1985). It is possible that senescent leaves are low in secondary plant substances and therefore are suitable for aphids like *A. pisum* and *H. atriplicis*. Or, according to Hille Ris Lambers (1979), it is a tendency of the aphids to exploit particularly abundant species of plants growing in the same or adjoining habitats. *Acyrthosiphon pisum* is oligophagous on Papilionaceae plants while *H. atriplicis* has so far only been recorded from *Chenopodium* (Baloch and Ghaffar, 1984).

Myzus persicae is considered to be the most important virus vector; but, in some cases, high levels of virus infection can be caused by other species, e.g. *H. atriplicis, S. graminum* and *A. pisum*. *Hayhurstia atriplicis* is known as a vector of CMV (Quiot et al., 1982)

and has been proved, contrary to the results of Ryden et al. (1982), to be a vector of PVY.

The low proportion of virus vectors, among alates trapped alive, indicate that most of the virus infection observed in the field can be attributed to aphids moving from plant to plant. A similar phenomenon was observed by Raccah et al. (1988).

REFERENCES

Baloch, G.M. & Ghaffar, A. (1984): Natural emenies of *Chenopodium* spp. in Pakistan with notes on *Trioza chenopodii* (Hemiptera: Psyllidae), a promising biocontrol agent. Entomophage, **29**. 409-414.

Carlebach, R., Raccah, B. & Loebenstein, G. (1982): Detection of potato virus y in the aphid *Myzus persicae* by enzyme-linked immunosorbent assay (ELISA). Annual Applied Biol., **101**. 511-516.

Clark, M.F. & Adams, A.N. (1977): Characteristics of the mikroplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J. General Virol., **34**. 475-483.

Dadd, R.H. & Krieger, D.L. (1968): Dietary amino acid requirements of the aphid *Myzus persicae*. J. Insect Physiol., **14**. 741-764.

Dixon, A.F.G. (1985): Aphid Ecology. Blackie and Son Limited, Bishopbriggs, Glasgow, 157 pp.

Hille Ris Lambers, D. (1979): Aphids as botanists? Symbolae Botanicae Upsaliensis, **22**. 111-119.

Kuroli, G. (1971): Paradicsom es paprika fontosabb virus es mikoplazma fetegsegeinek, a rovarvektorok biologiajanak es a vedekezes lehetosegeinek vizsgalata. Diss. Mosonmagyarovar, 285 pp.

Loebenstein, G., Cohen, J., Shabtai, S., Coutt S, R.H.A. and Wood, K.R. (1977): Distribution of cucumber mosiac virus in systematically infected tobacco leaves. Virol., **81**. 117-125.

Quiot, J.B., LaBonne, G. and Marrou, J. (1982): Controlling seed and insect-borne viruses. 95-123 pp. *In,* Harris, K.F. & Maramorosch, K. (Editors). Pathogens, vectors and plant diseases: Approaches to control. Academic Press, New York, 310 pp.

Raccah, B., Pirone, T.P. & Madden, L.V. (1988).   Correlation between the
    incidence of aphid species and the incidence of two non-persistent
    viruses in tobacco. Agricluture Ecosystems & Environment, **21**. 281-292.

Ryden, K., Brishammar, S. & Sigvald, R. (1982): Sambandet mellan
    frekvens vingade blaloss av olika arter och spridning av potatisvirus
    y i potatisfalt. Vaztskyddsrapporter No. 20, 182-184 pp.

APHID BIOLOGY AND SPRUCE FORESTS IN BRITAIN

Clive Carter
Forestry Commission Research Station
Alice Holt Lodge, FARNHAM, Surrey GU10 4LH, England

ABSTRACT

The list of aphids from spruce exceeds that of other conifers in Britain. Spruce is not indigenous to Britain and Sitka spruce is now the most extensively planted forest tree and is particularly favoured in the west where it thrives in the relatively mild oceanic climate. Most of the 14 known aphid species that have arrived here have retained their original holocyclic style of existence from their place of origin. One species, *Elatobium abietinum*, (Walker) is invariably anholocyclic and produces a succession of apterous generations throughout the winter months. If unchecked by freezing weather, the defoliation that occurs results in losses in tree growth which may lead to other aphid problems.

INTRODUCTION

Sitka spruce (*Picea sitchensis* [Bong.] Carr.) was introduced into Britain in 1832 from North America. It has grown particularly well in the high-rainfall areas of Britain, but was not planted on any significant scale for 100 years, after which large-scale upland afforestation took place (Ryle, 1969). By 1947 71,000 ha were under this species; this increased to 263,000 ha by 1963 and 525,000 ha by 1975 and now represents 28% of all tree species grown in high forest (Locke, 1987).

Thirteen species of aphids and adelgids have been recorded from *Picea sitchensis* in Britain (Carter 1983). Most are specialist *Picea* feeders and have retained their holocyclic condition. Two, (*Adelges cooleyi* (Gillette) and *Pineus similis* [Gillette]) are North American; the remainder have transferred from *Picea abies* (L.) Karst. which is also not

indigenous to Britain though widely distributed throughout
temperate Europe.   An additional British root-dwelling
pemphigine has also been suggested (Stroyan, 1975).   Only two
species are essentially anholocyclic, but the opportunity to
exploit the trees in the mild upland areas of western Britain
during the winter when natural enemies are least active has
enabled these to build up to large populations and cause
concern about tree growth.

MATERIALS AND METHODS

A system for extracting *Elatobium abietinum* from the
foliage of *Picea* shoots was developed from the Berlese funnel
principle.   A small diameter elongate cylinder (see Fig. 1)
was found to be the most effective.   Single shoots were placed
in the cylinders and 40W lamps above each one were kept on for
one hour;   the temperature in the centre of the cylinder
reaching 40°C.   The aphids were found to walk away from the
drying effect of the heat source and to fall below into a
small vial of 90% ethanol.

Root aphids are more difficult to collect by any hand
sorting especially by floatation with organic soils, so the
same method was used for organic litter and roots and found to
be most effective.   In both cases the host-plant substrate can
be recovered from the extraction cylinder and oven-dried to
relate its weight to the numbers of aphids present.

THE GREEN SPRUCE APHID, *Elatobium abietinum*

The green spruce aphid (*Elatobium abietinum*) has for many
years been recognised as a defoliating pest (Theobald, 1914).
It thrives particularly on needles of dormant spruce trees in
the mild winter weather conditions that prevail in the British
Isles (Carter, 1972).   It has also caused serious defoliation
from time to time elsewhere in Europe (Bejer-Petersen, 1962;
Ohnesorge, 1961) and also more recently in British Columbia
(J McLean and W Stanek, personal communication).   This aphid

species was first described from *Picea abies* growing in Britain over 100 years ago by Walker (1849). Distribution records suggest that it was originally associated with Norway spruce which is supported by the fact that this tree shows less reaction to its presence than does Sitka spruce (*P sitchensis*) or the majority of the North American species (Nichols, 1987). Although severe defoliations alone will seldom, if ever, completely kill established Sitka spruce, the loss in potential growth and the frequency of attack makes *E. abietinum* the major background insect pest of Sitka spruce crops in Britain (Carter, 1977).

The large numbers of aphids that can occur during the autumn to spring damaging-period are all viviparous females. As the population increases to a maximum in late spring a winged viviparous female form is produced. Flight of *E. abietinum* is a regular event and occurs more or less simultaneously all over Britain from late May to early June (Carter and Cole, 1977). Indeed, the annual dispersal flight means that spruce trees are exposed to a continual invasion pressure each year. Studies on the nutritional quality of the old needles where the aphids feed on phloem sap suggest that the immigrant winged aphids can acquire only a poor quality food supply during the summer months (Carter, unpublished, Fisher and Dixon, 1986). It is not until late summer to early autumn when the tree is producing hard terminal buds and is in or near a dormant shoot growth condition that aphids start to increase in numbers and are readily found.

E. abietinum always feeds on old needles and it is at on these that chlorotic bands develop; on Sitka spruce these needles rapidly senesce and are abscissed. Adjacent needles that have not been fed upon remain healthy and are not necessarily shed. The leader and upper crown are less often attacked, but in plantations the whole live tree crown may become completely defoliated in outbreak years. Young trees of up to 4 years old that have been heavily defoliated during the winter often have terminal buds that fail to break the

following spring (Carter, 1977).

Mild winter weather has been shown to be associated with attacks by *E. abietinum* (Bejer-Petersen, 1962; Ohnesorge, 1961). The air temperature threshold that will cause significant aphid mortality is -8°C, below which only a small proportion of aphids in the most sheltered situations will be able to survive, and as a result severe spring outbreaks are checked (Carter, 1972). Mild winters, on the other hand, are not necessarily followed by outbreaks. It seems likely that a particular host plant condition has to be achieved before the winter to enable the aphid to take advantage of the mild winter weather that may follow (Bevan and Carter, 1975). Periods of insect-increase correspond to an increase in the nutritive quality of the needles, especially the concentration of free soluble amino-acids.

THE SITKA SPRUCE ROOT APHID, *Pachypappa* sp.

The occurrence of a Pemphigine root-dwelling aphid on Norway spruce in Britain drew some attention in 1951 when aphids were found amongst flocculent white wax on roots that were growing in peat soil at Allerston, Yorkshire. Since then other infestations have been found to occur on Sitka spruce, invariably though when growing on the peaty organic soils in the upland afforested areas of Britain.

Stroyan (1975) in his descriptive account of *Pachypappa tremulae* (L.) and in discussing the spruce root aphids in Britain suggested that as well as a *Stagona* species (probably *S. xylostei* Mordvilko) there seemed also to be a third species present belonging to the *Asiphum/Pachypappa* group. The apterous root-generations of these aphids are very similar; the alate viviparous females, when they appear, show more features that could perhaps be used for identification of species. A number of these alate individuals have now been reared from Sitka spruce root colonies and a biometric description will be published in another article.

Aphid infested roots on Sitka spruce are abundant in the Rhondda plateau forest above the South Wales Coalfield. This forest is an even aged monoculture of Sitka spruce. Prior to afforestation, some 30 years ago, it was moorland dominated by purple moor-grass (*Molinia caerulea* (L.) Moench) and grazed by sheep. There are no trees or shrubs that have become established except very few *Sorbus aucuparia* L. and *Salix capraea* on rocky outcrops where forest roads have been constructed. Similar land is afforested in northern England, South Scotland and Northern Ireland; root aphids are also present in these places to some degree, but their comparative status is yet to be assessed.

In the Rhondda forest plateau (elevation 500m) the average annual rainfall is 2,500mm, and in very wet years is between 3,500 and 4,000mm. Boreholes in these peaty soils show a high yet fluctuating water table which results in shallow tree roots to a depth of only 10-25cm. Many of the fine feeding roots of spruce can be seen ramifying amongst the *Molinea* litter or under the carpet of fallen spruce needles caused by *Elatobium* defoliation. It is just at these surfaces or on the side of old plough furrows made at tree planting time that extensive root-aphid colonies can be seen.

Such colonies were extensively sampled for the first time on 24 October 1986, the date being approximately chosen from recorded observations in previous years when a small proportion of yellowish alatoid nymphs were present. Roots with aphid colonies intact were cultured on moist filter paper in small polystyrene boxes covered by a lid and kept in the laboratory. Alatae were only produced over a brief period of 10 days after sampling. Twelve of these were separately confined to freshly cut shoots of *Populus tremula* or *P. canescens*. The aphids did not settle to feed on these nor did they reproduce.

Subsequent field sampling at various times throughout summer and winter has revealed colonies to be present at each occasion. It would seem that colonies can withstand temporary inundation from heavy rainfall.

DISCUSSION

In Britain *E. abietinum* usually reaches its peak in numbers in the late spring, after which winged forms are produced and the population declines rapidly. This period of increase coincides with high concentration of amino-acids present in the needles just before bud burst (Carter and Nichols, 1988).

The early cessation of growth brought about by unusually dry weather in 1972 and 1973 in many parts of Britain produced foliage of a quality favourable for aphid development in the autumn months (Bevan and Carter, 1975). A higher concentration of foliar amino-acids at the onset of the bud setting period would then occur at a time when temperatures were still high enough for the aphid population to increase rapidly. It has been on rare occasions such as these and under glasshouse conditions that alate males and oviparae have been produced. These have only occurred in very low numbers in late October and early November.

Although a primary host plant for this *Pachypappa* species has not been ruled out in the South Wales area, it seems unlikely to be of much significance at the present time, especially as colonies can survive the year-round under periodically saturated ground conditions. Under more favourable ground conditions for tree growth, the root aphids presumably may influence the uptake of water and nutrients. The thick covering of wax filaments over the colony acts as an effective hydrophobic barrier for the aphid (Bevan and Carter, 1980) and consequently the root.

