ACTA
SILVATICA
&
LIGNARIA
HUNGARICA

AN INTERNATIONAL JOURNAL
IN FOREST, WOOD
AND ENVIRONMENTAL
SCIENCES

VOLUME 5
2009

ACTA SILVATICA ET LIGNARIA HUNGARICA
AN INTERNATIONAL JOURNAL IN FOREST, WOOD AND ENVIRONMENTAL SCIENCES
issued by the Forestry Commission of the Hungarian Academy of Sciences

Acta Silvatica et Lignaria Hungarica (ASLH) publishes original reports and reviews in the field of forest, wood and environmental sciences in English or German language.

ASLH is published in serial volumes. It is freely accessible electronically under:
http://aslh.nyme.hu

The journal is financially supported by the
Hungarian Academy of Sciences (HAS),
Faculty of Forestry, University of West Hungary (FF-UWH),
Faculty of Wood Sciences, University of West Hungary (FWS-UWH),
Hungarian Forest Research Institute (HFRI)
Instiute of Wildlife Management, University of West Hungary (IWM-UWH).
Sopron Scientists' Society of the Hungarian Academy of Sciences

HU ISSN 1786-691X (Print)
HU ISSN 1787-064X (Online)

Manuscripts and editorial correspondence should be addressed to
MAGDOLNA STARK, ASLH EDITORIAL OFFICE
UNIVERSITY OF WEST HUNGARY,
PF. 132, H-9401 SOPRON, HUNGARY

Phone: +36 99 518 122
Fax: +36 99 329 911
E-mail: aslh@nyme.hu
Information and electronic edition: http://aslh.nyme.hu

The journal is indexed in the CAB ABSTRACTS database of CAB International; by Scopus, Elsevier's Bibliographic Database and by EBSCOhost database

Published by UNIVERSITY OF WEST HUNGARY PRESS
Cover design by ANDREA KLAUSZ
Printed by LŐVÉR-PRINT KFT., SOPRON

Contents

Short Communications

Tartalomjegyzék

Rövid közlemények

Acta Silv. Lign. Hung., Vol. 5 (2009) 9-17

Allelopathic Effects of Invasive Woody Plant Species in Hungary

Ágnes CSISZÁR[*]

Department of Botany and Nature Conservation, Faculty of Forestry, University of West Hungary, Sopron, Hungary

Abstract – Allelopathy may play an important role in the invasion success of adventive plant species. The aim of this study was to determine the allelopathic potential of invasive woody plant species occurring in Hungary. Juglone index of fourteen invasive woody plant species in Hungary was determined by the method of Szabó (1997), comparing the effects of juglone and substance extracted of plant species with unknown allelopathic potential on the germination rate, shoot length and rooth length of white mustard (*Sinapis alba* L.) used as receiver species. Results have proven a more or less expressed allelopathic potential in case of all species. The juglone index at higher concentration extracts (5 g dry plant material extracted with 100 ml distilled water) of almost every studied species approaches to 1 or is above 1, this means the effect of the extracts is similar to juglone or surpasses it. In terms of juglone index, the allelopathic potential of false indigo (*Amorpha fruticosa* L.), tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) and hackberry (*Celtis occidentalis* L.) were the highest. Besides these species the treatment with the extracts of black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Ehrh.) and green ash (*Fraxinus pennsylvanica* MARSH. var. *subintegerrima* (Vahl) Fern.) reduced extremely significantly the germination rate, shoot and root length, compared to the control.

species / allelopathy / juglone index / germination inhibition / growth inhibition

Kivonat – Magyarországon előforduló fás szárú özönfajok allelopatikus hatásának vizsgálata. Az allelopátia egyes adventív növényfajok inváziós sikerében jelentős szerepet tölthet be, ezért jelen vizsgálat a Magyarországon előforduló, fás szárú özönnövények allelopatikus potenciáljának megállapítását tűzte ki céljául. A vizsgálat során tizennégy, hazánkban inváziós fás szárú növényfaj juglon-indexe került meghatározásra Szabó (1997) által leírt módszer szerint, amely az ismeretlen allelopatikus potenciálú növényfajból készített kivonat hatását a juglonéval hasonlítja össze a fehér mustár (*Sinapis alba* L.) tesztnövény csírázási százalékára, gyökér- és hajtáshosszúságára nézve. A vizsgálat eredményeként bebizonyosodott, hogy a Magyarországon előforduló, fás szárú inváziós növényfajok mindegyike rendelkezik kifejezett vagy kevésbé kifejezett allelopatikus potenciállal, a magasabb koncentrációjú kivonatok (5 g szárított növényi anyag 100 ml desztillált vízben kivonva) esetén csaknem mindegyik faj juglon-indexe közelít az 1-hez vagy meghaladja azt, vagyis hatása a juglonéhoz közelít, vagy azét felülmúlja. A juglon-indexet tekintve kiemelkedő a gyalogakác (*Amorpha fruticosa* L.), a bálványfa (*Ailanthus altissima* (Mill.) Swingle) és a nyugati ostorfa (*Celtis occidentalis* L.) allelopatikus potenciálja. E fajokon kívül a fekete dió (*Juglans nigra* L.), a kései meggy (*Prunus serotina* Ehrh.) és a zöld kőris (*Fraxinus pennsylvanica* Marsh. var. *subintegerrima* (Vahl) Fern.) kivonatával történt kezelés mind a csírázási százalék, mind a hajtáshosszúság, mind pedig a gyökérhosszúság esetén rendkívül szignifikáns eltérést mutatott a kontrollhoz képest.

fás szárú özönfajok / allelopátia / juglon-index / csírázásgátlás / növekedésgátlás

---

[*] keresztlapu@emk.nyme.hu; H-9401 Sopron, POB 132, Hungary

1 INTRODUCTION

Records about allelopathy are known since ancient times, however the inhibitory effect was not attributed to the secondary metabolites (Plinius Secundus 1st century AD cit. Rice 1984). After introducing the term allelopathy by Molish (1937), the definition has undergone several changing and widening of meaning (Csontos 1997, Brückner – Szabó 2001), nowadays it refers to the positive or negative, direct or indirect effect by one plant, fungus or microorganisms to the other through the production of chemical compounds that escape into the environment (RICE 1984). Most observations of allelopathy connected with agriculture, several weeds are known which are allelopathic to cultivated plants (Terpó – Kotori 1974, Mikulás 1981, Kazinczi et al. 1991), plant species allelopathic to weeds can offer a selective and an environmentally friendlier way of weed biocontrol.

Because of the complexity of allelopathy and problems of its practical applications the beneficial effects of allelopathy have not been exploited in the forestry yet, although the competition and allelopathic effects are more explicit in the forested plant communities because of huge biomass of canopy and root layers (Pellissier – Gallet – Souto 2002). It is also notable that almost one third of allelopathic plant species are woody plants in Hungary (Szabó 1997). Allelopathy can influence the succession, determine the pattern of cut area, inhibit the forestation and forest regeneration; understory species can inhibit the germination of woody plants therefore the secondary metabolites of woody plant species can greatly influence the pattern of understory (Lodhi 1975, 1976, 1978, Kuiters – Denneman 1987, Csontos 1991). The effect of understory species can be expressed indirectly through the microbiological activity of the soil (Szabó et al 1987), however the effect can show different rate in laboratory experiments and under field conditions (Fekete 1974). The role of allelopathy in the forest ecosystem has been proven by Čaboun (2004) in the seed production, forest regeneration and protection, forest structure and production of biomass. According to Carroll (1994): „Within the forest ecosystem allelochemical interaction plays a much larger role than previously thought, affecting growth, germination, plant succession, and vegetative patterning of forest ecosystem."

It is not surprising that the percentage of alien species among the allelopathic plants is very high; since the species living close to each other were able to adapt to metabolites produced by the other species during the evolution, and an alien species is more likely to emit chemicals that native plants are less resistant to (Callaway – Aschehoug 2000). Many studies suggest that allelopathy may contribute the ability of an alien species to become dominant in invaded plant communities (Ridenour – Callaway 2001, Hierro – Callaway 2003). Among native plant communities the forests are especially endangered by the invasion of alien plant species in Hungary (Bartha 2002), the number of alien woody plant species can exceed the native woody species locally. Among invasive woody plant species occurring in Hungary the allelopathic effect of Manitoba maple (*Acer negundo* L.), false indigo (*Amorpha fruticosa* L.), black locust (*Robinia pseudoacacia* L.), black walnut (*Juglans nigra* L.), white mulberry (*Morus alba* L.), tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle), hackberry (*Celtis occidentalis* L.), black cherry (*Prunus serotina* EHRH.) and Russian-olive (*Elaeagnus angustifolia* L.) has been proven (Čaboun 1994, Nandal et al. 1994, Elakovich – Wooten 1995, 1996, Heisey 1996, Szabó 1999). This study aimed at investigating the allelopathic effects of invasive woody plant species occurring in Hungary under the same conditions providing comparison of allelopathic potential of species and results which can contribute to understanding of complex function of forest ecosystems and hereby the protection and conservation of our forests.

2 MATERIALS AND METHODS

Juglone index (SZABÓ 1999) was chosen to study the allelopathic potential of invasive woody plant species in Hungary. Juglone is a strong allelopathic naftoquinone has been isolated from Persian walnut (*Juglans regia* L.), black walnut (*Juglans nigra* L.) and many species in the *Juglandaceae* family; it is washed into the soil by the rain from leaves (DAGLISH 1950, PRATAVIERA et al. 1983). Juglone has an inhibitory effect on germination and seedling growth of several plant species (Kocacaliskan – Terzi 2001), this inhibition is expressed by reduced intensity of photosynthesis and respiration (Hejl et al. 1993, Jose – Gillespie 1998), and increased oxidative stress (Segura-Aguilar et al. 1992). ERCISLI et al. (2005) treated day-neutral strawberry (*Fragaria* x *ananassa* L.) by juglone and found that the fruit yield per plant, the number of fruit per plant, average fruit weight, crowns per plant, number of leaves, leaf area, fresh root weight, total soluble solid (TSS), vitamin C, acidity and uptake of some nutrient element decreased. Method of juglone index was introduced by SZABÓ (1999), it is based on comparing the effects of treatment with 1 mM juglone and substance extracted of plant species with unknown allelopathic potential. Juglone index is a quotient created by the germination rate, shoot length and root length of white mustard (*Sinapis alba* L.) treated with juglone and substance with unknown allelopathic potential. If this quotient is above 1, the allelopathic potential is more expressed than the juglone's and the inhibitory effect is stronger; if it is below 1, the allelopathic potential is less expressed than the juglone's and the inhibitory effect is weaker. If the juglone index is smaller than 0,5, we can not practically speak about an allelopathic potential (Szabó 1999). The juglone index (I_j /x) of a substance with unknown allelopathic potential is:

$$I_j / x = (H_j + R_j + G_j) / (H_x + R_x + G_x)$$

Abbreviations: H_j : average of shoot lengths of 3 times 10 white mustard seeds treated with 1 mM juglone (mm), R_j: average of root lengths of 3 times 10 white mustard seeds treated with 1 mM juglone (mm), G_j: average of germination rates of 3 times 100 white mustard seeds treated with 1 mM juglone (number), H_x: average of shoot lengths of 3 times 10 white mustard seeds treated with substance from species "x" with unknown allelopathic potential (mm), R_x: average of root lengths of 3 times 10 white mustard seeds treated with substance from species "x" with unknown allelopathic potential (mm), G_x: average of germination rates of 3 times 100 white mustard seeds treated with substance from species "x" with unknown allelopathic potential (number).

For the examination shoots of invasive woody plants were collected in May 2008 and dried at room temperature. The studied species were the following: Manitoba maple (*Acer negundo* L.), false indigo (*Amorpha fruticosa* L.), black locust (*Robinia pseudoacacia* L.), black walnut (*Juglans nigra* L.), white mulberry (*Morus alba* L.), tree-of-heaven (*Ailanthus altissima* (Mill.) SWINGLE), hackberry (*Celtis occidentalis* L.), black cherry (*Prunus serotina* EHRH.), Russian-olive (*Elaeagnus angustifolia* L.), thicket creeper (*Parthenocissus inserta* (A. Kern) Fritsch), golden currant (*Ribes aureum* PURSH), riverbank grape (*Vitis riparia* MICHX.), common hoptree (*Ptelea trifoliata* L.), red ash (*Fraxinus pennsylvanica* Marsh. var. *austini* Fern.) and green ash (*Fraxinus pennsylvanica* Marsh. var. *subintegerrima* (Vahl) Fern.).

Aqueous extracts were prepared at two different concentrations by soaking 1 g and 5 g dried plant material (leaves and stems) of the donor species in 100 ml distilled water at 20 °C for an hour, shaken in every 10 minutes and filtered through filter paper. White mustard seeds were germinated between two filter papers wetted with 5 ml extract, in darkness, placed in a biological thermostat at 20 °C. 100 white mustard seeds were placed in each petri dishes, I repeated the experiment with each concentration and species three times. Germination rate, shoot and root length were registered on the 6th day counted from the beginning of imbibition. The effects of the different plant species extracts on the germination rate, shoot and root length of white mustard were compared to the treatment with using distilled water (control). The statistical analysis of the results was made by using Chi-square test in case of germination rate, with Mann-Whitney test in case of shoot and root length using the InStat statistical program (InStat 1997). During the statistical analysis the categories of InStat statistical program [extremely significant ($P < 0.001$), very significant ($P < 0.01$), significant ($P < 0.05$), not quite significant ($P \leq 0.1$), not significant ($P > 0.1$)] were used.

3 RESULTS

Regarding juglone index of invasive woody plant species in Hungary it is conspicuous, that the juglone index at higher concentration extracts of almost every studied plant species approaches to 1 or is above 1, this means the effect of the extracts is similar to juglone or exceeds it *(Table 1)*. *Amorpha fruticosa* is preeminent among the species, its juglone index is the highest at both concentrations, and it is the only one which juglone index is more than 1 at lower concentration extract. In case of higher concentration extracts *Amorpha fruticosa* was followed by *Ailanthus altissima* and *Celtis occidentalis* with juglone index 1.49 and 1.36. *Juglans nigra*, *Prunus serotina*, *Ptelea trifoliata*, *Fraxinus pennsylvanica* var. *subintegerrima* and *Robinia pseudoacacia* have a juglone index higher than 1. The juglone index of *Acer negundo*, *Parthenocissus inserta*, *Vitis riparia*, *Elaeagnus angustifolia* and *Ribes aureum* are only with some hundreth lower than 1. *Morus alba* and *Fraxinus pennsylvanica* var. *austini* can be characterized by the lowest juglone index in case of higher concentration extracts. Lower juglone index belonged to lower concentration extracts than to higher concentration extract in case of every species, although this difference was more considerable in case of species having a higher juglone index.

Table 1. Juglone index of invasive woody plant species occurring in Hungary

Species	Juglone index	
	at lower concentration extract (1 g plant material extracted with 100 ml distilled water)	at higher concentration extract (5 g plant material extracted with 100 ml distilled water)
Acer negundo L.	0.93	0.99
Ailanthus altissima (MILL.) SWINGLE	0.80	1.49
Amorpha fruticosa L.	1.11	2.00
Celtis occidentalis L.	0.86	1.36
Elaeagnus angustifolia L.	0.74	0.93
Fraxinus pennsylvanica Marsh. var. *austini* Fern.	0.79	0.85
Fraxinus pennsylvanica Marsh. var. *subintegerrima* (Vahl) Fern.	0.76	1.01
Juglans nigra L.	0.80	1.08
Morus alba L.	0.80	0.86
Parthenocissus inserta (A. Kern) Fritsch	0.76	0.96
Prunus serotina Ehrh.	0.77	1.04
Ptelea trifoliata L.	0.73	1.03
Ribes aureum Pursh	0.77	0.91
Robinia pseudoacacia L.	0.84	1.01
Vitis riparia Michx.	0.81	0.94

Species can be ranked based on expression of their allelopathic potential using the juglone index at different concentrations of extracts, but it does not give any information about how the species inhibit the growth and development of the test plant. To find this out I compared the germination rate, shoot and root length data in case of each plant species and concentration to the data of control (treatment with distilled water) *(Table 2)*.

Table 2. Inhibitory effects of extracts of invasive woody plant species in Hungary on the germination of Sinapis alba L. according to the analysis by Chi-square test and Mann-Whitney test

Donor species	Weight of plant material (g)	Germination rate	Shoot length	Root length
Acer negundo L.	5	*	***	***
	1	-	-	***
Ailanthus altissima (Mill.) Swingle	5	***	***	***
	1	-	-	***
Amorpha fruticosa L.	5	***	***	***
	1	**	***	***
Celtis occidentalis L.	5	***	***	***
	1	-	-	***
Elaeagnus angustifolia L.	5	-	-	***
	1	-	-	***
Fraxinus pennsylvanica Marsh. var. *austini* Fern.	5	-	-	***
	1	-	o	***
Fraxinus pennsylvanica Marsh. var. *subintegerrima* (Vahl) Fern.	5	***	***	***
	1	-	-	***
Juglans nigra L.	5	***	***	***
	1	-	-	***
Morus alba L.	5	-	o	***
	1	-	-	***
Parthenocissus inserta (A. Kern) Fritsch	5	*	*	***
	1	-	*	***
Prunus serotina Ehrh.	5	***	***	***
	1	-	-	***
Ptelea trifoliata L.	5	***	**	***
	1	-	*	**
Ribes aureum Pursh	5	-	-	***
	1	-	-	***
Robinia pseudoacacia L.	5	**	o	***
	1	-	-	***
Vitis riparia Michx.	5	***	*	***
	1	-	*	***

Abbreviations: The inhibitory effect: ***: extremely significant, **: very significant, *: significant,
o: not quite significant, -: not significant

Examining the germination rate the treatment with higher concentration extracts of *Ailanthus altissima, Amorpha fruticosa, Celtis occidentalis, Fraxinus pennsylvanica* var. *subintegerrima, Juglans nigra*, *Prunus serotina*, *Ptelea trifoliata* and *Vitis riparia* considered extremely significantly different compared to the control. The germination rates were very significantly lower than the control following the treatment with higher concentration extract eof *Robinia pseudoacacia* and the treatment with lower concentration extract of *Amorpha fruticosa*. There were significant difference between the control and the treatment with higher concentration extracts of *Acer negundo* and *Parthenocissus inserta*. Treatment with other extracts did not show significant difference to the control.

Analyzing the shoot length data the effects of various species and concentrations divided more considerably: eight extracts caused extremely significant, one very significant, five significant, three not quite significant and thirteen not significant differences. Higher concentration extracts of *Acer negundo, Ailanthus altissima, Amorpha fruticosa*, *Celtis occidentalis, Fraxinus pennsylvanica* var. *subintegerrima, Juglans nigra* and *Prunus serotina* and lower concentration extract of *Amorpha fruticosa* resulted extremely significant difference to the data of control. Higher concentration extract of *Ptelea trifoliata* reduced very significantly the shoot length. After the treatment with lower concentration extract of *Ptelea trifoliata* and both concentration extracts of *Vitis riparia* and *Parthenocissus inserta* the shoot lengths were significantly shorter.

The root lengths influenced with treatment using different species and concentrations brought more unified results. With the exception of lower concentration extract of *Ptelea trifoliata* – which showed very significant difference compared to the control – extracts at both concentration in case of every species reduced extremely significantly the root length.

4 CONCLUSION

The results of study have proven that every invasive woody plant species occurring in Hungary has a more or less expressed allelopathic potential. These allelopathic effects are known from the literature in case of some studied species, but there are not any publications or there are some ones about the allelopathy of other studied species such as *Fraxinus pennsylvanica* var. *austini*, *Vitis riparia*, *Parthenocissus inserta*, *Ptelea trifoliata* and *Ribes aureum*. In term of juglone index the allelopathic potential of *Amorpha fruticosa*, *Ailanthus altissima* and *Celtis occidentalis* were the most preeminent. Besides these species the treatment with *Juglans nigra*, *Prunus serotina* and *Fraxinus pennsylvanica* var. *subintegerrima* extracts reduced extremely significantly the germination rate, shoot and root length, compared to the control.

The comparison of the juglone index of investigated adventive woody species with the values of adventive herbaceous species reported by Szabó (1999), revealed that for higher concentrations extracts, juglone indices of woody species were in general similar, around 1. No extreme values were found comparable to Eastern daisy fleabane (*Erigeron annuus* (L.) Pers.) with a juglone index of 8.77 (Szabó 1999). In case of *Elaeagnus angustifolia,* I found at lower extract concentration an index lower by 0.14, at higher concentration higher by 0.18, respectively, than reported by Szabó (1999). This difference is not considerable and does not reduce the authenticity of methods; on the other hand it highlights the fact, that the concentration of allelopathica is influenced by several biotic and abiotic factors and may have seasonal variability.

It is known, that Petri dish bioassays could greatly overestimate the allelopathic effect compared to realistic field conditions (Keeley 1988, Wardle et al. 1998). The explanation of different allelopathic effects can be the transformation of allelochemicals by organic and anorganic compounds of soil, adsorption by colloids and dilution by the precipitation (Brückner – Szabó 2001). During these processes the allelochemicals can lose their allelopathic effects although it can be preserved too. To sum up in vitro researches are suitable for determining the allelopathic potential, but allelopathic effect should be proven under field conditions too.

Nowadays several uses of allelochemicals are known. Undesirable deciduous plants were controlled successfully in Canada sowing allelopathic plant species to the understory or incorporating barley, oat and wheat residues in soil (Jobidon et al. 1989). As the results of HEISEY's (1997) studies the ailanthone, the allelochemicals of tree-of-heaven was considered a broad-spectrum, pre- and postemergent herbicide. Most herbicides derived from plants are biodegradable and usually considered to be safer from human health and environmental point of view (Rizvi – Rizvi 1992). The invasive alien species cause considerable environmental, economical and human health harm worldwide, therefore we can agree with findings of Hierro and Callaway (2003 p. 29): „We do not recommend allelopathy as a 'unifying theory' for plant interactions, nor do we espouse the view that allelopathy is the dominant way that plants interact, but we argue that non-resource mechanisms should be returned to the discussion table as a potential mechanism for explaining the remarkable success of some invasive species."

Acknowledgements: I would like to express my thanks to Prof. Dénes Bartha for useful advice and critique. I am grateful to Prof. László Gy. Szabó and Prof. Péter Csontos for useful instructions and advice helping the experiment. Thanks to Ms. Mária Csanády for laboratory work and to the Institute of Sylviculture and Forest Protection for lending biological thermostat.