Both *Elatobium abietinum* and this *Pachypappa* sp. are now well established on Sitka spruce in Britain. Recurrent infestations seem likely as both species seem well able to persist anholocyclicly, and perhaps take advantage of the mild although very wet winter conditions where Sitka spruce is being grown extensively.

Figure 1.   Diagram of aphid extraction apparatus used for removing living aphids from samples of foliage and small roots, drawn to scale.
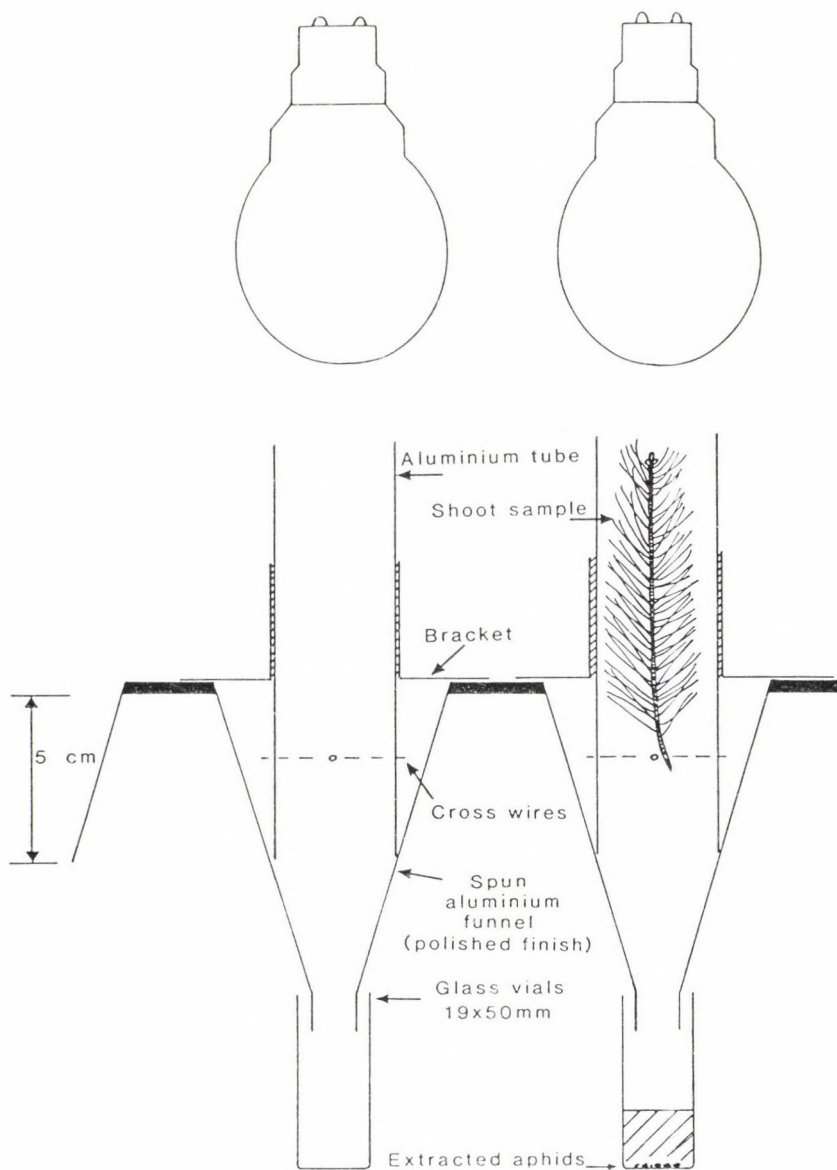
LITERATURE

Bejer-Petersen, B. (1962). Peak years and regulation of numbers in the aphid *Neomyzaphis abietina* (Walker). *Oikos* 13, 155-168.

Bevan, D. and Carter, C.I. (1975). Host plant susceptibility. *Forestry Commission Report on Forest Research 1975*, 37. HMSO, London.

Bevan, D. and Carter, C.I. (1980). Frost proofed aphids. *Antenna* 4, 6-8.

Carter, C.I. (1972). *Winter temperatures and survival of the green spruce aphid*. Forestry Commission Forest Record 84. (10 pp.). HMSO, London.

Carter, C.I. (1977). *Impact of the green spruce aphid on growth*. Forestry Commission Research and Development Paper 116. (8 pp.) Forestry Commission, Edinburgh.

Carter, C.I. (1983). Some new aphid arrivals to Britain's forests. *Proc. Trans. Br. Ent. Nat. Hist. Soc.* 16, 81-87.

Carter, C.I. and Cole, J. (1977). Flight regulation in the green spruce aphid (*Elatobium abietinum*). *Annals of Applied Biology* 86, 137-151.

Carter, C.I. and Nichols, J.F.A. (1988). The green spruce aphid and Sitka spruce provenances in Britain, *Forestry Commission, Occasional Paper* 19, (7pp). Forestry Commission, Edinburgh.

Fisher, M. and Dixon, A.F.G. (1986). Role of photoperiod in the timing of dispersal in the green spruce aphid *Elatobium abietinum*. *Journal of Animal Ecology* 55, 657-667.

Locke, G.M.L. (1987). Census of Woodlands and Trees 1979-82. Forestry Commission Bulletin 63, (123pp). HMSO, London.

Nichols, J.F.A. (1987). Damage and performance of the green spruce aphid, *Elatobium abietinum* on twenty spruce species. *Entomologia Experimentalis et Applicata* 45, 211-217.

Ohnesorge, B. (1961). Wann sind Schäden durch die Sitkalaus zu erwarten? *Allgemeine Forstzeitung* 27/28, 408-410.

Ryle, G. (1969). Forest Service: The first forty-five years of the Forestry Commission of Great Britain. Newton Abbot: David & Charles (340pp).

Stroyan, H.L.G. (1975). The life cycle and generic position of Aphis tremulae L., 1761 (Aphidoidea: Pemphiginae), with a description of the viviparous morphs and a discussion of spruce root aphids in the British Isles. *Biol. J. Linn. Soc.* 7, 45-72.

Theobald, F.V. (1914). Notes on the green spruce aphis (*Aphis abietina* Walker). *Annals of Applied Biology* 1, 23-36.

Walker, F. (1849). Description of aphides. *Annals and Magazine of Natural History* 3 (2), 301-302.

SYSTEMIC FUNGICIDES AS ANTIFEEDANTS: A CASE STUDY USING ACYRTHOSIPHON PISUM

SUZAN A. EL-BASSIOUNY

Plant Protection Institute of the Hung. Acad. Sci.

Budapest, pf. 102, H-1525, Hungary

ABSTRACT

Two systemic fungicides, Fundazol 0.5% and Bayleton 3% were tested for their antifeedant effect on *Acyrthosiphon pisum* reared on *Vicia faba* under green-house conditions. The results indicated that the effect lasted for a comparatively long time, and satisfactorily protected the youngest parts of the plants from aphids attack. Fundazol drastically decreased the number of progeny per female. The effect were extended to the third generations.

INTRODUCTION

Chemical treatment is still the main method of pest control. Several problems have arisen as a result of continuous and extensive use of pesticides (e.g. see data at Forgash, 1985).

Experience shows that many chemicals are capable of inhibiting the feeding of phytophagous chewing or sucking insects even on the optimal host plant. Wright (1963) reported that antifeedant compounds adversely affect only the pests which feed on the crop, and not beneficial natural enemis. For instance, the

compound 20455 (6-dimethyl triazeno acetanilidae) inhibited the
feeding of army worm caterpillars, Mexican beetle larvae, and
other chewing insects, but not the piercing and sucking species.
Such an antifeedant can be more effective and economic to use if,
(1) it is persistent, (2) it easily pentrates and is translocated
in plant. A compound exhibiting both of these properties would
give satisfactory level on control with few treatments (Jermy
and Matolcsy, 1967).

Systemic fungicides that are regularly applied to control
plant disease may also inhibit the feeding of sucking phyto-
phagous insect. Several experiments have shown such effect for
several systemic fungicides (Murbach and Corbaz, 1963; Ascher,
1964; Ascher and Nissim, 1965; Ascher and Meisner, 1969; Ascher
and Rones, 1969; Abo Eyghar et al., 1971; Abdel-Meeged et al.,
1974; Hare, 1984).

The present study investigates the effects of two systemic
fungicides on the feeding and progeny production of *Acyrthosiphon
pisum*.

MATERIAL AND METHODS

Apterous females of *A. pisum* were obtained from a culture
maintained on green house-grown bean *(Vicia faba)*. Experiments
were conducted with 5-7 day old insects.

Vicia faba plants individually potted were grown to a height
of approx. 15 cm. At this time some plants received one watering
with 10 ml of the fungicide suspension and watering was continued
with distilled water only. Others were only watered with amount

of distilled water. Pots were placed in Petri dishes to retain
excess water.

Concentrations (w/v) were prepared using ready-made wettable
powders suspended in distilled water. The concentrations used
refer to the active ingredients. The following systemic fungi-
icdes were used: Chinoin-Fundazol (50 WP: 50% benomil), and
Bayleton.

The following experimental arrangement was used to compare
the effectiveness of both Fundazol and Bayleton in inhibiting
feeding. Apterous 5-7 day old aphid were marked with enamel
paints using a camel hair brush and then placed onto plants that
had 48 hours breviously been watered with the chemicals. Marking
facilitated behavioural observations (movement on the plant) of
the mother. Small cages held one mother were attached to the
highest and lowest leaves of the plant. The cages were removed
after 48 hours, when light nylon sleave-cages were placed over
the plants. The experiment was evaluated 48 hours later. The
number of replicates was 19. In another experiment the same pro-
edure was employed using the concentrations used in the previous
test, in order to determine the fungicides persistence within
the plants. Evaluation of the effects: numbers of the progeny
counted at intervals of 48 hours; weight of progeny and behav-
ioural observation of the mother on the plant were used. In
order to study the long term effects of the fungicides on the
insects some of the progeny were transferred to normal plants
for several generations. Each experiment was repeated 4 times
at least.

RESULTS

Both fungicides caused a reduction in the number of progeny produced per female relative to the control group (Table 1). While Fundazol gave an inhibitory effect at a low concentrations, Bayleton was only effective at a higher concentration. These concentrations greatly reduced the number of progeny produced without any apparent toxic affect on the plant (Table 1).

Table 1
Mean number of offspring produced/female during 5 days on control and treated *Vicia faba* plants. (mean+S.D.)

Treatment	number of aphid/female
Control	15.5 + 4.4 e
Bayleton	
0.1%	15.3 + 3.9 e
1.0%	12.3 + 3.2 d
2.0%	10.8 + 7.2 c
Fundazol	
0.01%	10.3 + 5.9 c
0.2 %	7.3 + 3.4 b
0.5 %	4.3 + 3.3 a

Means signed with the same letter(s) are not significantly different at P=1% (DNMR-test).

At the beginning of the experiment the effect or the fungicides as antifeedants seemed slight with no significant difference in the number of aphids on control and treated plants (Table 2). The effect became evident after 96 hours. Control plants had a greater number of progeny on the highest than the lowest leaf of the same plants. The opposite situation as found on treated plants with the number of progeny on the lowest leaves greater than on the highest leaves.

The behavioural observations of the aphids on plants 2 days after treatment showed that aphids first fed on the lower leaf then moved to the highest one. On the other hand, the insects on

Table 2

Mean number of offspring produced/female on control and treated
Vicia faba plants after different periods of time and according
to position occupied by the aphids on the leaves (mean $\pm$ S.D.).

Treatment	time/ hour	leaf position	
		highest	lowest
Control	48	11.8+3.9a	9.4+2.9a
Bayleton 3%	48	7.9+5.3a	8.3+4.3b
Fundazol 0.5%	48	6.6+5.1a	5.2+3.3b
Control	96	10.9+2.1a	10.4+2.0a
Bayleton 3%	96	6.4+2.4a	7.2+3.6b
Fundazol 0.5%	96	4.2+3.8a	6.2+2.9b
Control	120	12.1+3.1a	11.8+3.9a
Bayleton 3%	120	6.1+3.2a	10.3+2.4a
Fundazol 0.5%	120	6.7+4.8a	8.3+4.7a
Control	144	15.5+2.7a	13.4+4.5a
Bayleton 3%	144	4.8+4.2b	6.5+4.7a
Fundazol 0.5%	144	3.2+3.6b	4.5+4.0b

Mean signed with the same letter(s) are not significantly
different at P=1% (DNMR-test).

control plants moved onto the uppermost leaves and stayed and
produced their progeny there. then some of the progeny moved
onto the stem and slowly occupyied the whole plant.

The weight of the progeny (Fig. 1) decreased significantly
as a result of the fungicide treatments. The weight-decrease
was more marked in the case of Fundazol.

The inhibitory effect of Bayleton affected the second genera-
tion, while that of Fundazol affected even the third generation.

DISCUSSION

The results obtained indicate that both fungicides are
effective antifeedants. The refusal of the aphids to colonize
the top leaves and the stem is an indirect proof for translocation
of the fungicides within the plant, although other factors could
have also contributed. The results of Ascher and Meisner (1969),
Sherrod et al. (1983) and Hare (1984) are similar. The decrease

in the number of the progeny produced on the youngest (top) leaf compared with the oldest (lowest) leaf, especially long after watering with chemicals is indirect proof of persistence. The inhibition of progeny productions proves that the fungicides have a physiological effect on the insect. Jermy and Matolcsy (1967) concluded that systemic properties of fungicides would undoubtly improve their antifeedants properties.
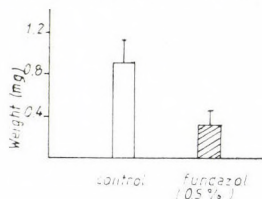
Fig. 1. Mean weight of apterous aphids on *Vicia faba* (mean±S.D.) (Student's t-test for unequal sample size, $t_{calc.}$ 0.30901, df= 45, P= 0.1%).
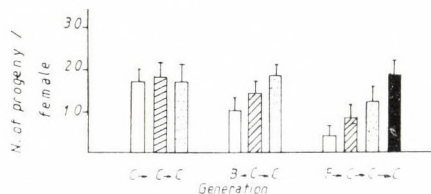
Fig. 2. Mean number of progeny of subsequent generations, after the first selected mother as trans. to control plant (control = C, Bayleton= B, Fundazol= F).

CONCLUSION

It concluded that systemic fungicides applied against pathogens may simultaneously affect of chewing/sucking phytophagous insect pests. Moreover, not only feeding but progeny production can also be affected for an extended period of time (for some generations). The experimental design employed here does not closely follow cultural practice where treatments are usually separated by longer intervals time, i.e. the long-term beneficial effect of persistence seen in this study may not occur in the field.

REFERENCES

Abdel-Megeed, M.I., Zidan, Z.H. and Kbalid, R.A., (1974): Response of the greasy cut worm, *Agrotis ypsilon* Rott to certain antifeedants. Z. angew. Entomol. 76, 106-110.

Abo-Elghar, M.R., Elbadry, E.A. and Radwan, H.S., (1971): Some toxic and antifeedant effects of Du-Ter on the cotton leafworm *Spodoptera littoralis* Boisd. Z. angew. Entomol. 69, 177-181.

Ascher, K.R.S., (1964): Organotin compounds and their potential use in pest control. World Rev. Pest control 3, 198-210.

Ascher, K.R.S. and Meisner, J., (1969): The antifeeding effect of organometalics for larvae of the potato tuber moth *Gnorimoschema operculella* Zell.): A laboratory screening on leaves of eggplants. Z. Pflkr. Pflschutz 76, 564-575.

Ascher, K.R.S. and Nissim, S., (1969): Quantitative aspects of antifeeding: comparing "antifeedant" bioassay with *Prodenia litura* Inter. Pest Control 7, 21-23.

Ascher, K.R.S. and Rones, G., (1969): Fungicides has residual effect on larval feeding. Inter. Pest Control 6, 6-8.

Forgash, A.J., (1985): Insecticide resistance in the Colorado potato beetle. In Ferro, D.N., Voss, R.H. (Eds.). Proceedings of the symposium on the Colorado potato beetle XVIIth Inter. Congress of Entomology., 33-53 pp.

Hare, T.D., (1984): Suppression of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Col.: Chrysomelidae), on solanaceous crops with a copper-based fungicide. Environ. Entomol. 13, 1010-1014.

Jermy, T. and Matolcsy, G. (1967): Antifeeding effect of some systemic compounds on chewing phytophagous insects. Acta Phytopath. Acad. Sci. Hung. 2, 219-224.

Murbach, R. and Corbaz, R., (1963): Influence de trois types de fongicides utilisés en Suisse contre le mildiou de la pomme de terre (Phytophthora infestans (Mont) de Bary) sur la densité de la population du doryphore (*Leptinotarsa decemlineata* Say). Phytopathol. Z. 47, 182-188.

Sherrod, D.W., Linduska, J.J. Hofmaster, R.N. and Franeis, J.A., (1983): Interaction of synthetic pyrethroid-foliar fungicides combination for Colorado potato beetle control in tomato and Irish potato. J. Can. Entomol. Soc. 18, 419-424.

Wright, D.P., (1963): Antifeeding compounds for insect control. Adv. Chem. Seri. 41, 56-63.

SUCTION TRAPPING OF APHIDS IN WESTERN NORTH AMERICA

(EMPHASIS ON IDAHO)

S. Halbert, J. Connelly & L. Sandvol

University of Idaho, SW Idaho Research & Extension Center,

29603 U of I Lane, Parma, ID 83660 USA.

ABSTRACT

The North American Western Regional Aphid Suction Trapping Network
has more than 60 traps in nine U.S. states and one Canadian province.
Data from trap collections are used to alert growers of potential
outbreaks of crop pests or epidemics of aphid transmitted plant viruses
such as barley yellow dwarf virus and potato leaf roll virus. The traps
have been used to track the establishment of *Diuraphis noxia*
(Mordvilko), a serious new pest of small grains in North America, and
to detect other species new to North America [*Hyadaphis tataricae*
(Aizenberg) and *Tinocallis saltans* (Nevsky)].

Diuraphis noxia was first detected in Idaho in June, 1987 when one
specimen was caught in the trap at Parma. By August, 1988, virtually
every wheat-producing area in the state was infested. In 1987, the 17
suction traps in Idaho collected 29 *D. noxia*. In the following season,
the same traps collected over 27,000 *D. noxia*. Initial trap collections
of *D. noxia* coincided with initial colonization of spring-sown cereal
crops. Presence of *D. noxia* in autumn trap samples indicated that there
was sufficient flight activity to warrant delayed planting of fall wheat
or use of an at-planting systemic insecticide.

Trap collections probably reflect flight activity within a 20-50 mile radius of the trap. Species composition of the samples can be accounted for by the composition of local vegetation.

The timing of peak flights of *D. noxia* in 1988 paralleled average lilac bloom dates (a widely used phenological indicator) for Idaho trapping locations. We think Idaho collections reflect phenological influences rather than large-scale migration of aphids.

INTRODUCTION

The European suction trap network has demonstrated the usefulness of monitoring aphid flights for the purpose of forecasting aphid pest populations and the potential for virus spread (Taylor, 1973; Tatchell, 1985a,b; Tatchell et al., 1988). Patterned after the European system, a network of suction traps has been established in western North America to detect and track the establishment of species new to the area, to provide a basis for alerting growers when flights of aphid pests occur and to better understand the phenology of aphid flight activity. This paper will discuss the entire network in a general way and focus in detail on our experience in the state of Idaho.

MATERIALS AND METHODS

The Western Regional Suction Trap Network has over 60 traps in nine Western States and one Canadian Province. Traps are located in strategic agricultural sites with particular emphasis on cereal production. There are 21 traps in Idaho (Figure 1). The traps are 8 m high with a diameter of 30 cm after the Allison & Pike (1988) design. The airflow is 570m3/hr, about 1/5 that of the Rothamsted traps which are 12.2 m high with a diameter of 24.4 cm (Macaulay et al., 1988).

Samples are collected weekly during the cropping season and mailed to identification centers in various states. Some regional centers (Colorado, Wyoming, Utah, California) identify only common pests, while others (Idaho, Washington) identify all the aphids at least to genus.

The data are compiled into data bases for subsequent analysis, and collections of pest species are entered into the nationwide NAPIS computer network. Weekly summaries of flight activity of economic species are distributed by regional identification centers to fieldmen, extension agents, interested growers, and researchers.

1.   Bonners Ferry
2.   Moscow
3.   Lewiston
4.   Craigmont
5.   Parma
6.   Caldwell
7.   Mountain Home
8.   Kimberly
9.   Picabo
10. Burley
11. INEL
12. Aberdeen
13. Neeley Area
14. Arbon Valley
15. Rockland Valley
16. Holbrook
17. Preston
18. Soda Springs
19. Shelley
20. Ririe
21. Tetonia
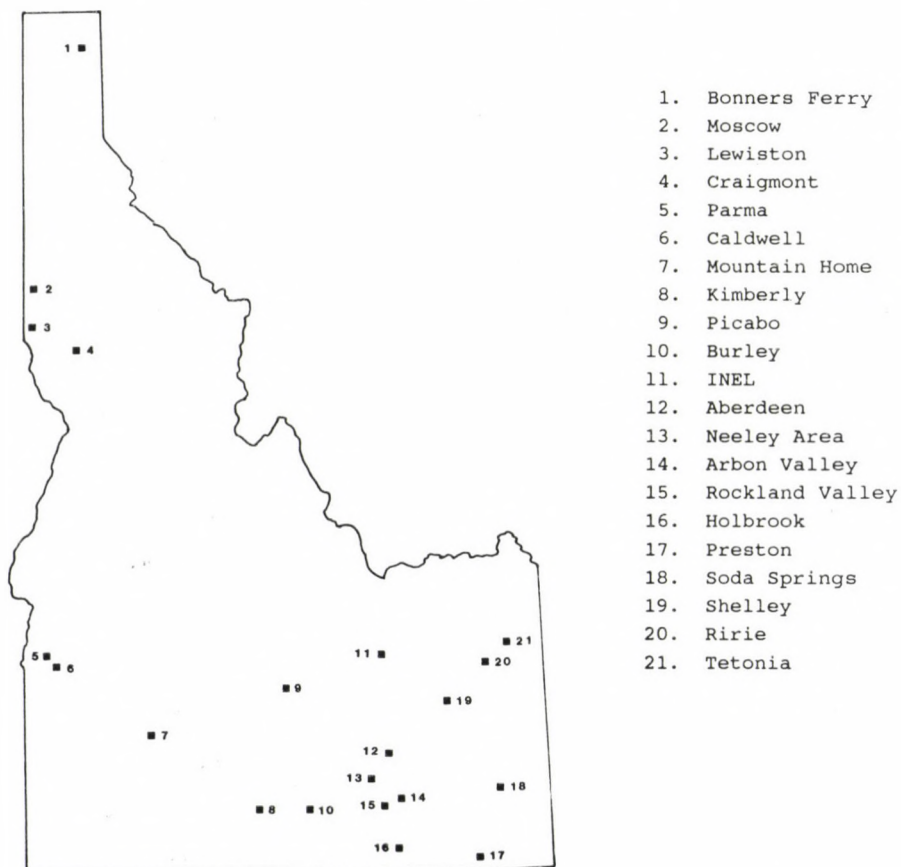
Fig. 1. Map of Idaho showing suction trap locations.

RESULTS AND DISCUSSION

The suction traps have been used to provide service to growers and to study content and biology of the aphid fauna. These aspects of our work are discussed below as they pertain to the state of Idaho.

Detection of Species New to the Region

One of the purposes of the trapping network is to detect and track the distribution of species new to the region. In Idaho, we have experience with three.

1. *Diuraphis noxia* (Mordvilko) (the Russian wheat aphid), by far the most important of the three, was introduced into Mexico in the late 1970's and early 1980's and was officially first detected in the United States in Texas in 1986 (Stoetzel, 1987). By the end of that season, it had become a serious pest as far north as southern Wyoming. In late June, 1987, one specimen was collected in the suction trap in Parma, Idaho. A few days later, Feng Ming-guang found a small infestation in a field of late planted wheat about 30 km from the trap. No *D. noxia* had been found in routine cereal surveys prior to that time.

We were surprised to find that *D. noxia* showed up first in western Idaho in Canyon County when all previous records were east of Idaho. We believe this can be explained by elevation-related phenology. Western Idaho is lower in elevation than eastern Idaho and thus warms up much earlier in the spring. We suspect that *D. noxia* was widely distributed across southern Idaho at low densities early in the spring of 1987. In western Idaho, populations reached levels detectable by the traps earlier than they did farther east because of earlier prolonged mild temperatures. Very few *D. noxia* were collected the first season, but first collections across the state coincided with the appearance of detectable field populations.

The next season's trap samples documented the establishment of

D. noxia in Idaho.   In 1987, a total of 29 *D. noxia* were collected.   In

1988 the same traps collected over 27,000.   In 1987, *D. noxia* made up

0.05 percent of the sample.   In 1988, 34.2 percent of the sample was

D. noxia.   First collections in northern Idaho traps coincided with

occurrence of field colonies there, and first collections in general

coincided with the occurrence of detectable populations on spring-sown

cereal crops.

In 1989, the *D. noxia* population in Idaho declined sharply,

probably due to the hard winter.   No *D. noxia* were collected in the

suction traps until most cereal crops had matured beyond the point where

economic injury could be expected.   Insecticide treatment for *D. noxia*

was negligible in Idaho in the spring of 1989.