REFERENCES

BARTHA D. (2002): Adventív fa- és cserjefajok Magyarországon. [Adventive tree- and shrub species in Hungary.] Erdészeti Lapok 137: 63-65. (in Hungarian)

BRÜCKNER D.J. – SZABÓ L.GY. (2001): Az allelopátia modern értelmezése. [New approaches to allelopathy.] Kitaibelia 4 (1): 93-106. (in Hungarian with English summary)

ČABOUN, V. (1994): Allelopathy research in forest ecosystems of Slovakia. In: Narwal, S.S. – Tauro, P. (eds.): Allelopathy in Agriculture and Forestry. Scientific Publ., Jodhpur.

ČABOUN, V. (2004): Results of allelopathy research in Slovak forest ecosystems. Second European Allelopathy Symposium „Allelopathy – from understanding to application". 3rd - 5th June 2004, Pulawy, Poland. 24 p.

CALLAWAY, R.M. – ASCHEHOUG, E. T. (2000): Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290: 521-523.

CARROLL, M. (1994): Allelopathic interactions in a temperate forest setting by higher woody plants and understory components. EN570 Term Report, Colorado State University.

CSONTOS P. (1991): Allelopathic interactions and pattern generation of herbs in oakwood clearings. (Preliminary studies). Abstracta Botanica 15: 25-30.

CSONTOS P. (1997): Az allelopátia kutatásának hazai eredményei. [Allelopathy in Hungary: a review of literature.] Természetvédelmi Közlemények 5-6: 27-40 (in Hungarian with English summary)

DAGLISH, C. (1950): The determination and occurrence of hydrojuglone glucoside in the walnut. Biochemical Journal 47: 45-462.

ELAKOVICH, S.D. – WOOTEN, J.W. (1995): Allelopathic woody plants I. *Abies alba* through *Lyonia lucida*. Allelopathy Journal 2/2: 117-146.

ELAKOVICH, S.D. – WOOTEN, J.W. (1996): Allelopathic woody plants II. *Mabea* through *Zelkova*. Allelopathy Journal 3/1: 9-32.

ERCISLI, S. – ESITKEN, A. – TURKKAL, C. – ORHAN, E. (2005): The allelopathic effects of juglone and walnut leaf extracts on yield, growth, chemical and PNE compositions of strawberry cv. Fern. Plant, Soil and Environment 51 (6): 283-287.

FEKETE G. (1974): Interspecifikus kapcsolatok, kölcsönhatások és az ökológiai niche elemzése tölgyerdei fajokon. [Interspecific relations, interactions and analysis of the ecological niche on oak forest species.] Akadémiai doktori értekezés, kézirat, MTA Kézirattár Budapest. (in Hungarian)

HEISEY, R.M. (1996): Identification of an allelopathic compound from *Ailanthus altissima* and characterization of its herbicidal activity. Journal of Botany 83: 192-200.

HEISEY, R.M. (1997): Allelopathy and the Secret Life of *Ailanthus altissima*. Arnoldia (1997 Fall): 28-36.

HEJL, A.M. – EINHELIIG, F.A. – RASMUSSEN J. (1993): Effects of juglone on growth, photosynthesis and respiration. Journal of Chemical Ecology 19: 559-568.

HIERRO, J. L. – CALLAWAY, R. M. (2003): Allelopathy and exotic plant invasion. Plant and Soil 256: 29-39.

INSTAT 1997: GraphPad InStat Demo, Version 3.00 for Win 95/NT. GraphPad Software Incl., San Diego.

JOBIDON, R. – THIBAULT, J.R. – FORTIN, J.A. (1989): Phytotoxic effect of barley, oat and wheat mulches in eastern Québec forest plantations 1. Effects on red raspberry (*Rubus idaeus* L.) Forest Ecology and Management 29: 277-294.

JOSE, S. – GILLESPIE, A. R. (1998): Allelopathy in black walnut (*Juglans regia* L.) alley cropping: II. Effects of juglone on hydroponically grown corn (*Zea mays* L.) and soybean (*Glycine max* L. Merr.) growth and physiology. Plant and Soil 203: 199-205.

KAZINCZI G. – BÉRES I. – HUNYADI K. – MIKULÁS J. (1991): A selyemmályva (*Abutilon theophrasti* Medic.) allelopatikus hatásának és kompetitív képességének vizsgálata. [Study of allelopathic effect and competitive ability of *Abutilon theophrasti*.] Növénytermelés 40 (4): 321-331. (in Hungarian with English summary)

KEELEY, J.E. (1988): Allelopathy. Ecology 69: 293-294.

KOCACALISKAN, I. – TERZI, I. (2001): Allelopathic effects of walnut leaf extracts and juglone on seed germination and seedling growth. Journal of Horticultural Science and Biotechnology 76: 436-440.

KUITERS, A.T.– DENNEMAN, C.A.J. (1987): Water-soluble phenolic substances in soils under several coniferous and decidous tree species. Soil Biology and Biochemistry 19: 765-769.

LODHI, M.A.K. (1975): Soil-plant phytotoxicity and its possible significance in patterning of herbaceous vegetation in a bottomland forest. American Journal of Botany 62: 618-622.

LODHI, M.A.K. (1976): Role of allelopathy as expressed by dominanting trees in a lowland forest in controlling the productivity and pattern of herbaceous growth. American Journal of Botany. 63: 1-8.

LODHI, M.A.K. (1978): Allelopatic effects of decaying litter of dominant trees and their associated soil in a lowland forest communitiy. American Journal of Botany 65: 340-344.

MIKULÁS J. (1981): A fenyércirok (*Sorghum halepense* L.) allelopátiája a gyom és kultúrnövényekre. [Allelopathy of Sorghum halepense L. to weeds and cultivated plants.] Növényvédelem 17 (10-11): 413-418. (in Hungarian)

MOLISCH, H. (1937): Der Einfluß einer Pflanze auf die Andere. Allelopathie. Gustav Fischer Verlag, Jena. 106 p.

NANDAL, D.P.S. – BISLA, S.S. – NARWAL, S.S. – KAUSHIK, J. C. (1994): Allelopathic interactions in agroforestry systems. In: Narwal, S.S. – Tauro, P. (eds.): Allelopathy in Agriculture and Forestry. Scientific Publ., Jodhpur.

PELLISSIER, F. – GALLET, C. – SOUTO, X. C. (2002): Allelopathic interactions in forest ecosystems. In: Reigosa, M.J. – Nuria P. – Sanchez-Moreiras, A.M. – Gonzales, L. (eds.): Allelopathy: from molecules to ecosystems. Science Publishers, Enfield, New Hampshire. 257-269.

PRATAVIERA, A.G. – KUNIYUKI, A.H. – RYOGO, K. (1983): Growth inhibitors in xylem exudates of Persian walnut (*Juglans regia* L.) and their possible role in graft failure. Journal of the American Society of Horticultural Science 108: 1043-1050.

RICE, E.L. (1984): Allelopathy. Second Edition. Academic Press, Orlando, 422 p.

RIDENOUR, W.M. – CALLAWAY, R.M. (2001): The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126: 444-450.

RIZVI, S.J.H. – RIZVI, V. (1992): Exploitation of allelochemicals in improving crop productivity. In: Rizvi, S.J.H. – Rizvi, V.: Allelopathy: Basic and applied aspects. Chapman and Hall, London. 443-473.

SEGURA-AGUILAR, J. – HAKMAN, I. – RYDSTROM J. (1992): The effect of 5-OH-1,4 naphtoquinone on Norway spruce seed during germination. Plant Physiology 100: 1955-1961.

SZABÓ L.GY. (1997): Allelopathy – Phytochemical potential – Life strategy. JPTE, Pécs. 188 p.

SZABÓ L. GY. (1999): Juglone index – a possibility for expressing allelopathic potential of plant taxa with various life strategies. Acta Botanica Hungarica 42 (1-4): 295-305.

SZABÓ L. – VARGA I. – KEVEY B. (1987): Allelopátia és gombatevékenység erdei ökoszisztémákban. [Allelopathy and fungal activity in forest ecosystems] Mikológiai Közlemények 2-3: 109-119. (in Hungarian with English summary)

TERPÓ A. –KOTORI E.P. (1974): Allelopátiás hatások előidézése termesztett növények csírázó magvain. [Allelopathic effects on germinating seeds of cultivated plants.] A Kertészeti Egyetem Közleményei: 38: 274-282. (in Hungarian)

WARDLE, D.A. – NILSON, M.-C., – GALLET, C. – ZACKRISSON, O. (1998): An ecosystem-level perspective of allelopathy. Biol. Rev. 73: 301-309.

Acta Silv. Lign. Hung., Vol. 5 (2009) 19-25

Wood-Inhabiting Macrofungi Proposed for Conservation from the Primeval Bog of Bátorliget

Imre RIMÓCZI[a*] – Lajos BENEDEK[a] – Heinz FORSTINGER[b]

[a] Department of Botany and Soroksár Botanical Garden, Faculty of Horticultural Science,
Corvinus University of Budapest, Hungary
[b] A-4910 REID/Innkreis, Konrad L. str. 1., Austria

Abstract – Short description and evaluation of the wood-inhabiting macrofungi proposed for conservation in the primeval bog of Bátorliget is presented here for the species *Irpex lacteus* (Fr.) Fr., *Kavinia himantia* (Schw.: Fr.) Erikss., *Perenniporia fraxinea* (Bull.: Fr.) Ryv., *Phlebia livida* (Pers.: Fr.) Bres., *Artomyces pyxidatus* (Pers.: Fr.) Jülich, *Antrodia albida* (Fr.: Fr.) Donk, *Antrodiella semisupina* (Berk. et Curt.) Ryv. et Johansen, *Ceriporiopsis resinascens* (Rom.) Domanski, *Oxyporus latemarginatus* (Dur. et Mont.) Donk, *Spongipellis pachydon* (Pers.) Kotl. et Pouzar, and *Pleurotus cornucopiae* (Paulet: Pers.) Roll.

xilophagous macrofungi / Fraxino pannonicae–Ulmetum / Convallario–Quercetum roboris tilietosum / conservation of macrofungi

Kivonat – Fán élő védendő nagygombák a Bátorligeti Ősláp társulásaiban. A Bátorligeti ősláp területén előforduló fán élő, védendő nagygombák közül az alábbiak rövid ismertetését és értékelését adjuk: *Irpex lacteus* (Fr.) Fr., *Hydnocristella himantia* (Schwein.) R. H. Petersen, *Perenniporia fraxinea* (Bull.: Fr.) Ryv., *Phlebia livida* (Pers.: Fr.) Bres., *Artomyces pyxidatus* (Pers.: Fr.) Jülich, *Antrodia albida* (Fr.: Fr.) Donk, *Antrodiella semisupina* (Berk. et Curt.) Ryv. et Johansen, *Ceriporiopsis resinascens* (Rom.) Domanski, *Oxyporus latemarginatus* (Dur. et Mont.) Donk, *Sarcodontia pachydon* (Pers.) Spirin, *Pleurotus cornucopiae* (Paulet: Pers.) Roll.

xilofág nagygombák / keményfa ligetredők / hárssal elegyes gyöngyvirágos tölgyes / védendő nagygombák

1 INTRODUCTION

The primeval bog of Bátorliget was discovered in 1914 by János Tuzson. The outstanding diversity of its flora originates from the beech and birch-pine epoch of the Great Hungarian Plain (Boros 1932, Soó 1934, Simon 1991).

The macrofungi of the region were listed by Ubrizsy (1937, 1940, 1941, 1943, 1953, 1957) for the first time. The latest monograph on the primeval bog of Bátorliget contains (Mahunka 1991) no information on the macrofungi, though several works have been published discussing thoroughly the macrofungi of other protected areas and of national parks.

---

[*] Corresponding author: imre.rimoczi@uni-corvinus.hu; H-1118 Budapest, Ménesi út 44., Hungary

The macrofungi of the Bog has been continuously investigated since 1995 (Lenti–Máté 1995, 1996, Rimóczi 2002). Moreover, today the survey involves also the nearby 'great pasture' of Bátorliget (Leni et al. 2004) and the Fényi forest (Lenti 2007).

2 METHODS

We regularly documented the mushroom species inhabiting living and dead wood in the two plant communities, that cover the majority of the Bog: in the lowland oak woodlands mixed with lime (Convallario–Quercetum roboris tilietosum) and in the oak-elm-ash woodlands (Fraxino pannonicae–Ulmetum). The first results of this survey were published in 1997 (Rimóczi et al. 1997). This work, however, did not discuss the conservation status of these fungi, since the plan of the Red List of our mushrooms has been developed simultaneously (Rimóczi 1997). The revised version of the Red List, which is still today valid for the Hungarian macrofungi, was published in 1999 (Rimóczi et al. 1999). Fungal species being under legal protection (35 species altogether) are compiled in the governmental decree № 23/2005 (VIII. 31.) Ministry of Environment and Waters. This list of the Ministry, containing astonishingly and inexplicably few species, is not reasonable from any scientific aspect.

The above mentioned facts led us to the decision, that in the present article we describe such species of the wood-inhabiting macrofungi of Bátorliget, that are included in the Red List, but their legal protection was rejected by the Ministry. Some species of our compilation were found in the Bog in the past few years and are published here for the first time.

3 RESULTS

Irpex lacteus (Fr.) Fr.

Annual basidiocarps are effuse, effuse-reflexed or composed of shelf-like pilei with a diameter of 1–2 cm. Reflexing surfaces are crinite, velvety. The trama is quite varying: composed of narrow pores when young, then the pores elongate forming lamellae, finally split into teeth and spines. The sporocarps can be observed throughout the year: from the early spring right till the persistent frosts. This saprotrophic species causes white-rot. It fruits on standing or lying trunks and logs of deciduous trees.

In 1783, Batsch regarded this species as a member of Hydnaceae. Fries classified it into its current genus in 1818, under the name *Irpex pavichii*. Pilát considered it as a lamellate polypore: *Trametes lacteae* (Fr.) Pilat.

According to Igmándi (1999), in Hungary this species is widespread from the lowlands to the mountains. It fruits not only on *Fagus*, *Quercus*, *Prunus* and *Populus* species, but also on *Robinia* and *Ailanthus*, and rarely even on the wood of *Pinus*. He does not assign this species to any community.

Krieglsteiner (2000) describes it as a rare species, which is characteristic of oak-elm-ash woodlands and ash-alder swamp woodlands. He observed it mostly on the wood of *Fraxinus excelsior*, *Frangula alnus, Betula pendula* and *Salix* species in the forests of the lowland and the hills, less frequently in the mountains of medium elevation.

We found it on the twigs of *Fraxinus angustifolia* subsp. *pannonica* and *Betula pendula*. Nature conservation status: very rare in the Netherlands and in Italy, rare in Sweden, Germany and Switzerland. On our Red List, this species belongs to Category '3', because it prefers principally the wetlands, the communities of which are also proposed for conservation (Borhidi – Sánta 1999).

Hydnocristella himantia (Schwin.) R. H. Petersen

(= Kavinia himantia (Schw.: Fr.) Erikss.)

(= *Clavaria himantia* Fr.)

The widely effused sporocarp is thin, soft and felty, often with risomorphs. The odontoid trama is composed of dense, needle-shaped, rarely branching teeth of 2-7 mm length, hanging down from the sporocarp ('Hängezähnchen').

Spore print is pale yellow. *Kavinia himantia* fruits on decayed, often mossy trunks and logs, in autumn or in late autumn. It is a characteristic circumpolar species of the riverine woodlands, found on the timber of *Salix*, *Fraxinus* and *Carpinus*. In Bátorliget we found it on the fallen trunk of *Fraxinus angustifolia subsp. pannonica*. This fungus is distributed in the sub-Atlantic regions of the temperate zone of Europe. It is a very rare species of the Red List.

Perenniporia fraxinea (Bull.: Fr.) Ryv.

(= *Fomes cytisinus* [Bk.] Gill.), (= *Fomitopsis cytisina* [Berk.] Bontd. et Sing.)

This species lives as a parasite of deciduous trees on the fringes of riverine woodlands, and it can also be found as a saprotrophic polypore, on logs and fallen dead wood in tree lines. It turns the timber white and soft. Fruit bodies may also be observed in the sunny areas of parks. Contrary to its scientific name, it is more frequent on black locust, than on ash. *Perenniporia fraxinea* can be come across throughout the whole year; partially because it is perennial, and also because new sporocarps may be produced in almost each months. The basidiocarp is broadly attached to the substratum. Its diameter is 10-20 cm, even reaching 50 cm, if several fruitbodies coalesce. The margin is irregularly crispate. The sporocarp often encloses plant remnants by its growth. Pores of the young fruit body are narrow, later they may become larger cream-coloured, turning brown if pressed.

It is rare (Netherlands, Germany, Switzerland) or sporadic (Italy) in Europe. On our Red List it belongs to Category '4', principally because of its preference of humid riverine habitats. However, it also lives in antropogenic habitats, even on the trunk of *Robinia* or *Aesculus*.

Phlebia livida (Pers.: Fr.) Bres.

(= *Corticium lividum* Pers.)

The effused sporocarp forms a 2-4 mm thick, wax-like crust on the surface of decaying deciduous trees. The trama is smooth or granulose, warty, involute, cracking with drying. Its colour is quite varying.

Phlebia livida fruits throughout the whole year, but most frequently in late autumn. It causes the white-rot of deciduous trees, in the intermediate phases of decay. We have observed it on the lying trunks of *Fraxinus angustifolia* subsp. *pannonica* and *Alnus glutinosa*. According to the literature, it inhabits also the timber of *Quercus*, *Carpinus* and *Fagus* (Kreigsteiner 2000), beside that of *Betula*, *Tilia* (Arnolds et al. 1995), or *Picea* (Breitenbach-Kränzlin 1986). It is considered rare in the Netherlands. It is not frequent anywhere in Europe. It belongs to Category '3' of our Red List, because it primarily lives in mesophilic woodlands and riverine forests.

Artomyces pyxidatus (Pers.: Fr.) Jülich

(= *Clavicorona pyxidata* /Pers: Fr./ Donk)

The terminal branches of *Artomyces pyxidatus* (crown-tipped coral fungus) end in minute cups with tapering edge. Its flesh is tough, yellowish or greyish brown, turning brown with aging. Its taste is hot spicy, and the fungus is inedible. It fruits from the beginning of summer till late autumn, on decaying and mossy wood.

On the first sight, its fruiting body resembles a well-developed coral fungus, though it is not a relative of them. The terminal branches form small cups. From the edges of these cups, 4-6 thin branches derive that end in even smaller cups. The edges of the smallest cups bear only small, needle-like outgrowths. Its flesh is springy, whitish yellow when young, changing into brown with a flesh tint with aging. Its smell is very spicy, later it becomes stinking. Its taste turns gradually ever bitter, finally burning hot.

Artomyces pyxidatus fruits on the logs and lying trunks of deciduous trees (and rarely those of *Pinus* or *Abies*) in the intermediate and final decay phases, from the mid-summer till the first frosts. This Holarctic species (Corner 1970) was observed in Bátorliget on thick, well-decayed fallen trunks of *Populus, Salix* and *Fraxinus angustifolia* subsp. *pannonica*, in the heart of riverine forests that are always moist. It is under protection everywhere in Europe, becoming more and more rare due to the lack (or insufficient amount) of dead wood in the natural riverine forests. It belongs to Category ‘2’ on our Red List.

Antrodia albida (Fr.: Fr.) Donk

(= *Lenzites albida* Fr.) (= *Antrodia serpens* (Fr.: Fr.) G. Karst.)

Sporocarp is effused, or emerges at the margins, forming hat-like structures, which arrange above each other in a tile-like manner. Its surface is slightly felty, white or cream-coloured. Pores are whitish, wide and slightly angular at the effused parts of the sporocarp, while at the hat-like emergences they gradually turn into lamellae, elongating in a labyrinth-like way, . It fruits from early summer till late autumn, and the basidiocarps pulverize by the next spring. *Antrodia albida* is a rare species everywhere in Europe. It causes the brown-rot of the trees in *Salix* and *Alnus* forests and in other riverine woodlands. In Bátorliget, we found it on the timber of poplar and ash. It belongs to the Category ‘3’ on our Red List.

Antrodiella semisupina (Berk. et Curt.) Ryv. et Johansen

Fruit bodies appear as mycelial patches, attached close to the substratum, later they become effused, conchiform. Its thickness is some mm, and the sporocarp tapers into a stem-like stalk near the substratum. Its surface is slightly undulate with irregularly lobed margin. Pores of the underside are round, or slightly elongated. Flesh is white, quite elastic, almost rubber-like. Its smell is uncharacteristic, its taste is sweetish.

This fungus lives in beech forests mixed with hornbeam, and in oak-elm-ash or alder woodlands of the Great Plain. It fruits on lying, well-decomposed twigs and trunks, being in the intermediate and terminal phases of decay. Sporocarps often turn up on the soil-facing side of the trunks. It causes white-rot.

The fresh fruiting body can be observed from the beginning of June till the persistent frosts. It distributes throughout Europe, but it is not a frequent species. It lives from the sub-Mediterranean region to the boreal forests, where it was found also on the trunks of spruce and fir.

In Bátorliget we have found it on the trunks of ash, English oak and poplar. Often inhabiting humid, semi-natural habitats, *Antrodiella semisupina* may become endangered in the future.

Ceriporiopsis resinascens (Rom.) Domanski

(= *Poria aneirina* [Somm.] Sacc.) (= *Tyromyces polyetes* Parm.)

Sporocarp is closely attached to the substratum, forming a 1-2 mm thick, wax-like crust. Its surface is finely porous, whitish or cream white when young, turning ochre and dark orange-brown with aging. Pores are initially round, later becoming angular or elongated.

It is the characteristic species of alder and willow forests, and also of riverine woodlands. It fruits from the end of summer, even over milder winters, mainly on the lying and standing decayed trunks of *Salix,* but it also to be found on the wood of *Populus*, *Fraxinus* and even *Sambucus*. It causes white-rot. In Bátorliget we found it on the fallen twigs of *Salix* and *Populus*.

This Holarctic species is rare throughout Europe. This fungus of humid, semi-natural habitats would worth legal protection even in Hungary.

Oxyporus latemarginatus (Dur. et Mont.) Donk

(= *Poria ambigua* Bres.)

Oxyporus latemarginatus is the characteristic species of riverine woodlands. It fruits on the lying, well-decayed twigs and trunks of poplar and alder. It prefers the quickly warming, open parts of the forests. It is sporadic everywhere in the sub-Mediterranean regions of Europe and also in Central Europe. Bánhegyi – Bohus – Kalmár – Ubrizsy (1953) mentioned it several times, as a rare wood-rotting mushroom, but they never described the accurate location of the species. Igmándy (1991) regards it as a sporadic species in Hungary, fruiting on decomposing trunks and branches of deciduous trees. In Bátorliget, we found it on the branches of *Ulmus*, *Fraxinus* and presumably *Salix*.