Suction traps generally detected *D. noxia* before economic

infestations occurred in spring sown cereal crops.   Peak flights

reflected emigration from maturing fields.

2.   *Hyadaphis tataricae* (Aizenberg) was first detected in the

United States in Illinois in 1979 (Voegtlin, 1981).   It causes dwarfing

of the terminal leaves and a severe "witch's broom" distortion of

growing tips of many varieties of *Lonicera* spp.   The damage is often

mistaken for a plant disease.   In the spring of 1986, three specimens

were caught in the Parma suction trap.   As with *D. noxia*, the first

collection occurred in the mildest part of the state.   In 1987,

specimens were collected in eastern and northern Idaho as populations

reached detectable levels in cooler areas.   *Hyadaphis tataricae* is not

abundant in trap samples, but it is now collected consistently

throughout the state, and extension agents receive numerous samples of

infested bushes from homeowners.

3. *Tinocallis saltans* (Nevsky) was first collected in September
1986 in the Parma suction trap. This is a new record for North America,
and it is unknown where or when this Asian elm aphid was introduced.
Because Idaho is an inland state, it is unlikely that the original
introduction occurred here. By 1988, trap samples indicated that
T. saltans was present throughout the state. In the spring of 1989, it
was one of the most common species collected in western Idaho. The
aphid has also been collected on *Ulmus pumila* in Caldwell, Parma, and
Mountain Home.

Crop Protection Forecasting

The original purpose for the suction traps in Idaho was to
determine safe fall planting dates for dryland winter wheat,
particularly in the high mountain valleys of eastern Idaho where barley
yellow dwarf virus (BYDV) epidemics occur fairly regularly. Several new
snow mold resistant varieties of wheat have become popular in these
areas, and in order for the snow mold resistance to reach its full
potential, the wheat must be planted as early as mid-August, which puts
it at risk for BYDV. The primary vector under these conditions is
Schizaphis graminum (Rondani) (the greenbug).

Peak collections of cereal aphids coincide with maturation of the
crop, usually in late July or early August. Populations decline after
that at a rate dependent upon environmental conditions. Our experience
has shown that if growers plant untreated wheat when local suction traps
are collecting approximately 40 or more *S. graminum* per week, fall
problems with BYDV are likely. If numbers are still high in mid-August,
we recommend delayed planting or at-planting systemic insecticide
treatment. We hope to refine this threshold to include infectivity data
as is done at Rothamsted (Plumb & Lennon, 1982).

The trapping network is used to alert growers to potential *D. noxia* infestations in the spring. Colonization of spring-sown cereals coincides with initial collections of *D. noxia* in the suction trap. Fall wheat can become heavily infested though very few *D. noxia* are caught in the suction trap (Table 1). The fall threshold may be too low to be detectable using our suction traps; however, if the suction traps are collecting any *D. noxia*, damaging infestations in the area are likely.

Potatoes are one of Idaho's major crops. Tubers of Russet Burbank, the most widely grown variety, develop a condition known as net necrosis if they are infected with potato leaf roll virus (PLRV). Bishop and others (Bishop & Guthrie, 1964; Byrne & Bishop, 1979) developed a pest management program for PLRV which depends upon monitoring numbers of *Myzus persicae* (Sulzer) (green peach aphid), the most important vector.

The suction traps are now used in conjunction with yellow pan traps and direct field scouting to alert potato growers of *M. persicae* movements. Usually, yellow pan traps will collect *M. persicae* before it is collected in suction traps (Table 2), but specimens are generally collected in suction traps before damaging infestations occur.

Aphid Biology

We believe that our traps reflect aphid flight activity within a 20-50 mile radius of the trap. We suspect that some of the aphids collected have flown at least 20 miles. One trap is located at the Idaho National Engineering Laboratory (INEL) in a desert site which is about 20 miles from the nearest agricultural development. It collects large numbers of cereal aphids which would not survive in the desert in significant numbers at the time of year when they are caught (Table 3).

Table 1   Suction trap collection of and percent plants infested with
           Diuraphis noxia (Mordvilko) in wheat fields in Canyon County,
           Idaho. 1987, 1988.

	Cummulative Average Suction Trap Collections from 15 Sept (2 traps)	Average % Plants Infested (8-10 fields surveyed)
5 Nov 1987	1	2.8
19 Nov 1987	1	17.6
5 Oct 1988	4	2.0
1 Nov 1988	11.5	12.6
1 Dec 1988	13.5	35.3

Table 2   Initial collections of *Myzus persicae* (Sulzer) in yellow pan
           traps and suction traps, and first date economic threshold
           was exceeded in Canyon County, Idaho. 1985-1989.

Year	Yellow Pan Traps	Suction Traps	Economic Threshold Exceeded
1985	19 June	6 July	22 July
1986	16 June	29 June	30 June
1987	8 June	11 May	25 August
1988	16 June	24 June	18 July
1989	26 June	7 July	Never Exceeded

*In each year there were 10 yellow pan traps with a surface area
of 1200 cm^2, two suction traps and 10 scouting fields.

Table 3   Cereal aphids* collected at INEL (desert site) & Aberdeen
           (agricultural site) in eastern Idaho, July & August 1987-1989.

Year	INEL	Aberdeen
1987	506	2101
1988	187	379
1989 (July only)	1487	2502

Rhopalosiphum padi, Rhopalosiphum insertum, Rhopalosiphum maidis,
Metopolophium dirodum, Sitobion avenae, Schizaphis graminum, Diuraphis
noxia, Sipha elegans.

Table 4   Contribution of aphids with native desert hosts to total suction
           trap collections at selected locations. Idaho, 1987, 1988.

Location	% Desert Aphids 1987	% Desert Aphids 1988	Vegetation
INEL	3.4	1.9	Desert
Arbon Valley	2.2	1.8	Desert and Dryland Cereal Production
Parma	0.4	0.02	Irrigated Agriculture
Kimberly	0.1	0.05	Irrigated Agriculture
Moscow	0.0	0.0	Dryland Cereals, Legumes, Rapeseed and Forest

Though some of the aphids caught have flown 20 miles or more, we think trap collections for the most part represent emigration from local crowded colonies rather than long distance migration. Several observations support this hypothesis. Few if any species are caught more than 100 miles from the closest host plant. Aphids infesting native desert shrubs such as *Artemisia tridentata* and *Atriplex canescens* are host specific. The contribution made by these species is small because of the overwhelming numbers of crop pests, but relative percentages of desert species reflect the composition of surrounding plant communities (Table 4). Collections of large numbers of pest species can virtually always be accounted for by heavy infestations in local crops.

Relative numbers of aphids collected in the traps reflect phenological development. In 1986, peak flights of *Metopolophium dirhodum* (Walker) occurred progressively later at increasing elevations across Idaho (Figure 2). Everson & Caprio (1974) developed a phenology
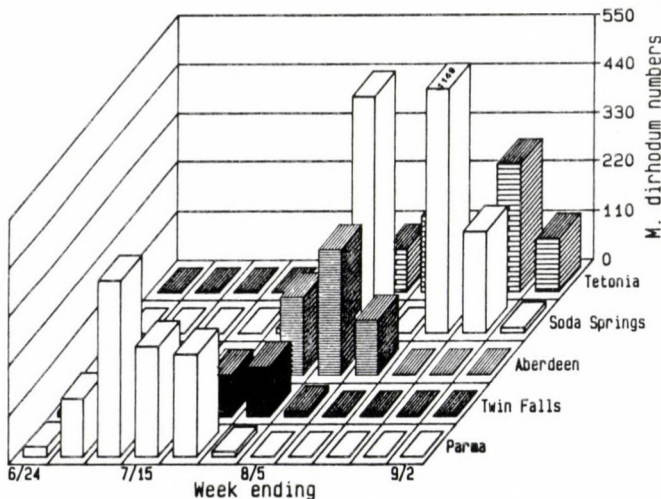
Fig. 2. Suction trap collections of *Metopholophium dirhodum* at sites increasing in elevation from Parma (700 m) to Tetonia (1800 m), Idaho, USA, 1987.
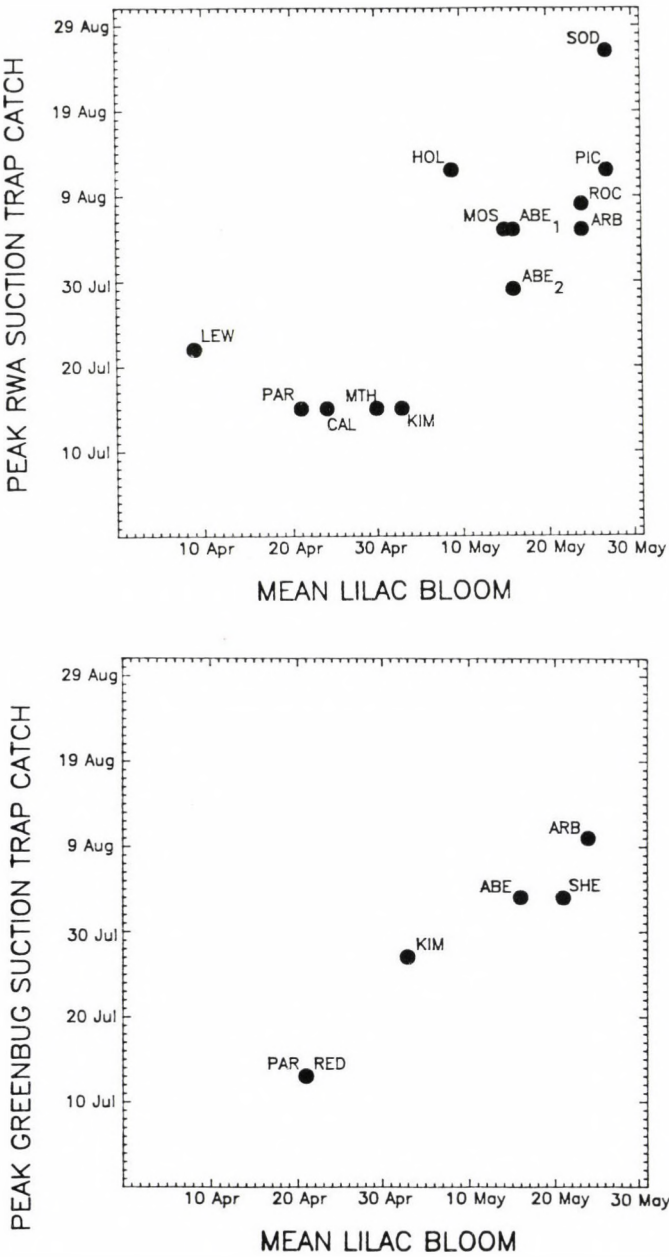
Fig. 3. For Idaho, USA, scatter plots of lilac bloom dates & peak suction
   trap collections of *Diuraphis noxia* (1985) and *Schizaphis graminum* (1988).

map of Idaho based upon average lilac bloom date. Peak flights of

Schizaphis graminum in 1985 occurred later at locations with later lilac

bloom dates (Figure 3). The correspondence was not as good for *D. noxia*

in 1988, possibly because *D. noxia* is still in the process of becoming

established in Idaho.

CONCLUSIONS

Suction traps have been useful in detecting and monitoring

establishment of aphid species new to Idaho. Populations reach

detectable levels first in the mildest areas, and subsequent collections

reflect elevation and latitude related phenology.

The trapping network has also been useful in crop pest forecasting,

particularly for cereal crops.

ACKNOWLEDGEMENTS

REFERENCES

Allison, D. & Pike, K.S. (1988): An inexpensive suction trap and its use
    in an aphid monitoring network. J. Agric. Entomol., **5**. 103-107.

Bishop, G.W. & Guthrie, J.W. (1964): Home gardens as a source of the
    green peach aphid and virus diseases in Idaho. Amer. Potato J., **41**.
    28-34.

Byrne, D.N. & Bishop, G.W. (1979): Relationship of green peach aphid
    numbers of spread of potato leaf roll virus in southern Idaho.   J.
    Econ. Entomol., **72**. 809-811.

Everson, D.O. & Caprio, J.M. (1974): Phenological map of average date
    when lilacs start bloom in Idaho.   Misc. Publ. No. 18, Idaho
    Agricultural Experiment Station.

Macaulay, D.M., Tatchell, G.M. & Taylor, L.R. (1988): The Rothamsted
    Insect Survey "12-metre" Suction Trap.   Bull. Entomol. Res., **78**. 21-9.

Plumb, R.T. & Lennon, E. (1982): Aphid infectivity and the infectivity
    index.   Report of the Rothamsted Experimental Station for 1981, Part 1
    pp. 195-197.

Stoetzel, M.B. (1987): Information on and identification of *Diuraphis
    noxia* (Homoptera: Aphididae) and other aphid species colonizing
    leaves of wheat and barley in the United States.   J. Econ. Entomol.,
    80. 696-704.