Sarcodontia pachydon (Pers.) Spirin

(= Spongipellis pachydon (Pers.) Kotl. et Pouzar)

Its sporocarp is effused, or forms pilei growing above each other, in a tile-like manner. It fruits from early spring till late autumn. The surface of the fruiting body is finely felty, partly becoming glabrous. Its cream white colour turns light brown with aging. The trama is composed of flattened, spiny projections (or teeth), sometimes of 10–15 mm length. At the edge of the sporocarp, these spines fuse to form lamellae. Its flesh is cartilaginous when young, turning brittle with aging.

The fruit bodies of *Spongipellis pachydon* occurs in deciduous forests, on standing dead trunks or on fallen branches or logs. It causes white-rot. In Bátorliget, we found this species on the twigs of *Populus* and *Quercus robur*. It is a rare species all over Europe, being under protection. It belongs to Category ‘3’ on our Red List, i.e. it is ‘endangered’.

Pleurotus cornucopiae (Paulet: Pers.) Roll.

In deeply shaded habitats the cap is bright yellow, turning paler in the more sunny ones. The dense gills are white, often with a pink tint. They are running right down the stem, where they anastomose reticularly. Its snow-white flesh is soft when young, later becoming fibrose. It is slightly flour-flavored, delicious.

Most often, thus also in Bátorliget, it fruits on the decomposing logs and fallen trunks of *Ulmus*, always forming groups of numerous fruit bodies. Sometimes it is found on other deciduous trees, like poplar or ash.

This species is characteristic of oak-elm-ash woodlands. It fruits from early summer till the first frosts. It is a rarefying species throughout Europe. It belongs to Category ‘3’ on the Hungarian Red List. The main reasons for this position are the decline of its habitats, diminishing of its substrata, and also its delicious taste. It is the most delicate oyster mushroom, containing the ‘least amount of fibres’. Its cultivation has been under development for decades.

Approximately 120-140 species from 75 genera of the order Aphyllophorales lives in Bátorliget. 55-70% of them are characteristic of the area, which can be assigned to a certain plant community.

REFERENCES

ARNOLDS, E. – KUYPER, TH. W. – NOORDELOOS, E. M. (1995): Overzicht van der paddestoelen in Nederland. Nederlandse Mycologische Vereniging, Wijster.

BÁNHEGYI, J. – BOHUS, G. – KALMÁR, Z. – UBRIZSY, G. (1953): Magyarország nagygombái. [Macrofungi of Hungary] Akadémiai Kiadó, Budapest. (in Hungarian)

BORHIDI, A. – SÁNTA, A. (szerk.) (1999): Vörös Könyv Magyarország növénytársulásairól 1.-2. [Red Book of the Hungarian plant communities 1-2.] Természet BÚVÁR Alapítvány Kiadó, Budapest. (in Hungarian)

BOROS, Á. (1932): A Nyírség flórája és növényföldrajza. [Flora and plant geography of the Nyírség.] Tisza István Tud. Társ. Honism. Biz. Kiadványai, Debrecen, 7.: 25-26. (in Hungarian)

BREITENBACH, J. – KRÖNZLIN, F. (1986): Pilze der Schweiz, Band 2, Vertag Mykologia, Luzern.

CORNER, E. J. H. (1970): Supplement to „A monograph of Clavaria and alkied genera.” Beiheft z. Nova Hedwigia, 33.

IGMÁNDI, Z. (1991): A magyar erdők taplógombái. [Polypores of the Hungarian forests] Akadémiai Kiadó, Budapest. (in Hungarian)

KRIEGLSTEINER, G.J. (2000): Die Grosspilze Baden-Württembergs. Bd. 1-2. Verlag Eugen Ulmer, Stuttgart (Hohenheim).

LENTI, I. – MÁTÉ, J. (1995): A Bátorligeti-ősláp mikológiai vizsgálata I. [Mycological study of the premival bog of Bátorliget I.] MTA Sz. Sz. B. Megyei Tud. Test. 4. Ülésének Kiadványa, Nyíregyháza, 28. (in Hungarian)

LENTI, I. – MÁTÉ, J. (1996): Fungi in the Bátorliget Ancient. Bog. Symp. on Cur. Top. in microbiol. Uzhgorod.

LENTI, I. – RIMÓCZI, I. – BORONKAY, F.né (2004): A Bátorligeti nagylegelő gombái. [Mushrooms on „Bátorligeti-nagylegelő”] Mikol. Közlem., 43. (1-3): 47-60. (in Hungarian)

LENTI, I. (2007): A bátorligeti Fényi-erdő nagygombái [Mushrooms of the Fényi forest, Bátorliget] Szabolcs-Szatmár-Beregi Szemle, XLII./2.: 203-217. (in Hungarian)

MAHUNKA, S. (ed.) (1991): The Bátorliget Nature Reserves – after forty years. Hung. Nat. Hist. Museum, Budapest.

RIMÓCZI, I (1997): Magyarország nagygombáinak természetvédelmi helyzete és Vörös Könyvének terve [Plan of the Red Book and position in nature conservation of the hungarian mushrooms.] Mikol. Közlem., 36.: 65-108. (in Hungarian)

RIMÓCZI, I. (2002): A Bátorligeti-ősláp nagygombáinak rendszertani és társulástani jellemzése. [Taxonomical and cenological characterization of macrofungi from the premival bog of Bátorliget] In: Lenti, I. – Aradi, Cs. (eds.) Bátorliget élővilága – ma. Bátorliget Önkormányzata, Bátorliget. 109-139. (in Hungarian)

RIMÓCZI, I. – MÁTÉ, J. – LENTI, I. (1997): Osztott bazidiumú- és nem lemezes nagygombák a Bátorligeti-őslápon. [Phramobazidiomycetidea and Aphyllophorales at Bátorliget mire Nature Reserve] Mikol. Közlem., 36. (2-3): 13-34. (in Hungarian)

RIMÓCZI, I. – SILLER, I. – VASAS, G. – ALBERT, L.– VETTER, J. – BRATEK, Z. (1999): Magyarország nagygombáinak javasolt Vörös Listája. [Proposed Red List of Hungarian mushrooms] Mikol. Közlem. 38. (1–3): 107-132.

SIMON, T. (1991): Nature conservation values of the Bátorliget area. In: Mahunka S. (ed.) The Bátorliget Natura Reserves 1. Hung. Nat. Hist. Mus., Budapest. 19-23.

SOÓ, R. (1934): Nyírségkutatásunk florisztikai eredményei. [Floristic results of the survey of the Nyírség] Bot. Közlem. 218-252. (in Hungarian)

TUZSON, J. (1914): A Magyar Alföld növényformációi. [Plant assemblages of the Great Hungarian Plain] Bot. Közlem. 51. (in Hungarian)

UBRIZSY, G. (1937): Válasz bírálóimnak [Response to the critiques] Szabolcsi Szemle, 4.: 129-131. (in Hungarian)

UBRIZSY, G. (1940): Adatok a Nyírség gombavegetációjának ismeretéhez. [Data on the macrofungi of the Nyírség] Acta Geobot. Hung., 3.: 66-77. (in Hungarian)

UBRIZSY, G. (1941): A Nyírség gombavegetációja. [The macrofungi of the Nyírség] Acta Geobot. Hung., 5.: 43-91. (in Hungarian)

UBRIZSY, G. (1943): Szociológiai vizsgálatok a Nyírség gombavegetációján. [Sociological survey of the macrofungi of the Nyírség] Acta Geobot. Hung. 5.: 251-279.

UBRIZSY, G. (1953): Mycophyta = Gombák. [Mycophyt=Fungi] In: SZÉKESSY, V. (eds.): Bátorliget élővilága. Akadémiai Kiadó, Budapest: 23-25.

UBRIZSY, G. (1957): Újabb vizsgálatok az erdőtípusok talajlakó nagygombáinak társulási viszonyairól. [Recent cenological results on the terrestrial macrofungi of different forest types] Növ. véd. Kut. Int. Évkönyve, 7.: 409-444.

Acta Silv. Lign. Hung., Vol. 5 (2009) 27-45

Stress Sensitivity of Correlation between POD and PPO Activities in Plants

Zsolt István NÉMETH[a*] – Mónika POZSGAI-HARSÁNYI[a] –
Borbála GÁLOS[b] – Levente ALBERT[a]

[a] Department of Chemistry, Faculty of Forestry, University of West Hungary, Sopron, Hungary
[b] Institute for Environmental and Earth Sciences, Faculty of Forestry,
University of West Hungary, Sopron, Hungary

Abstract – In the leaf extracts of two plant species (*Quercus robur* L. and *Phaseolus vulgaris* L.), peroxidase (POD) and polyphenol oxidase (PPO) activities have been measured by the methods of Shannon et al (1966) and Flurkey and Jen (1978). The oxidative activities regarded as semi-empirical biochemical variables have distributions in the plant foliage and between them a linear correlation has been observed. In this work the resultant oxidative activities of POD and PPO isoenzymes of plant foliages, the measuring uncertainties of their values and their correlation are interpreted. For the effects of cold shock and lack of illumination, significant alterations in the correlation have been revealed that are also reflected by the parameters of the regression. The correlation of POD and PPO has been established to be stress sensitive by the application of covariance analysis (ANCOVA).

plant stress / enzyme correlation / *Quercus robur* L./ *Phaseolus vulgaris* L. / peroxidase / polyphenol oxidase

Kivonat – Növényi oxidatív aktivítás-korreláció stressz-érzékenysége. Két növényfaj (*Quercus robur* L. és *Phaseolus vulgaris* L.) lombozatából peroxidáz (POD) és polifenol oxidáz (PPO) aktivitásokat határoztunk meg Shannon et al (1966), ill. Flurkey-Jen (1978) módszerével. A félempirikus biokémiai változóknak tekintett oxidatív aktivitások a növényi lombozatban eloszlással rendelkeznek. Értékeik között lineáris korrelációt tapasztaltunk. Dolgozatunkban a POD és PPO izoenzimek eredő oxidatív aktivitásait, értékeik bizonytalanságát és korrelációjukat egyaránt értelmezzük. Hideg sokk és fényhiány hatására a regressziós paraméterek által visszajelzett szignifikáns változásokat észleltünk a POD versus PPO korrelációban. A kovariancia analízis (ANCOVA) alkalmazásával ez a korreláció statisztikai értelemben stressz-érzékenynek bizonyult.

növényi stressz / enzimkorreláció / *Quercus robur* L. / *Phaseolus vulgaris* L. / peroxidáz / polifenol oxidáz

---

[*] Corresponding author: nemeth.zsolt@emk.nyme.hu; 9401 Sopron, POB 132, Hungary

1 INTRODUCTION

The plant cells have a complex antioxidant system. Its primary role is to minimize the amount of hydrogen-peroxide produced in the SOD-ASC-GSH cycle during the photosynthesis (Polle 2001) and to oxidize some metabolites, respectively. Various peroxidases (POD isoenzymes) and polyphenol oxidases (PPOs) take part in the oxidation of the metabolites. The higher plants have several classes and types of PODs, reaching up to 160 isoenzymes in some plants such as cereals (Dunford 1999). The same is true for PPO (Mayer 2006). In their activity controls, there were found both up and down regulated isoenzymes (Boss et al. 1994, Kim et al. 2001, Li – Steffens 2002, Thipayong et al. 2004, Wang – Constabel, 2004). In cases of these two enzyme classes it is necessary to emphasize the activity overlapping between them, too. For example, 10 isoenzymes of PODs in tobacco leaves can also produce PPO activity (Sheen–Calvert 1969).