Tatchell, G.M. (1985a): Aphid-control advice to farmers and the use of
    aphid-monitoring data.   Crop Protection, **4**. 39-50.

Tatchell, G.M. (1985b): Forecasting aphids and the diseases they
    transmit.   Proceedings of the Seminar on Agrometeology and Pest
    Forcasting, Fulmer Grange, U. K.   pp. 81-88.

Tatchell, G.M., Plumb, R.T. & Carter, N. (1988): Migration of alate
    morphs of the bird cherry oat aphid (*Rhopalosiphum padi*) and
    implications for the epidemiology of barley yellow dwarf virus.   Ann.
    Applied Biol., **112**. 1-11.

Taylor, L.R. (1973): Monitoring change in the distribution and abundance
    of insects.   Rothamsted Report for 1973, Part 2 pp. 202-238.

Taylor, L.R., French, R.A., Woiwod, I.P., Dupuch, M.J. & Nicklen, J.
    (1980): Synoptic monitoring for migrant insect pests in Great Britain
    and Western Europe I.   Establishing expected values for species
    content, population stability and phenology of aphids and moths.
    Rothamsted Report for 1980, Part 2 pp. 41-104.

Voegtlin, D. (1981): Notes on a European aphid (Homoptera: Aphididae)
    new to North America.   Proc. Entomol. Soc. Wash., **83**. 361-362.

WEATHER, LIFE CYCLE STRATEGY AND SPRING POPULATIONS OF APHIDS

R. Harrington, G.M. Tatchell and J.S. Bale*

Department of Entomology and Nematology, AFRC Institute of

Arable Crops Research, Rothamsted Experimental Station,

Harpenden, Hertfordshire, AL5 2JQ, England.

*Department of Pure and Applied Biology, University of Leeds,

Leeds, LS2 9JT, England.

ABSTRACT

The numbers of fourteen aphid species sampled in spring
and early summer using the Rothamsted 12.2 m suction trap, and
their time of first appearance in the trap, are compared by
linear regression with temperature data from December to
June. There are good correlations for largely anholocyclic
species, especially with winter temperatures, but for most
holocyclic species the correlations are poor. The potential
value of such relationships in forecasting aphid problems and
in suggesting areas for complementary laboratory and field
studies on aphid overwintering is discussed.

INTRODUCTION

The winter of 1988/89 was the mildest in Britain for many
years. This led to the expectation that the aphid *Myzus
persicae* (Sulzer) which is largely anholocyclic in Britain,
would be detected in suction trap samples earlier than usual
(Bale, Harrington & Clough, 1988; Harrington, Dewar & George

1989), and that the risk of problems from virus spread in
potatoes and sugar beet would be greater than after cold
winters which delay the spring migration. An unusually warm
spring followed the mild winter and severe aphid problems were
reported in many crops.

The relationship between temperature in winter and
early spring and the time of the first suction trap record of
nine potato and cereal aphid species in Scotland was studied
by Turl (1980). Using up to nine years of data she found a
significant negative relationship between temperature and the
date of first record for seven of the nine species; February
being the most significant month for most species. Turl
suspected that more significant relationships were occurring
for those species comprising populations with a high
proportion of anholocyclic clones, active individuals being
less cold tolerant than eggs, but did not have data to confirm
this. The relationship between winter weather and first
suction trap record for *Sitobion avenae* (Fabricius) and *S.
fragariae* (Walker) was examined over a range of latitudes
(Walters & Dewar, 1986). No relationship was found for *S.
fragariae* which is largely holocyclic at all latitudes in
Britain, nor for *S. avenae* in the north where it is largely
holocyclic. However in the south, where *S. avenae* is largely
anholocyclic, a significant negative relationship was found
between winter temperatures (particularly in January and
February) and first suction trap record.

In this paper, 21 years of data from Rothamsted are used
to look at the relationship between suction trap records and

temperature for 14 aphid species ranging from those being
entirely anholocyclic to those entirely holocyclic in southern
Britain.   The findings are discussed in relation to life cycle
strategy and an attempt is made to evaluate the relative
importance of mild winters and warm springs in causing aphid
epidemics in Britain.

METHODS

Aphid data: The Rothamsted Insect Survey (Taylor, 1986), has
operated a 12.2 m. suction trap (Macaulay, Tatchell & Taylor,
1988) at Harpenden, England since 1965.   All aphids caught
have been identified but data from 1968 to 1988 only were used
here, as prior to that some species of interest were not
separated from other closely related species.   Thirteen pest
species and one common tree aphid were studied and classified
according to the degree of holocycly.   This cannot be precise
and will vary to some extent from year to year, but the
classifications used are thought to represent the general
situation in southern Britain.   The date (day number since 1
January) of the first and third record of each species in the
suction trap, and the numbers caught ($\log_{10}$ (N + 1)) until 1
July and 15 July were extracted for examination with
temperature data.

Temperature data: Temperature data from the meteorological
station at Rothamsted were extracted from the Agriculture and
Food Research Council's 'ARCMET' database.   Screen mean
temperatures for each individual month and each combination of
consecutive months from December to June were calculated from

December 1967 until June 1988.

Comparison of aphid and temperature data: Linear regression

analyses of each aphid variable (y) on each temperature

variable (x) were done.   Correlation coefficients were used to

assess the significance of relationships found.   Where

December temperature is used it refers to the December prior

to the year of aphid data.

RESULTS

The significance levels for all the correlations of

temperature data with the date of first suction trap record

and with the number of aphids caught until 1 July are shown in

Tables 1 and 2 respectively.   Examples of the regression lines

for *M. persicae* are shown in Figures 1 and 2 and points for

1989 are included.   The date of the third record and the

numbers caught until 15 July generally gave similar or

marginally worse fits and are not shown.

The correlations between temperature and first suction trap

record are negative, with the exception of that for

Drepanosiphum platanoidis (Schrank).   Thus, in general, high

temperature over winter and spring corresponds to an early

date of first record.   For the largely anholocyclic species

there is a good relationship between winter temperature and

first record with high significance being found by using

temperature data to March.   The best combination of months

varies between the species but there is generally little to be

gained by considering temperatures beyond March.   February

is generally the most significant individual month.   Similar

results are found for *Brevicoryne brassicae* (L.) and for

Brachycaudus helichrysi (Kaltenbach). For other species

temperature data from later months is generally required, but

fewer significant correlations are found.

The correlations between temperature data and number of

aphids caught to 1 July are positive with the exception of *D.*

platanoidis. Thus, high temperature over winter and spring

usually corresponds with large numbers of aphids trapped.

Again the best correlations are for the largely anholocyclic

species and for *B. brassicae*, with the winter months being

most important. A similar result is found for *Rhopalosiphum*

padi (L.). Few significant correlations are found for other

species, although temperatures from April to June are related

to numbers of *Acyrthosiphon pisum* (Harris) and *Metopolophium*

dirhodum (Walker) trapped.

DISCUSSION

It is apparent that winter temperature is more closely

related than spring temperature to the time of the first

appearance of the largely anholocyclic species studied, and to

their numbers in early summer. It may be that there are

generally a sufficient number of anholocyclic clones of *B.*

brassicae and *R. padi* for similar relationships to be found.

Brachycaudus helichrysi is unusual in that eggs hatch in

autumn rather than in spring so that, although largely

holocyclic, it passes the winter as active stages and may thus

be influenced by temperature in a similar way to the largely

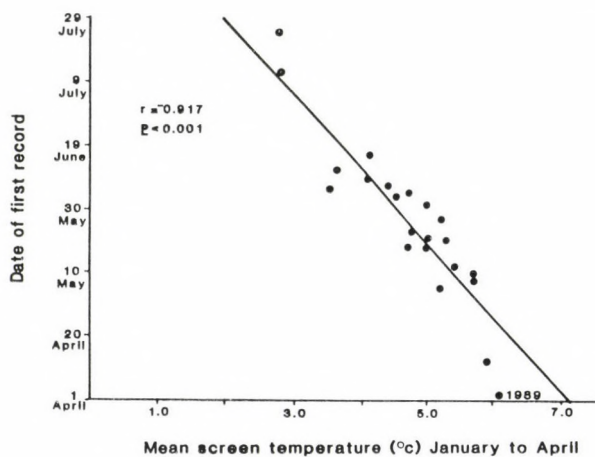anholocyclic species. *Drepanosiphum platanoidis* is

Fig. 1. Date of first record of *Myzus persicae* in suction trap
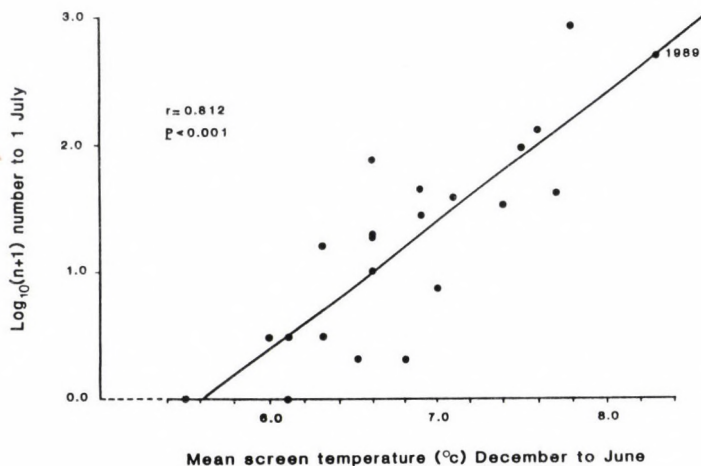vs January - April mean screen temperature (Rothamsted, 1968 -
1988)

Fig. 2. Numbers ($\log_{10}(n + 1)$) of *Myzus persicae* in suction
trap up to 1 July vs December - June mean screen temperature
(Rothamsted, 1968 - 1988)

TABLE 1 Significance of correlation between date of first suction trap record and screen mean temperature at Rothamsted, 1968-1988.

3 = P<0.001   2 = P<0.01   1 = P<0.05
All correlations are negative except for *D. platanoidis*

First Month

(Row labels D–J at left represent the "Last Month"; each species block has sub-columns D J F M A M J.)

LARGELY ANHOLOCYCLIC SPECIES

Myzus ascalonicus

Last Month	D	J	F	M	A	M	J
D	1						
J	2	1					
F	3	2	1				
M	2	1					
A	3	2	1				
M	3	1					
J	2	1					

Macrosiphum euphorbiae

Last Month	D	J	F	M	A	M	J
F	1	2	3				
M	2	2	3				
A	2	2	3	1			
M	2	2	3	1			
J	2	2	3				

Myzus persicae

Last Month	D	J	F	M	A	M	J
J	2	2					
F	3	3	3				
M	3	3	3				
A	3	3	3	1			
M	3	3	3	2			
J	3	3	3	1			

Sitobion avenae

Last Month	D	J	F	M	A	M	J
J	1	2					
F	3	3	3				
M	3	3	2				
A	3	3	2				
M	3	3	3	2	1		
J	3	3	3	1			

SPECIES COMMONLY BOTH ANHOLOCYCLIC AND HOLOCYCLIC

Acyrthosiphon pisum

Last Month	D	J	F	M	A	M	J
M			1				
J			1				

Brevicoryne brassicae

Last Month	D	J	F	M	A	M	J
J	2	2					
F	2	3					
M	1	2					
A	2	2					
M	2	3	1				
J	3	3	2	1	1		

Cavariella aegopodii

Last Month	D	J	F	M	A	M	J
A	1		1				
M	2	2	3				
J	1						

Rhopalosiphum padi

Last Month	D	J	F	M	A	M	J
F	1						
A	1	1					
M	1						
J	1	1					

LARGELY HOLOCYCLIC SPECIES

Brachycaudus helichrysi

Last Month	D	J	F	M	A	M	J
F	1	2	2				
M	1	1	1				
A	2	2	2	1	2		
M	2	2	2	2	2		
J	2	2	2				

Metopolophium dirhodum

Last Month	D	J	F	M	A	M	J
F			1				
A			1				
M			1	1			
J			1				

Aphis fabae

Last Month	D	J	F	M	A	M	J
J						1	

Phorodon humuli

Last Month	D	J	F	M	A	M	J
F	1	1					
A	1						
M	1	2	2	2	3	2	
J	1	2	3	2	1		

Hyperomyzus lactucae

Last Month	D	J	F	M	A	M	J
F		1					
M		1					
A		1					
M	1	2	1	1			
J		1					

Drepanosiphum platanoidis

Last Month	D	J	F	M	A	M	J
M	1	2	1				
A		1					

TABLE 2 Significance of correlation between number in suction trap until July 1 and screen mean temperature at Rothamsted, 1968-1988.