The plant antioxidant enzyme system has been proved to be stress sensitive. The stress sensitivity of these two enzyme groups, the POD and the PPO enzymes have in turn been experienced in a numerous cases of environmental and stress effects. Their susceptibility can be related to their gene transcriptions influenced by abiotic and biotic stress factors. Their investigations are very important part in the researches of plant physiological states and these state alterations (Sárdi–Stefanovits-Bányai 2006, Jaleel et al. 2009). The knowledge about the stress dependence of POD and PPO activities has continuously been broadening. Recently, in the investigations of *Catharanthus roseus* (Jaleel et al. 2008), cowpea (Chandra et al. 2007), spinach (Ozturk et al. 2008), *Polygonum vivparum* (Wang et al. 2009) and bean (Sárdi – Stefanovits – Bányai 2006), the POD and/or PPO activities are significantly altered by sodium chlorite, triadimefon, *Rhizoctonia solani* inoculation, ethephon, different altitudes and *Pseudomonas savastanoi* infection. However, the relative large standard deviations of the results greatly limit the characterization of stress with enzyme activities. In many cases, the establishment of significant difference between the two means requires many simultaneous experiments, that can improve the statistical comparability. Based on determination of enzyme activities, a substantial condition of stress qualifying conception is to decrease the standard deviation of the measurements. The reduction of standard deviations demands that we know the reasons and the origin of the activity differences. The standard deviation of the enzyme activity results from the stochastic error of analytical methods, uncertainty of fixation of the developmental stage and different intensities of metabolisms. The difference in metabolic intensities among the cells has the dominant role. In consequence, efficiency of the stress investigations carried out by the measurement of enzyme activities can be augmented if there is a possibility to decrease or avoid metabolic intensity deviations of biological samples.

Observations of the existence or non-existence of the correlations between biochemical variables are important establishments that suggest a synchronized potential regulation of the variable values in the metabolism. Seeking the origin of the correlations, the conditions of the existence of state-dependent correlation have been declared in one of the recent articles and a theoretical equation was successfully deduced to the linear regression symbolizing state-dependent correlation of two biochemical variables (Németh et al. 2009a):

$$x_1 = \frac{\sigma_1}{\sigma_2} x_2 + \frac{\sigma_2\mu_1 - \sigma_1\mu_2}{\sigma_2} \quad (1)$$

where $\mu_i = \lim_{n\to\infty}\left(\overline{x_i}\right) = \lim_{n\to\infty}\left(\frac{1}{n}\sum_{j=1}^{n} x_{i_j}\right), \overline{x_i}$ is the mean of variable x_i,

$\sigma_i = \lim_{n\to\infty}\left(s_i\right) = \lim_{n\to\infty}\left(\sqrt{\frac{\sum_{j=1}^{n}\left(x_{i_j} - \overline{x_i}\right)^2}{n-1}}\right)$ and s_i is the i^{th} empirical standard deviation,

where, x_1 and x_2 are the biochemical variables in the correlation (e.g. metabolite concentrations, enzyme activities, etc). μ_1 and μ_2 are the expected values of the variables x_1 and x_2. σ_1 and σ_2 are the theoretical standard deviations of distributions of variables x_1 and x_2. Applying equation 1 to enzyme concentrations, the relationship of enzyme correlation is obtained:

$$[E_1] = \frac{\sigma_{E_1}}{\sigma_{E_2}}[E_2] + \frac{\sigma_{E_2}\mu_{E_1} - \sigma_{E_1}\mu_{E_2}}{\sigma_{E_2}} \qquad (2)$$

where, μ_{E_1} and μ_{E_2} are the means of concentration distributions of E_1 and E_2 enzymes. σ_{E_1} and σ_{E_2} are the theoretical standard deviations of the distributions of enzyme concentrations.

The correlations belonging to the same sampling time are considered as state-dependent correlations. State-dependent correlation is a concept that is based on the physiological state of organism. The slope and the intercept of state-dependent regression can alter in time. It makes an opportunity to characterize the physiological states or state alterations with the correlation of biochemical variables. The state-dependent correlation is regarded as sensitive to state alteration if the slope and/or the intercept of regression straight line, ergo if the theoretical standard deviations and/or the expected values of distributions of biochemical variables can significantly change during the state alteration (Németh et al. 2009a). By a correlative investigation in this paper, we show that the physiological stages of biological systems can be distinguished from each other in a more sensitive way in relation to only the comparisons of the means of correspondent variables. By using the ANCOVA method statistical identity or deviation has effectively been established among the state-dependent regressions of some plant stresses.

Resultant activities of both POD and PPO isoenzymes are often tracked by spectrophotometrical methods (Chisari et al. 2008, Nunes et al. 2007, Toralles et al. 2005; Rajeswari – Paliwal 2008). In these protocols, the *in vitro* abilities of the crude leaf extract, which degrade *o*-dianizidine and catechol substrates, have primary been monitored. The correlative approximation has been extended to the investigation of the resultant activities of peroxidase (POD) and polyphenol oxidase (PPO) isoenzymes. Via a model investigation, the existence of the correlation of resultant oxidative activities was discussed. Moreover, the correlations of some biochemical variables (carbohydtrate contents, levels of quaterneric ammonium compounds, etc) have been proven to be susceptible to some plant stresses. As a result of this phenomenon, the stress syndromes of some plants have been characterized with the state-dependent regressions having various slopes and intercepts (Németh et al. 2009b). Thus, for the investigation of stress sensitivity we have tried to choose these two universal activities whose roles are related to high-flux backbone of the metabolism and which can be stress sensitive. The alterations of POD and PPO activities have been investigated in the leaves of a herbaceous plant and a forest tree species exposed to cold shock and lack of illumination.

2 MATERIALS AND METHODS

2.1 Plants

Individual characteristics of the investigated pedunculate oak trees (*Quercus robur* L.) located in the Botanical Garden at the University are the next: (a) first tree. No 1.; GPS:47.67780 °N. 016.54928 °E; age: 27 years; (b) second tree. No 2; GPS:47.67960 °N. 016.57364 °E; age: 32 years; third tree. No 3; GPS: 47.67963 °N. 016.57360 °E; age: 32 years.

Peroxidase (POD) and polyphenol oxidase (PPO) activities were determined in pedunculate oak seedlings with six leaves, in the leaves of pedunculate oak trees and also in leaves of large white bean plants (*Phaseolus vulgaris* L.). All experiments were performed at the Department of Chemistry of the University of West Hungary. Fresh acorns originated from West Hungary (Vitnyéd) were stored in refrigerator at 2°C and 80% relative humidity until used.

The germination of oak acorns and bean seeds for growing seedlings and plants were carried out in a wet bed of Florasca B soil (Florasca Ltd. Sopron. Hungary) under greenhouse condition.

2.2 Extraction of enzymes

All reagents came from Merck Chemical Co. (Germany) and Reanal Chemical Co. (Hungary). After sampling the sample clean-up was carried out immediately and all measurements were made in triplicate. The fresh leaves were homogenized with equal quantity of quartz sand. For enzyme extraction, the samples of 1.20 g were extracted with 15.00 cm^3 amounts of K-Na-phosphate buffer (pH = 6.0) solutions at 4°C for 20 minutes and then centrifuged at 6000 rpm for 10 minutes.

2.3 Assay for oxidative activity of POD isoenzymes

Resultant activity of POD isoenzymes (EC. 1.11.1.7) with *o*-dianizidine as chromogen reagent was determined by spectrophotometry at 480 nm. The reaction mixture contained 1.7 mL of buffer (pH=6.0), 30 μL of 0.3 % H_2O_2 and 20 μL of *o*-dianizidine as substrates. The reactions were started by the addition of 10 or 20 μL of extracts (Shannon et al. 1966)**.** The increase was followed for 4 minutes. 1 POD Unit = 0.01 absorbance unit·min^{-1}.

2.4 Assay for oxidative activity of PPO isoenzymes

By monitoring of the increase in absorbance at every 10th second with a Hitachi U-1500 spectrophotometer at 420 nm, resultant activity of PPO isoenzymes (EC 1.10.3.1) with catechol substrate was measured. The increase was tracked for 3 minutes. The reaction mixture contained 1mL of buffer (pH=6.0), 1 mL of 0.2 M catechol as a substrate and 0.5 mL of extract (Flurkey–Jen 1978)**.** All measurements were performed at room temperature. Each sample was assay in triplicate. 1 PPO Unit = 0.001 absorbance unit·min^{-1}.

2.5 Protein determination

All enzyme activities were expressed as units per microgram of protein weight (Uμg $protein^{-1}$). The determination of protein amounts in the extracts was carried out with Bradford's method (Bradford 1976)**.**

3 RESULTANT EFFECT OF ISOENZYMES

Biochemical researches with reductionist approximation had a penchant for the application of spectrophotometrical technique in order to detect the enzymes and to confirm their ubiety within a given tissue, respectively. During enzyme catalysis, chemical conversion of the substrates added to the extract of biological sample to the products could be tracked according to Beer's law of spectrophotometry. For detecting the activities of various enzymes a lot of photometrical protocols have been developed. Until the middle of the seventies, the spectrophotometrical protocols had been dominant and quickly feasible indirect methods of enzyme kinetical investigations. Determination of the values of enzyme activities on the basis of biochemical reaction models (e.g. Michaelis-Menten kinetic, Ping-pong mechanism, etc) was taken back to quantitative alterations of substrate or product in time. Since finding of the existence of isoenzymes, these bioanalytical protocols have become semi-empiricals because they are directly not able to distinguish the different isoenzymes or their catalitical properties. With spectrophotometrical investigations of the activities, POD and PPO isoenzymes degrading the same substrate can not be distinguished from each other. The investigation of enzyme activities has been relocated to the analytical techniques including the separation of isoenzymes (e.g. protein electrophoresis). In spite of development of isoenzyme investigations, the applications of spectrophotometrical activity measurements has not sunk into oblivion since the semi-empirical information provided by them are/were characteristic of the biological systems. Physiological states can be characterized and their significant differences can be revealed by the measurements of semi-empirical activities, respectively. Spectrophotometrical activity protocols integrate the activities of the isoenzymes. They reflect the resultant effect of the isoenzymes as the activity of a hypotethical enzyme, wich substitute the roles of each isoenzymes in the investigated biochemical reaction. The resultant effect of the isoenzymes can be interpreted as a specific capability or activity of biological extract. The effects of POD and PPO isoenzymes in the sample extract on given substrates (e.g. catechol and o-dianizidine) are named as substrate specific oxidative activities of *in vitro* biological system.

The reaction rate (v) depends on the converting capability of biological system (Ψ) and the biochemical driving force (φ). The driving force of biochemical reactions, $\varphi([S])$ is influenced by substrate concentration and the value of Ψ is determined by product of rate constant (k) and enzyme concentration ($[E_0]$). The rate of i^{th} reaction catalyzed by i^{th} isoenzymes:

$$v_i = \frac{d[P]_i}{dt} = \Psi(k_i, [E_{i0}]) \cdot \varphi([S]) = k_i [E_{i0}] \cdot \varphi([S]), \quad i = 1,2, ...,\mathrm{n} \tag{3}$$

where $\varphi([S]) \in [0, 1]$. n is the number of isoenzymes. $[P]$ is the biochemical product. $[S]$ is the substrate concentration, $[E_{i0}]$ is the total amount of i^{th} isoenzyme and k_i is the rate constant of product formation in the i^{th} reaction.