3 = P<0.001 2 = P<0.01 1 = P<0.05
All correlations are positive except for *D. platanoidis*

First Month

LARGELY ANHOLOCYCLIC SPECIES

	Myzus ascalonicus	Macrosiphum euphorbiae	Myzus persicae	Sitobion avenae
	D J F M A M J	D J F M A M J	D J F M A M J	D J F M A M J
D				
J	1 1	1 1	1 2	1
F	3 3 2	3 3 2	3 3 2	2 2 1
M	2 2	2 2 1	3 3 1	1 2
A	2 2	3 2 1	3 3 1	2 2 1
M	3 2 1 1	3 2 1	3 3 2	2 2 1
J	3 3 2 1 1	3 3 3 1	3 3 3 2	3 3 2 1 1

SPECIES COMMONLY BOTH ANHOLOCYCLIC AND HOLOCYCLIC

	Acyrthosiphon pisum	Brevicoryne brassicae	Cavariella aegopodii	Rhopalosiphum padi
	D J F M A M J	D J F M A M J	D J F M A M J	D J F M A M J
D				
J		2 3		1 3
F		2 3		1 2
M		1 1		1
A		1 1		
M		2 2		2 1
J	3 2 2	3 3 1 2 1 1 1		2 2 2 2 1

Last Month (row label at left)

LARGELY HOLOCYCLIC SPECIES

	Brachycaudus helichrysi	Metopolophium dirhodum	Aphis fabae	Phorodon humuli
	D J F M A M J	D J F M A M J	D J F M A M J	D J F M A M J
D	1			
J	1			
F	2			
M	2			
A	1			
M	1			
J	1	1 3 2 2		

	Hyperomyzus lactucae	Drepanosiphum platanoidis
	D J F M A M J	D J F M A M J
D		
J	2 2	
F	1 1	
M		1 1 1 2
A		1 1
M		
J		

exceptional in that early records and large numbers are related to low temperature, especially in February and March. It would be interesting to examine other monoecious tree-dwelling species in this respect.

For the largely anholocyclic species, it is thus possible to forecast by February or March whether early and large flights of aphids in spring are likely and this clearly has potential value in crop protection (Dewar & Carter, 1984). It is important to complement such studies with laboratory and field work to establish causal relationships between temperature and aphid records. Where relationships are not found, investigations of other weather variables, other temperature indices or non-meteorological factors may help explain spring population levels and enhance forecasting efforts.

REFERENCES

Bale, J.S., Harrington, R. & Clough, M.S. (1988): Low temperature mortality of the peach-potato aphid *Myzus persicae*. Ecol. Ent., 13, 121-129.

Dewar, A.M. & Carter, N. (1984): Decision trees to assess the risk of cereal aphid (Hemiptera: Aphididae) outbreaks in summer in England. Bull. ent. Res. 74, 387-398.

Harrington, R., Dewar, A.M. & George, B. (1989): Forecasting the incidence of virus yellows in sugar beet in England. Ann. appl. Biol., **114** (in press).

Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988): The Rothamsted Insect Survey '12-metre' suction trap. Bull. ent. Res. 78, 121-129.

Taylor, L.R. (1986): Synoptic dynamics, migration and the Rothamsted Insect Survey. J. anim. Ecol. 55, 1-38.

Turl, L.A.D. (1980): An approach to forecasting the incidence
    of potato and cereal aphids in Scotland. EPPO Bull. 10,
    135-141.

Walters, K.F.A. & Dewar, A.M. (1986): Overwintering strategy
    and the timing of the spring migration of the cereal
    aphids *Sitobion avenae* and *Sitobion fragariae*. J. appl.
    Ecol. 23, 905-915.

LABORATORY STUDIES ON THE GROWTH AND REPRODUCTION OF
SITOBION AVENAE F. (HOMOPTERA; APHIDIDAE)

Gergely Kalmár and Géza Kuroli

Plant Production System of Kisalföld, Győr, Pásztor u. 17

H-9024, Hungary

PANNON University of Agricultural Sciences, Faculty of

Agricultural Sciences, Mosonmagyaróvár, Vár 2 H-9201, Hungary

ABSTRACT

1. The lower temperature threshold for development was
    5.9 °C.

2. The duration of developmental time varied from 7-11
    days and was on average 8.7 days.

3. The prereproductive period of adults is short; usually
    a few hours.

4. The reproductive period lasted 6-8 days. During this
    time an average of 20.8 offsprings were produced. Adults
    died shortly after the birth of their last offspring.

5. The average total nymphal developmental time was 8.7
    days and adult life 7.1 days.

INTRODUCTION

It is well known that Sitobion avenae Fabricius causes
large losses in grain producing countries. According to Müller
/1961/, Valencia et al. /1976/, Zuñiga and Suzuki /1976/ this
aphid occurs in the Palearctic and Nearctic regions and

Catherall /1974/ has reported it from New Zealand and Chiang
/1977/ from the Oriental region.

The damage it causes and its way of life in Hungary have
been reported by Szalay-Marzsó /1970/, Andrásfalvy /1971/,
Kovács et al. /1973/ and Kalmár /1980/.

The summer generations of this aphid develop on cultivated
plants, and frequently reach high numbers on wheat and maise.

In addition to the direct damage caused by S. avenae, it
is an effective vector of maize dwarf mosaic virus /Horváth,
1972/. Although this aphid is often abundant, little information
is available on its biology in the field, and it is therefore
difficult to control. If we are to follow the development of
populations of this aphid on commercial grain crops, we need to
know its rate of development and potential fecundity.

MATERIAL AND METHODS

In order to establish the lower temperature threshold for
development and the number of day degrees necessary for the
development of each instar of apterous virginoparae, the aphid
was reared in climatic chambers.

For the purpose of the investigations we used L_1 degree
instars originated from virgo generations line. We put the
instars at the age of 8 days on the back side of the wheat
leaves /B 1/ isolated individually.

Observations were made every 24 hours and the time between
moults and the number of offspring produced noted.

In the first part of the investigation the development of
the individuals, kept at one of 3 different temperatures /17,

21, 25 $^{\circ}$C/ was investigated.

From the average developmental times the lower temperature threshold for development was calculated. The total number of day degrees /T/ needed for development was calculated from:

$$T = \frac{K}{t - a}$$

where K is effective temperature sum /$^{\circ}$C/, t is temperature /$^{\circ}$C/ and a is lower development temperature /$^{\circ}$C/.

In the second part of the investigation the time between moults was determined at 21 $^{\circ}$C. The aphids were inspected every 24 hours, when any cast skins were removed from the cages with a fine brush.

From the time of each moult the duration of each instar was determined. Adult life span was calculated from the last moult to the time of death.

In the third part of the investigation the reproductive period of the adults and their average offspring production was determined.

Offspring were removed each day, so that the maximum and minimum number offspring produced by each adult could be determined.

RESULTS

The developmental times of the instars of <u>S. avenae</u> reared at 3 different temperatures on the leaves of wheat are summarized in Table 1.

Table 1

The duration of development of the instars of <u>Sitobion avenae</u> /F./ reared at
3 different temperatures on the leaves of wheat

Instar	17 °C Development time /days/			Effective temperature sum °C	21 °C Development time /days/			Effective temperature sum °C	25 °C Development time /days/			Effective temperature sum °C
	min.	max.	$\bar{x}$		min.	max.	$\bar{x}$		min.	max.	$\bar{x}$	
L_1	1	3	2.2		1	3	1.6		1	4	1.7	
L_2	2	5	4.0	130.4	0	5	2.3	130.4	1	5	3.0	218.4
L_3	2	5	2.4		2	4	2.5		2	5	3.6	
L_4	2	4	3.2		0	4	2.3		2	5	3.3	
Total	9	14	11.8		7	11	8.7		10	13	11.6	

Lower development temperature: 5.9 °C

The developmental time was shortest at 21 °C, 8.7 days
on average; at 17 °C and 25 °C it was 11.8, 11.6 days,
respectively.

The lower temperature threshold for development was calcu-
lated for the whole developmental period: it was 5.9 °C. Using
this value the total number of day degrees necessary for deve-
lopment of apterous virginoparae was determined.

The shortest average developmental time was 8.7 days at
21 °C. The minimum developmental time was 7 days and the
maximum 14. Overall the first instar took the shortest and
the second instar the longest time to complete their development.

The adults lived for 7.1 days on average. The shortest span
of life was 6 days and the longest 8 days. The combined life span
of instars plus adults was 15.8 days at 21 °C. The results of

the investigations on the length of adult life and progeny
production in <u>S. avenae</u> are shown in Fig. 1.
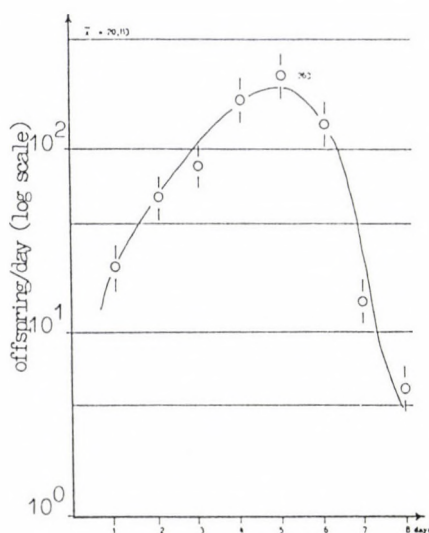
Fig.1. The average daily progeny production by Sitobion avenae (F.).

The prereproductive period was short, for most individuals
only a few hours. The reproductive period varied between 6-8
days, during which the adults produced an average of 20.8
offspring. The number of the offspring varied between 7-33
per adult. The postreproductive period lasted on average
0.5 day.

REFERENCES

Andrásfalvy, P. /1971/: A magyar faunában ismeretlen vagy ke-
    véssé ismert levéltetvek /Hom., Aphididea/. Fol. Ent. Hung.
    20: 229-238.

Catherall, P.L. /1974/: Chlorotic streaking in Italien Ryegrass.
    Pl. Pathl. 223: 116-117.

Chiang, H.C. /1977/: Pest management in the People's Republic.
    China-monitoring and forecasting insect populations in rice,
    wheat, cotton and maise. FAO Plant Prot. Bull. 25: 1-8.

Horváth, J. /1972/: Növényvirusok, vektorok, virusátvitel.
    Akad. kiad. Bp. 514.

Kalmár, G. /1980/: A buzát és kukoricát kárositó levéltetvek
    /Aphidoidea/ biológiája. Disz. Mosonmagyaróvár. 199.

Kovács, V. - Bánk, L. - Szalay-Marzsó, L. /1973/: A gabonale-
    véltetü elleni védekezés tapasztalatai Hajdu-Bihar megyében.
    Növényvédelem. 7: 327-328.

Müller, F.P. /1961/: Blattläuse am Mais. Nachr.Dtsch., Pflan-
    zenschutzdienst, 15: 46-53.

Szalay-Marzsó, L. /1970/: Adatok a hazai gabonalevéltetvek is-
    meretéhez. Növényvédelem, 6: 244-250.

Valencia, V.L. - Guerra, T.C. - Gutarra, F. /1976/: Los áfidos
    /Homoptera - Aphididae/ del Valle Mantaro, plantos hospedaras
    y enemigos naturales. Rev. Peruana de Ent., 18. 1: 90-97.

Zuñiga, E. - Suzuki, H. /1976/: Ecological and economic prob-
    lems created by aphids in Latin America. Outlook on Agri-
    cult. 8: 311-319.

APHIDS LIVING ON CULTIVATED PLANTS IN THE PROVINCE OF LEON (SPAIN)

E. Núñez Pérez and J.M. Nieto Nafría

Departamento de Biología Animal, Facultad de Biología, Universidad de
León, 24071 León, Spain.

ABSTRACT

In order to determine the pest status of aphids on cultivated plants in
the province of León, a list of the aphids with host plants was compiled.

Three sources were used:

1.- Previously published data, which refers mainly to species in the Aphidina
and the genus *Macrosiphum*.

2.- The insect collection of Departamento de Biología Animal, Universidad
de León.

3.- Samples collected from farm land.

From the compiled list of host plants, a total of 44 crops are now affected
by a total of 47 aphid species.

Additionally, various species of ants, principally of the genus *Lasius*,
have been collected with the aphids. Three species of *Coccinellidae* (*Adalia
bipunctata* (L.), *Coccinella septempunctata* L. and *Psyllovora vigintiduo-
punctata* L.) have also been found feeding on aphids. Various still to be
identified hover-flies and aphidiids were also collected.

INTRODUCTION

Aphids make up one of the most important groups which damage cultivated
plants of agricultural, forestry, ornamental and medicinal importance. Their
devastating action affect plants directly by causing sap loss or inducing
plant malformations or indirectly by allowing fungi to develop on their
honeydew or by transmitting various viruses. Either way, they cause a decrease
in plant vitality and thus in production.