If the substrate concentration is much larger than the values of Michaelis constants of their isoenzymes ($[S] >> K_{M1}, K_{M2}, ..., K_{Mi}, ..., K_{Mn},$) the biochemical reaction rates are particularly propotion to the concentrations of their isoenzymes ($\varphi([S]) \approx 1$). Anyway, this limitation is the necessary condition of the application of spectrophotometrical activity measurements. The overall reaction rate is determined by the amount of the rates of independent reaction steps.

$$\begin{aligned} v &= v_1 + v_2 + ... + v_i + ... + v_n = (k_1[E_{10}] + k_2[E_{20}] + ... + k_i[E_{i0}] + ... + k_n[E_{n0}]) \cdot \varphi([S]) \\ &= k^*[E_0]^* \cdot \varphi([S]) \approx k^*[E_0]^* \end{aligned} \tag{4}$$

$$v = v\big|_{\varphi([S])\approx 1} \approx k_1[E_{10}] + k_2[E_{20}] + \ldots + k_n[E_{n\S}] \tag{4.1}$$

v is the resultant reaction rate measured in *in vitro* manner. Adapted the nomenclature of specific enzyme reactions to this reaction rate, it can be regarded as the resultant activity of the isoenzymes $E_1, E_2, \ldots, E_n$, or as the converting activity of the extract.

$$[E_0]^* = [E_{10}] + [E_{20}] + \ldots + [E_{i0}] + \ldots + [E_{n0}] \tag{4.2}$$

$$k^* = \frac{k_1[E_{10}] + k_2[E_{20}] + \ldots + k_i[E_{i0}] + \ldots + k_n[E_{n0}]}{[E_{10}] + [E_{20}] + \ldots + [E_{i0}] + \ldots + [E_{n0}]} \tag{4.3}$$

3.1 Uncertainty of resultant activities

Stochastic error and/or measuring precision ($\pm\,\Delta v$) of the reaction rate *v* is collectively influenced by the values of rate constants $k_1, k_2, \ldots, k_n$, which are equivalent to turnover numbers, and stochastic deviations ($\pm\,\Delta[E_i]$) of isoenzyme activities $E_1, E_2, \ldots, E_n$. Applied the law of error propagation to equation (4.1) we obtained the equation (5).

$$\Delta v \approx k_1\Delta[E_1] + k_2\Delta[E_2] + \ldots + k_n\Delta[E_n] \tag{5}$$

On the basis of equation (5), model values of Δv, which have been determined at the combinations of identical and different hypothetical rate constants (cases A, B and C in the *Table 1*) and the same values of $\Delta[E_i]$ deviations (hypothetical absolute error: ± 0.1 or ± 1), respectively, are shown in *Table 1.*

Table 1. Effect of the turnover numbers (ki) and stochastic error of isoenzyme concentrations (Δ[Ei]) on the resultant reaction rate in a hypothetical case of three isoenzymes.

Combinations of reaction rates			A			B			C	
$v = \Sigma v_i =$ *constant*						*i*				
		1	2	3	1	2	3	1	2	3
$\Delta[E_i]$	$[E_i]$ k_i	$[E_1]=1$ $k_1=1$	$[E_2]=1$ $k_2=1$	$[E_3]=1$ $k_3=1$	$[E_1]=5$ $k_1=0.1$	$[E_2]=2$ $k_2=1$	$[E_3]=5$ $k_3=0.1$	$[E_1]=1$ $k_1=0$	$[E_2]=3$ $k_2=1$	$[E_3]=1$ $k_3=0$
± 0.1	$v_i=k_i[E_i]$	1	1	1	0.5	2	0.5	0	3	0
	$\Delta v_i=k_i\Delta[E_i]$	±0.1	±0.1	±0.1	±0.01	±0.1	±0.01	0	±0.1	0
	$\Delta v=\Sigma\Delta v_i$		**± 0.3**			**± 0.12**			**± 0.1**	
± 1	**$\Delta v=\Sigma\Delta v_i$**		**± 3**			**± 1.2**			**± 1**	

With the hypothetical value ± 0.1 of Δ[Ei] such a biological system (e.g. blood) is represented, in which the concentrations of the isoenzymes can be considered nearly constant. The absolute error is about ± 10% of the means or smaller than this limit. In these systems the stochastic deviations of isoenzyme quantities can primary be originated from the noises of gene operations (McAdams – Arkin 1999, Thattai – van Qudenaarden 2001, Arkin et al. 1998). In a hypothetical case of Δ[Ei] ≤ ± 1, in turn, such biological tissues (e.g. plant foliage) are modelled where the isoenzyme concentrations E1, E2, ..., En have some distributions. The absolute error is about ± 100% of the means or smaller than this limit. In the cases of the errors of both 10% and 100% , the value of Δv is minimal if the conversion of the substrate S to product P is carried out by only one isoenzyme. In case of collective catalysis of more isoenzymes (n), if the rate constants were equivalent (k1 = k2 = ... = ki = ... = kn) then Δv would be equivalent to nkiΔ[Ei]. The value of Δv will decrease if one of the rate constants becomes dominant with respect to the rest (kj >> k1, k2, ..., ki ,...., kn; j ≠ i). Besides the constancy of resultant reaction rate, the larger is the dominancy of kj, the smaller will be Δv.

The occurrence of this latter case within the metabolism is supported by reference data (Masanori et al. 1984, Chemnitius et al. 1982, Wu – Marletta 1988, Thongsook – Barrett 2005, Bogdanovic et al. 2005). Moreover, it has been established in our own experiments that the distributions of resultant oxidative activities cover the domains of about one magnitude order surrounding their expected values similarly to the distributions of other biochemical variables. These phenomena may also reflect the fact that the metabolic regulation mechanisms make every effort to minimize the uncertainty of biochemical reactions. During the improvement of control of metabolic fluxes the deacrease of flux noises must have ensured evolutional advantage to the organisms (Savageau 1976, Heinrich – Schuster 1996).

3.2 Correlation and state dependence of resultant activities

In a former paper it has already been proven that the values of two biochemical variables can produce state dependent linear correlation if their distributions are identical and if the regulation of their values in the metabolism is synchronized (Németh et al. 2009a). There is a linear correlation between the resultant activities of isoenzymes if the mentioned conditions are valid for the dominant isoenzymes or for all isoenzymes. In that case if some environmental state alteration is able to induce significant alteration in the physiological state of the organism then the isoenzyme activities can also change in significant manner. If, during the alteration of physiological state, the identity of the distributions and the synchronization of regulation of the activities to each other are maintained then the new environmental state will be characterized by a new correlation differing from the previous one. Various environmental states can be distinguished from each other by the correlation of resultant isoenzyme activities being susceptible for state alteration, for example, by the correlation of different oxidative activities of leaf extracts. According to the isoenzymes determining them, these oxidative activities are specific and significantly independent from each other. The oxidative activities measured by us were specific according to their POD and PPO isoenzymes. In such situations the correlations of oxidative activities are represented by regression straight lines. To distinguish them from each other is possible by using the covariance analysis (ANCOVA) (Sváb 1967). In the next, representing and modelling various environmental effects, oxidative activities, their linear correlations and covariance analysis of regression straight lines of the correlations are reported.

4 RESULTS AND DISCUSSION

To study the correlation between the oxidative activities produced by peroxidase and polyphenol oxidase isoenzymes we chose three pedunculate oak trees (*Quercus robur* L.) at the Botanical Garden of the University of West Hungary (Sopron, Hungary). The sampling of the leaves of the three trees was variously designed. Different leaf samplings were applied to get information about their effect on the investigated enzyme correlation. Six leaves from each tree were cut off and then they were analysed at once.

In case of the first tree (No 1) a random sampling of leaves was taken from the same branch. The leaves of the second tree (No 2) originated from six different branches. The leaf samples from the third tree (No 3) were gathered without assigning branches. The leaf samplings were taken for three days when the values of climatic parameters (e.g. temperature: 20,6 ± 0,9 ^{o}C; moisture: 68 ± 1 %, atmospherical pressure: 1012 ± 4 kPa; sunshine duration: 1.5 ± 0.2 h;) could be regarded as nearly the same. The protein contents of leaf samples provided the confidence interval of 7.24 ± 0.95 mg/g dry weight independent of the individual character of oak trees. Thus, the protein content in the leaves has been considered as constant in the statistical sense. The three trees were growing on brown earth soil.

The linear regression of enzyme activities provided the straight lines with about 0.93 values of the coefficients of determination, r^2. The results of enzyme activities are shown in *Table 2*. The influence of the trees (and different leaf samplings) on the correlations were investigated by covariance analysis (ANCOVA) and we found some answers to the next four questions.

I. May a total equation of linear regression be applied to incorporated results of the leaf samplings?
II. May the regression coefficients of different samplings be considered as the same? (Is there a significant deviation between the slopes of the straight lines?)
III. Are the regression of the mean enzyme activities and the regressions of the trees identical with each other?
IV. May the corrected PPO activities, treating them as independent variables, be regarded as almost the same?

With respect to the assumed normal distribution of enzyme activities, the ANCOVA analysis was carried out (Sváb 1967) by StatsDirect v2.6.5 software (StatsDirect Ltd, Altrincham, UK). These two covariance methods can give the answers to the question mentioned above. The statistical equations of applied covariance method can be found in the Supplemental Data.

After fitting straight lines in terms of the formulation of $[PPO] = b[POD] + a$ to the values of POD and PPO specific activities, to respond to our questions the investigations of following hypotheses are necessary:

I. H_0: $b_T \neq 0$ and H_a: $b_T = 0$, respectively. If the condition of $b_T \neq 0$ is met then there is a total linear relationship in the incorporated set of enzyme activities. (b_T – he slope of the total linear regression)
II. For the second question, the H_0: $b_W = b_1 = b_2 = b_3$ and respectively, H_a: $b_W \neq b_1 \neq b_2 \neq b_3$ hypotheses have to be checked, where b_W is the slope of the regression within the classes (or of the trees) and b_i is the slope of i^{th} class.
III. For the third case the investigation of H_0: $b_B = b_W$ resp. H_a: $b_B \neq b_W$ hypothesis give some answers. (b_B – the slope between the classes)
IV. H_0: $Y'_1 = Y'_2 = Y'_3$ is the hypothesis of the equivalence of corrected PPO specific oxidative activities.

The parameters of ANCOVA are shown in *Table 2* and their results and statements are recorded in *Table 3*.

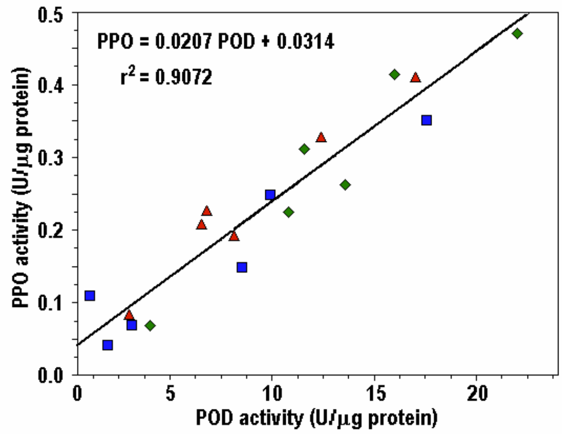
On the basis of ANCOVA, the leaf sampling did not show any influence on the investigated enzyme correlations. There was no significant deviation in the slopes and interceptions of the linear relationships. Thus, the incorporated set of activity data pairs can be characterized by a common regression straight line. The existence of the total regression is independent of the sampling and of the entity of the oak trees. The total correlation relationship between POD and PPO specific activities independent of the leaf sampling and the individual character of the tree is depicted in *Figure 1*.