In order to achieve more effective control of these aphids, it is necessary
to know their identity and biology and that of the fauna of important
aphidophages (*Diptera: Syrphidae; Coleoptera: Coccinellidae; Neuroptera:*

Chrysopidae), parasitoids (*Hymenotera: Aphidiidae*) and insects (*Hymenoptea: Formicidae*) which protect some species.

MATERIAL AND METHODS

The material came from previously published data on Aphidina species, collections the Departamento de Biología Animal, University of León collection and samples collected from farm land.

The samples were collected in the province of León from May to November, 1988; and a complete cross section of all types of farm land in this Province is represented. Each sample provides information on the relationship between the aphid and its host plant, and between the aphid and the ants and predators present when the sample was collected. Samples were held in a growth chamber for several days, so that predators which were caught as larvae and parasites could be reared.

Various sources, especially Blackman and Eastop (1984), were used to determine, the species of aphids. For ants, articles by Collingwood (1978, 1979) and Bernard (1968) were used; and for ladybirds those by Cardoso and Gomes (1986).

We have indicated the scientific name of the host plants with its Spanish and English common name in brackets. The aphid species are listed in alphabetical order, with the associated insects abbreviated as follows:

Formicidae: Dolychoderinae,   *Tapinoma nigerrimum* Nyl.=T.n.

                   Myrmicinae,   *Crematogaster scutellaris* Ol.=C.s.

                                      Myrmica ruginodis Nyl.=M.r.

                   Formicinae,   *Camponotus lateralis* Ol.=C.l.

                                      Cataglyphis iberica Em.=C.i.

                                      Formica cunicularia Latr.=F.c.

                                      Formica polyctena Foerst.=F.p.

                                      Lasius brunneus (Latr.) =L.b.

                                      Lasius flavus (F.) =L.f.

                                      Lasius niger (L.) =L.n.

Coccinellidae: *Adalia bipunctata* =A.bp.

                  Coccinella septempunctata =C.sp.

                  Psyllovora vigintiduopunctata =P.vp.

Chrysopidae =CHR.

RESULTS

A list of aphids and associated insects collected on farm lands, non-citric fruit trees, vegetables, fodder crops, commercial crops, cereals and medicinal plants is presented here.

Aphids marked with an asterisk (*) were not mentioned under this crop by Blackman and Eastop (1984).

A. Non-citric fruit trees

  1. With pips:

    Cydonia oblonga (Membrillero: quince tree)

      Ovatus (O.) insitus

      Rhopalosiphum insertum

    Malus domestica (Manzano: apple tree)

      Aphis (A.) fabae Scopoli, 1763

      Aphis (A.) pomi de Geer, 1773: L.n.

      Dysaphis (Pomaphis) plantaginea (Passerini, 1860): C.s., C.l., L.n., A.bp.

      Eriosoma (E.) lanigerum (Hausmann, 1802): L.n.

      Ovatus (O.) crataegarius (Walker, 1850)

      Ovatus (O.) insitus (Walker, 1849)

      Rhopalosiphum insertum (Walker, 1849): A.bp.

    Pyrus communis (Peral: pear tree)

      Dysaphis (Pomaphis) pyri (Boyer de Fonscolombe, 1841): A.bp.

      Melanaphis pyraria (Passerini, 1861)

      Rhopalosiphum insertum

  2. With stones:

    Prunus avium (Cerezo: cherry tree)

      Aphis (A.) fabae *

      Myzus (M.) cerasi (Fabricius, 1775): L.n.

      Rhopalosiphum padi (Linnaeus, 1758) * (alatae)

    Prunus domestica (Ciruelo: plum tree)

      Aphis (A.) fabae *

      Brachycaudus (B.) helichrysi (Kaltenbach, 1843): M.r, L.n.

      Hyalopterus pruni (Geoffroy, 1762): CHR.

      Phorodon humuli (Schrank, 1801)

    Rhopalosiphum padi

  Prunus persica (Melocotonero: peach tree)

    Aphis (A.) spiraecola Patch, 1914

    Brachycaudus (Acaudus) persicae (Passerini, 1860)

    Myzus (Nectarosiphon) persicae (Sulzer, 1776)

    Rhopalosiphum padi * (alatae)

  3. With fleshy fruits:

  Ficus carica (Higuera: fig tree)

    Aphis (A.) fabae *

  4. With nuts:

  Castanea sativa (Castaño: sweet chestnut tree)

    Lachnus roboris (Linnaeus, 1758)

    Myzocallis (M.) castanicola Baker, 1917: CHR.

  Corylus avellana (Avellano: hazelnut tree)

    Myzocallis (M.) coryli (Goetze, 1778): CHR.

  Juglans regia (Nogal: walnut tree)

    Chromaphis juglandicola (Kaltenbach, 1843)

    Panaphis juglandis (Goetze, 1778)

B. Vegetables

  1. With leaves or stems:

  Brassica oleracea subsp. *capitata* (Berza: cabbage)

    Brevicoryne brassicae (Linnaeus, 1758)

    Macrosiphum euphorbiae (Thomas, 1878)

    Myzus (Nectarosiphon) persicae

  Cichorium endivia form *crispa* (Escarola: endive)

    Acyrthosiphon lactucae (Passerini, 1860)

  Cichorium endivia form *latifolia* (Endibia: endive)

    Macrosiphum euphorbiae

  Lactuca sativa (Lechuga: lettuce)

    Acyrthosiphon lactucae

    Nasonovia (N.) ribisnigri (Mosley, 1841): L.n.

    Neotrama caudata (del Guercio, 1909): L.f.

    Pemphigus bursarius (Linnaeus, 1758) *: L.f.

  Petroselinum crispum (Perejil: parsley)

    Aphis (A.) fabae

    Cavariella (C.) aegopodii (Scopoli, 1763)

2. With fruits:

  Capsicum anuum (Pimento: chili pepper)

    Macrosiphum euphorbiae

    Myzus (Nectarosiphon) persicae

  Cucurbita pepo (Calabacín: marrow)

    Aphis (A.) fabae

    Aphis (A.) frangulae gossypii Glover, 1877

    Aulacorthum (A.) solani (Kaltenbach, 1843) *

    Macrosiphum euphorbiae

  Cucurbita pepo (Calabaza: pumpkin)

    Aphis (A.) fabae: P.vp.

    Aphis (A.) frangulae gossypii

    Aulacorthum (A.) solani *

    Macrosiphum euphorbiae: P.vp.

    Myzus (Nectarosiphon) persicae: P.vp.

  Fragaria vesca (Fresal: strawberry plant)

    Aphis (A.) forbesi Weed, 1889

    Chaetosiphon (Pentatrichopus) fragaefolii (Cockerell, 1901)

    Macrosiphum rosae (Linnaeus, 1758)

  Lycopersicon esculentum (Tomate: tomato plant)

    Aphis (A.) fabae

    Macrosiphum euphorbiae

    Myzus (Nectarosiphon) persicae

3. With flowers:

  Brassica oleracea subsp. *botrytis* (Coliflor: cauliflower)

    Brevicoryne brassicae

4. With roots, bulbs or tubers:

  Allium cepa (Cebolla: onion)

    Aphis (A.) fabae

    Rhopalosiphum padi

  Allium porum (Ajo-puerro: garlic-leek)

    Aphis (A.) fabae

  Brassica campestris subsp. *rapa* (Nabo: turnip)

    Brevicoryne brassica

    Macrosiphum euphorbiae *

    Myzus (Nectarosiphon) persicae

Daucus carota (Zanahoria: carrot)

    Aphis (A.) fabae

    Cavariella (C.) aegopodii: L.n., C.sp.

    Dysaphis (D.) crataegi (Kaltenbach, 1843): L.n., C.sp.

    Semiaphis dauci (Fabricius, 1775): T.n., F.p., C.sp.

Solanum tuberosum (Patata: potato)

    Aphis (A.) fabae: T.n., C.sp.

    Aulacorthum (A.) solani *

    Macrosiphum euphorbiae: C.sp., CHR.

    Myzus (Nectarosiphon) persicae: C.sp.

5. With leguminous greens:

Phaseolus vulgaris (Judía: french bean)

    Aphis (A.) craccivora (Koch, 1854): T.n.

    Aphis (A.) fabae: L.b., L.n., CHR.

    Macrosiphum euphorbiae: C.sp., P.vp.

    Myzus (Nectarosiphon) persicae: CHR.

Pisum sativum (Guisante: pea)

    Acyrthosiphon pisum (Harris, 1776)

    Aphis (A.) fabae: L.n.

    Macrosiphum euphorbiae

Vicia faba (Haba: broad bean)

    Aphis (A.) fabae: L.n., F.c., C.sp.

C. Fodder lands

  1. With cereals:

Zea mays (Maiz: maize)

    Aphis (A.) fabae

    Rhopalosiphum maidis (Fitch, 1856)

    Rhopalosiphum padi

    Sitobion fragariae (Walker, 1848) *: C.sp., P.vp.

  2. With leguminous plants:

Medicago sativa (Alfalfa: alfalfa)

    Acyrthosiphon pisum

    Aphis (A.) craccivora: T.n.

    Therioaphis (Th.) trifolii (Monell, 1882)

Trifolium pratense (Trébol: clover)

    Acyrthosiphon pisum

      Nearctaphis bakeri (Cowen, 1895)

      Therioaphis (Th.) trifolii

  3. With roots:

    Beta vulgaris (Remolacha: beet)

      Aphis (A.) fabae: C.i.

      Macrosiphum euphorbiae

      Myzus (Nectarosiphon) persicae

D. Commercial crops

  1. For sugar:

    Beta vulgaris (Remolacha azucarera: sugar-beet)

      Aphis (A.) fabae: L.n.

      Macrosiphum euphorbiae

      Myzus (Nectarosiphon) persicae

  2. For oil:

    Helianthus annuus (Girasol: sunflower)

      Aphis (A.) fabae: C.sp.

E. Grain cereals

    Avena sativa (Avena: oats)

      Sitobion avenae (Fabricius, 1775)

    Hordeum vulgare (Cebada: barley)

      Metopolophium dirhodum (Walker, 1849)

      Rhopalosiphum padi

      Sitobion avenae

      Sitobion fragariae

    Triticum aestivum (Trigo: wheat)

      Rhopalosiphum padi: C.sp.

      Sitobion avenae: C.sp.

F. Other farm crops

    Humulus lupulus (Lúpulo: hop)

      Phorodon humuli: CHR.

    Vitis vinifera (Vid: grape vine)

      Macrosiphum euphorbiae

G. Medicinal plants

    Matricaria chamomilla (Manzanilla: camomile)

      Aphis (A.) fabae: L.n.

      Macrosiphum euphorbiae

Mentha piperita (Menta: mint)

  Myzus (Nectarosiphon) persicae

  Ovatus (O.) mentharius (van der Goot, 1913)

Tilia argentea and *T. platyphyllos* (Tilo: lime tree)

  Eucallipterus tiliae (Linnaeus, 1758)

CONCLUSIONS

Aphids are frequently found on the agricultural crops studied, although rarely in very high numbers. We have rarely observed serious attacks, specially in vegetables and in somewhat isolated orchards, which are used by the farmer for their own food. The attacks are usually controlled by using insecticides, and rarely naturally.

It was very common to find ants tending the aphids, and *Lasius niger* was the most abundant species of ant collected.

The control carried out by ladybirds and green lacewings on aphids does not seem to be intense and is far less important than that carried out by hover-flies and aphidiids. This study is being continued not only with additional samples on agricultural crops but also with samples from suction and Moericke traps with the aim of broadening the knowledge of the aphid fauna on plants of agricultural importance.

REFERENCES

Blackman, R.L. and V.F. Eastop, (1984): *Aphids on the world's crops: An identification and information guide*. 466 pp. Ed. John Wiley and Sons. Chichester.

Bernard, F. (1968): *Les fourmis* (Hymenoptera Formicidae) *d'Europe Occidentale et Septentrionale*. 407 pp. Ed. Masson et Cie, Paris

Cardoso Raimundo, A.A. and M.L.Gomes Alves, (1986): *Revisao dos Coccinelideos de Rortugal*. 104 pp. Ed. Universidade de Evora.

Collingwood, C.A., (1978): A provisionae list of Iberian *Formicidae* with a key to the worker caste *(Hym., Aculeata)*. Eos, 52: 65-95.

Collingwood, C.A., (1979): *The* Formicidae (Hymenoptera) *of Fennoscandia and Denmark*. 174 pp. Scandinavian Sciense Press, Ser. Fauna Entomol. Scand., 8.

FORECASTING THE ABUNDANCE OF RHOPALOSIPHUM PADI (L.) BY MEANS SUCTION TRAP CATCHE AND METEOROLOGICAL DATA

M. Ruszkowska

Institute for Plant Protection, ul. Miczurina 20

60-318 Poznań, Poland

ABSTRACT

The analysis of 14 years of suction trap catches revealed
a correlation between the size of the spring-summer flights
and the autumnal flights of the previous year for
Rhopalosiphum padi (L.).

INTRODUCTION

As cereals aphids are of considerable economical importance
in Poland investigations have started into possibility
of forecasting their abundance (Stacherska and Ruszkowska 1978).
Rhopalosiphum padi (L.) is the most abundant aphid infesting
cereals growing under polish climatic and agricultural con-
ditions. As on holocyclic and heteroecious species it shows
seasonal peaks of flight activity in spring, summer and autumn.
The individuals that make up the three flights (emigrants,
alate exules, gynoparae and males) differ morfologically
and vary greatly in abundance (Ruszkowska and Złotkowski 1977).

METHODS

Johnson suction trap catches of aphids from taken at hight of 12.2 m - records the duration and intensity each of the flights.

RESULTS

Analysis of the suction trap catches from 1973 to 1986 reveal a good correlation between the size of the spring-summer flight and the autumnal flight of the previous year R. padi (Fig. 1). This correlation is improved if the meteorological factors listed in Table 1 are taken into consideration. The following weather factors have influence on the number of aphids: the number of days when the temperature exceeded $18^{\circ}C$ (positive), the number of days on which rainfall exceeded 0.25 mm (negative) and the number of hours of sunshine (positive) per day between May and October.

The seasonal flight activity of R. padi and meteorological factors measured over many years can be used to forecast the abundance of this species each year.

ACKNOWLEDGEMENTS

Table 1

Number of Rhopalosiphum padi (L.) caught by a Johnson suction trap in spring and summer, and autumn of each year from 1973 to 1986 in relation to some meteorological factors

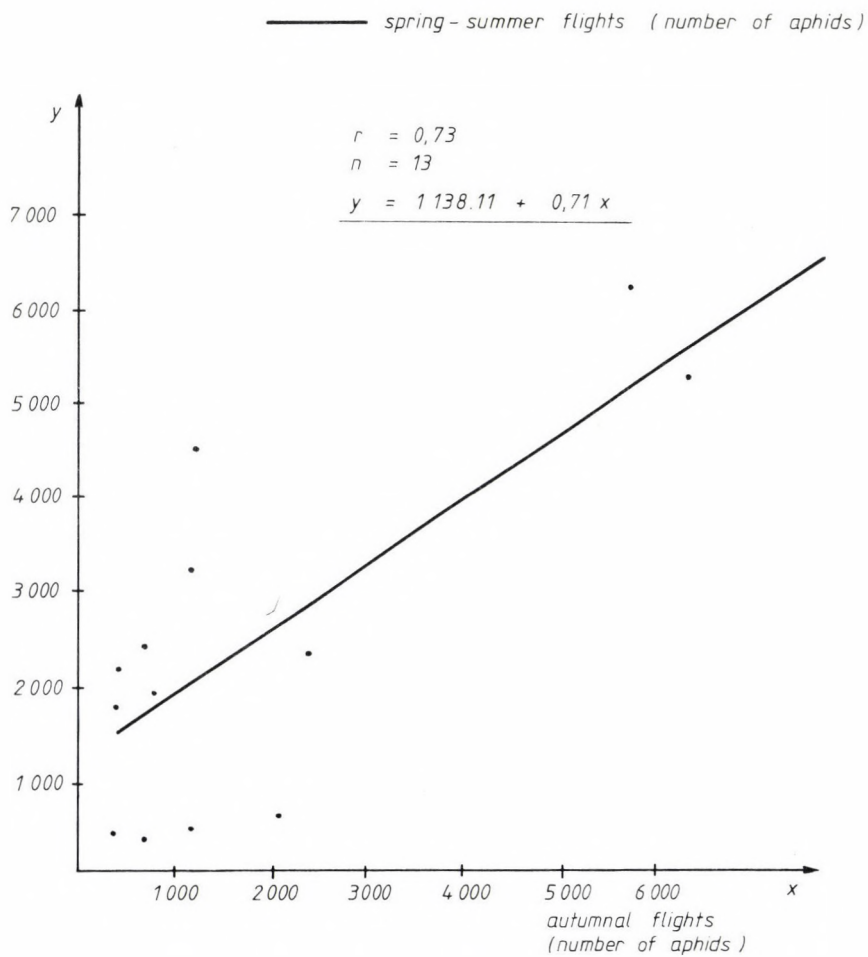| Year	spring-summer flight	autumnal flight	no. days temp.> 18°C	May-October rain> 0.25mm	hours of sunshine May-October
1973	5 178	1 081	118	46	1 271
1974	4 471	1 051	103	66	932
1975	3 067	5 597	122	41	1 231
1976	6 094	838	121	59	1 218
1977	354	6 334	105	62	1 108
1978	5 287	415	103	78	1 023
1979	1 717	2 025	122	46	1 069
1980	528	568	27	81	703
1981	2 352	341	112	91	950
1982	2 055	1 139	57	45	1 318
1983	438	2 332	111	50	1 289
1984	2 384	819	97	64	945
1985	1 880	380	118	67	1 074
1986	413	749	102	67	935

Fig. 1. The relation between the size of the spring - summer flight and the autumnal flight of the previous year in Rhopalosiphum padi (L.)

REFERENCES

Ruszkowska, M., Złotkowski, J. (1977) : Badania populacyjne
  nad ważnymi gospodarczo gatunkami mszyc na podstawie
  połowów z powietrza. Część II. Dynamika sezonowa.
  Prace Naukowe Instytutu Ochrony Roślin. XIX Z. No.2
  pp 125-144.

Stacherska, B and Ruszkowska, M. (1978): Prognozowanie
  nasilenia pojawu mszycy czeremchowo-zbożowej (Rhopalosiphum
  padi (L.) na podstawie jesiennych połowów mszyc z powietrza.
  Zeszyty Problemowe Postępów Nauk Rolniczych. No. 208
  pp 75-85.

ODE TO THE III. INTERNATIONAL SYMPOSIUM ON APHIDS

O. E. Heie

Ladies and Gentlemen:

I want to say a few words on this last day.

Excuse me for reading what I have written down to say.

English is not my first language, and I have no diary,

But I must say something about this wonderful symposium in Hungary.

The contents have been mannifold, and loss of time has been prevented.

Many interesting projects and new ideas have been presented.

Our dear, small creatures have been treated and into small pieces cut

From processus terminalis to the ectodermal hindgut.

Though we had a rather warm weather,

Many details have been put together,

And it has been tried to come through

Into a general ecological, genetical and systematical view.

Much had to be percepted,

Though not always without discussion accepted.

From four continents we came to share

Our common pleasure to treat the aphids with care.

We may put them into alcohol, but never beat them.

We may prevent them from doing harm, but never eat them.

That the field of aphidology is our preferred own land,

May be difficult for other people to understand.

To other people, even zoologists, they are only pests and bugs,

But we love them - though in another manner than the frogs.

So like a great family we have been.

Social connections across borders and independent on nationality we have

   seen.

To arrange such conditions and such an atmosphere is a huge work and not

   easy.

Our Hungarian hosts have indeed been both clever and busy.

The spiritual richness and social conditions have been well prepared,

And also our food, transportation and material wellfare.

Every one here has reason to thank Zsuzsa Basky and her

   committee and helpers very much

For making these days a series of happy and fruitful events

   by doing such:

Let us all on this happy day

Say very aloud: Hurrah, hurrah, hurray,

And lift our glasses!

LATIN ODE

Preface and Delivery by **J. Nieto Nafria**

Latin Text by **A. Binazzi**

English is not the mother language of the Latin group,

Italian and Spanish people.

Because of that, we would like to thank Zsuzsa

In our great mother language, Latin:

Grati nos tibi sumus, Zsuzsae,

Propter omnia quae nobis praebuisti

In hoc tempore quod in hac pulcherrima pannonica urbe egimus.

Periodicals of the Hungarian Academy of Sciences are obtainable at the following addresses:

AUSTRALIA
C.B.D. LIBRARY AND SUBSCRIPTION SERVICE
39 East Splanade
P.O. Box 1001, Manly N.S.W. 2095

AUSTRIA
GLOBUS, Höchstädtplatz 3, 1206 Wien XX

BELGIUM
OFFICE INTERNATIONAL DES PERIODIQUES
Avenue Louise, 485, 1050 Bruxelles
E. STORY-SCIENTIA P.V.B.A.
P. van Duyseplein 8, 9000 Gent

BULGARIA
HEMUS, Bulvar Ruszki 6, Sofia

CANADA
PANNONIA BOOKS, P.O. Box 1017
Postal Station "B", Toronto, Ont. M5T 2T8

CHINA
CNPICOR, Periodical Department, P.O. Box 50
Peking

CZECH AND SLOVAK FEDERAL REPUBLIC
MAD'ARSKA KULTURA, Národni třida 22
115 66 Praha
PNS DOVOZ TISKU, Vinohradská 46, Praha 2
PNS DOVOZ TLAČE, Bratislava 2

DENMARK
EJNAR MUNKSGAARD, 35, Nørre Søgade
1370 Copenhagen K

FEDERAL REPUBLIC OF GERMANY
KUNST UND WISSEN ERICH BIEBER
Postfach 10 28 44
7000 Stuttgart 10

FINLAND
AKATEEMINEN KIRJAKAUPPA, P.O. Box 128
00101 Helsinki 10

FRANCE
DAWSON-FRANCE S.A., B.P. 40, 91121 Palaiseau
OFFICE INTERNATIONAL DE DOCUMENTATION ET
LIBRAIRIE, 48 rue Gay-Lussac
75240 Paris, Cedex 05

GREAT BRITAIN
BLACKWELL'S PERIODICALS DIVISION
Hythe Bridge Street, Oxford OX1 2ET
BUMPUS, HALDANE AND MAXWELL LTD.
Cowper Works, Olney, Bucks MK46 4BN
COLLET'S HOLDINGS LTD., Denington Estate,
Wellingborough, Northants NN8 2QT
WM DAWSON AND SONS LTD., Cannon House
Folkstone, Kent CT19 5EE

GREECE
KOSTARAKIS BROTHERS INTERNATIONAL
BOOKSELLERS, 2 Hippokratous Street, Athens-143

HOLLAND
FAXON EUROPE, P.O. Box 167
1000 AD Amsterdam
MARTINUS NIJHOFF B. V.
Lange Voorhout 9-11, Den Haag
SWETS SUBSCRIPTION SERVICE
P.O. Box 830, 2160 Sz Lisse

INDIA
ALLIED PUBLISHING PVT. LTD.
750 Mount Road, Madras 600002
CENTRAL NEWS AGENCY PVT. LTD.
Connaught Circus, New Delhi 110001
INTERNATIONAL BOOK HOUSE PVT. LTD.
Madame Cama Road, Bombay 400039

ITALY
D. E. A., Via Lima 28, 00198 Roma
INTERSCIENTIA, Via Mazzé 28, 10149 Torino
LIBRERIA COMMISSIONARIA SANSONI
Via Lamarmora 45, 50121 Firenze

JAPAN
KINOKUNIYA COMPANY LTD.
Journal Department, P.O. Box 55
Chitose, Tokyo 156
MARUZEN COMPANY LTD., Book Department
P.O. Box 5050 Tokyo International, Tokyo 100-31
NAUKA LTD., Import Department
2-30-19 Minami Ikebukuro, Toshima-ku, Tokyo 171

KOREA
CHULPANMUL, Phenjan

NORWAY
S.A. Narvesens Litteraturjeneste
Box 6125, Etterstad
1000 Oslo

POLAND
WĘGIERSKI INSTYTUT KULTURY
Marszalkowska 80, 00-517 Warszawa
CKP I W, ul. Towarowa 28, 00-958 Warszawa

ROUMANIA
D. E. P., Bucuresti
ILEXIM, Calea Grivitei 64-66, Bucuresti

SOVIET UNION
SOYUZPECHAT — IMPORT, Moscow
and the post offices in each town
MEZHDUNARODNAYA KNIGA, Moscow G-200

SPAIN
DIAZ DE SANTOS Lagasca 95, Madrid 6

SWEDEN
ESSELTE TIDSKRIFTCENTRALEN
Box 62, 101 20 Stockholm

SWITZERLAND
KARGER LIBRI AG, Petersgraben 31, 4011 Basel

USA
EBSCO SUBSCRIPTION SERVICES
P.O. Box 1943, Birmingham, Alabama 35201
F. W. FAXON COMPANY, INC.
15 Southwest Park, Westwood Mass. 02090
MAJOR SCIENTIFIC SUBSCRIPTIONS
1851 Diplomat, P.O. Box 819074,
Pallas, Tx. 75381-9074
REDMORE PUBLICATIONS, Inc.
22 Cortlandt Street, New York, N.Y. 1007

YUGOSLAVIA
JUGOSLOVENSKA KNJIGA, Terazije 27, Beograd
FORUM, Vojvode Mišića 1. 21000 Novi Sad