Table 2. Activities (U µg protein-1) of POD and PPO isoenzymes in the leaf samples of Quercus robur L. and their statistical data. (Statistical equations can be found in Supplemental Data)

$j = 1...k$	j – the number of investigated oak trees								
$i = 1…n$	1.			2.			3.		
$k = 3$	Leaves from the same branch of the oak tree 1.			Leaves from six various branches of the oak tree 2.			Leaves from the tree 3 by chance.		
$n = 6$	POD	PPO		POD	PPO		POD	PPO	
i	X_{i1}	Y_{i1}	$X_{i1}Y_{i1}$	X_{i2}	Y_{i2}	$X_{i2}Y_{i2}$	X_{i3}	Y_{i3}	$X_{i3}Y_{i3}$
1	4.014	0.068	0.2729	8.496	0.150	1.2744	6.532	0.206	1.3456
2	22.018	0.470	10.349	1.074	0.110	0.1181	6.790	0.224	1.5210
3	13.564	0.262	3.5538	17.520	0.352	6.1670	3.018	0.082	0.2475
4	10.836	0.224	2.4273	3.120	0.070	0.2184	8.130	0.190	1.5447
5	11.594	0.312	3.6173	1.950	0.042	0.0819	17.034	0.408	6.9499
6	16.024	0.414	6.6339	9.882	0.250	2.4705	12.414	0.326	4.0467
Mean:	13.008	0.292	4.4756	7.007	0.162	1.7217	8.986	0.239	2.6093
□(…) :	78.050	1.750	26.853	42.042	0.974	10.330	53.918	1.436	15.656
□(…^{2}) :	1193.5	0.61308	182.78	491.48	0.22767	45.83	608.24	0.4082	71.25
[□(…)]^2 :	6091.8	3.063	721.12	1767.5	0.9487	106.72	2907.2	2.0621	245.10

Calculated statistical data

Grand means			
	SST(X) = 611.02	SST(Y) = 0.2875	SPT(XY) = 12.6240
	SSB(X) = 112.22	SSB(Y) = 0.0508	SPB(XY) = 2.2781
G(X) = 10.236	SSW(X) = 498.80	SSW(Y) = 0.2367	SPW(XY) = 10.3459
G(Y) = 0.2447	$SW(X)_1$ = 178.20	$SW(Y)_1$ = 0.1027	PW(XY)1 = 4.0891
G(XY) = 3.1082	$SW(X)_2$ = 196.89	$SW(Y)_2$ = 0.0696	PW(XY)2 = 3.5056
	$SW(X)_3$ = 123.72	$SW(Y)_3$ = 0.0645	PW(XY)3 = 2.7512



◆ - tree 1; ■ – tree 2; ▲ - tree 3,
Activity data are in *Table 2*.

Figure 1. Linear correlation between POD and PPO specific activities from different pedunculate oak trees and various leaf sampling designs. Total correlation equation: PPO = 0.0207 POD + 0.0314, r^2 = 0.9072; (Global solar radiation (GSR) = 4.82 MJ·m^{-2}·day^{-1})

Table 3. Variance table for the investigation of homogenity of the linear regressions. (F - variable of F test; Fcv - criterion value of F test at α = 0.05 significance level)

α = 0.05		Deviation from linear regression				
i	Source of variation	D_i	DFD_i	$MD_i = D_i / DFD_i$	*F*	F_{cv}
1	summarized for the samples $(D_1 = D_C)$	0.01928	12	0.00160		
2	within samples collectively $(D_2 = D_W)$	0.02213	14	0.00158		
3	between samples $(D_3 = D_B)$	0.00454	1	0.00454	$\frac{MD_3}{MD_1} = 2.84$	4.60
4	for total regression $(D_4 = D_T)$	0.02669	16	0.00167		
	Null Hyphothesis					
5	H_0: $b_T \neq 0$; There is a common regression equation $(D_5 = D_T - D_C)$	0.00741	4	0.00185	$\frac{MD_5}{MD_1} = 1.16$	3.26
6	H_0: $b_1 = b_2 = b_3 = b_W$; The slopes are almost the same $(D_6 = D_W - D_C)$	0.00285	2	0.00143	$\frac{MD_6}{MD_1} = 0.90$	3.89
7	H_0: $Y'_1 = Y'_2 = Y'_3$; Corrected *Y* means are almost the same $(D_7 = D_T - D_W)$	0.00456	2	0.00228	$\frac{MD_7}{MD_2} = 1.44$	3.74
8	H_0: $b_W = b_B$; $(D_8 = D_T - D_B - D_W)$	0.00002	1	0.00002	$\frac{MD_8}{MD_2} = 0.01$	4.60

The distributions of activities of POD and PPO isoenzymes were checked by Shapiro-Wilk test and the characterization of its distribution is depicted in the *Figure 2* by van der Waerden's methods (Buchan 2000). Note that in the plain of normal scores versus enzyme activities, scattering patterns of the points along their fitted straight lines are very similar. This similarity results from necessary condition of type identity of the distributions (Németh et al. 2009a). In the case of meeting the perfect type identity of the distributions, the normal scores of POD and PPO would provide the linear regression with r^2=1 (see *Figure 2c*).

$$NS = \Phi(p), \; p = \frac{R}{n+1} \tag{7}$$

where *NS* is the normal score for an observation, *R* is the rank for that observation, *n* is the sample size and $\Phi(p)$ is the p^{th} quantile from the standard normal distribution (Buchan 2000).

The results of Shapiro-Wilk test applied to the significance level of α = 0.05 did not contradict our hypothesis for the normal distributions of enzymes activities. As can be seen in the *Figure 2* the normal scores of activities determined by van der Waerden test versus the values of the activities represents linear relationships with a very good approximation.

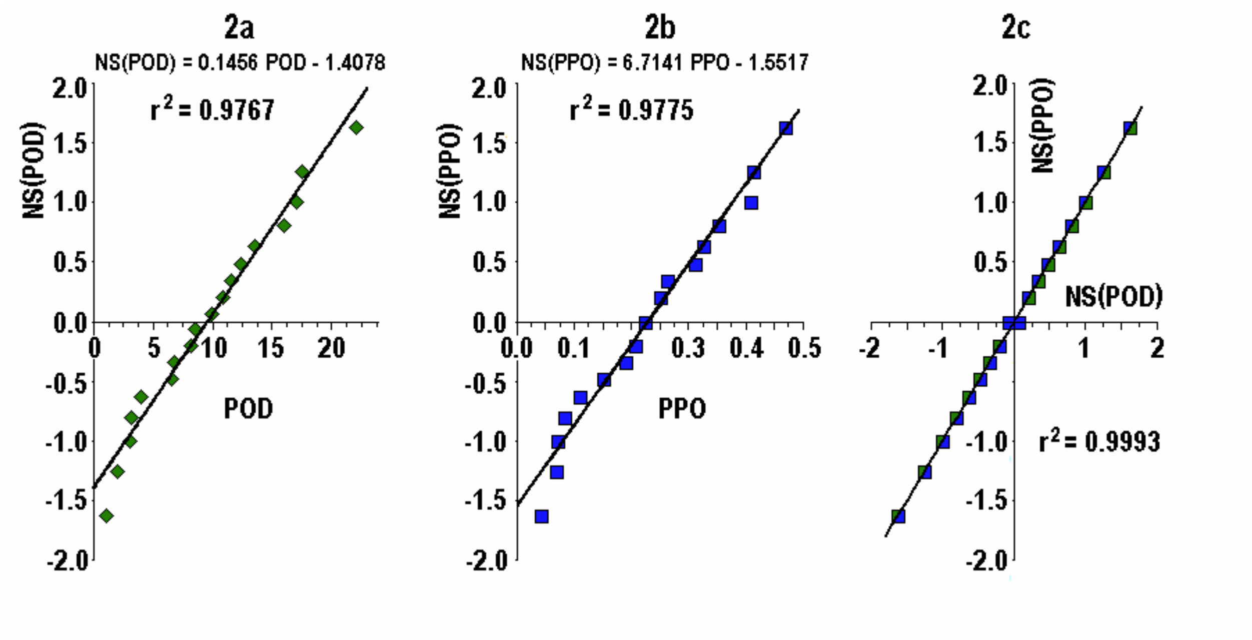
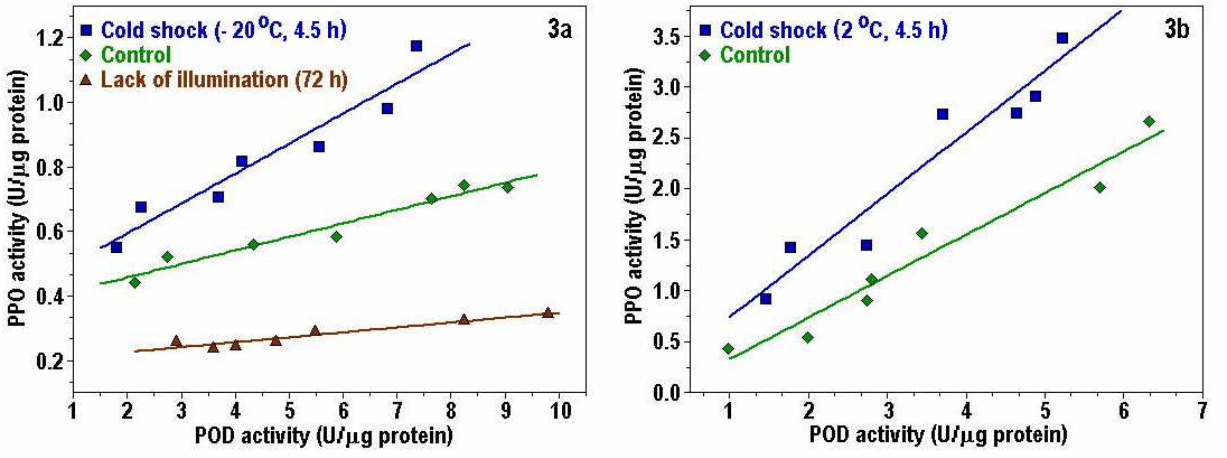


Figure 2. Investigation of distributions of POD and PPO activities in Table 2 by van der Waerden's test. (NS(POD), NS(PPO) – normal scores of enzyme activities POD and PPO)

The correlation between the resultant oxidative activities of POD and PPO isoenzymes, which showed an independence of tree entity, and which was found in pedunculate oak trees, has also been mapped for a herbaceous plant species and for the leaves of large white bean plant (*Phaseolus vulgaris* L.). Since the cold shock and absence of illumination are able to change some enzyme activities (Li et al. 2006, Prestano et al. 2004, Cohen et al. 1984, Fair et al. 1974) the role of these environmental effects on POD-PPO oxidative activity correlation has been investigated. For control and stress investigations oak acorns and bean seeds were germinated and full-grown bean plants and oak seedlings were exposed to the similar effects. Linear correlations between POD and PPO specific activities of both the oak seedlings and bean plants were found (*Figure 3*).

The ***measured*** protein contents in the control state, cold shock and lack of illumination of bean plants and oak trees were in the confidence intervals of 75.65 ± 3.97 and 6.32 ± 0.30 mg/g dry weight (□ = 0.05).

As an alternative statistical evaluation, the regression straight lines, whose data are depicted in the *Tables 4 and 5,* were compared to each other by the ANCOVA of StatsDirect v2.6.5 software (StatsDirect Ltd., UK). The results of this evaluation are enclosed in the sections II. and III. of Supplemental Data. From them it can be established that the investigated environmental effects induced significant alterations in the regression parameters of oxidative activities POD and PPO. These environmental conditions are characterized by significantly different POD versus PPO correlations. This correlation has been proven to be stress sensitive. With respect to the classical comparison of activity means, the stress sensitivity of the correlation can reveal extra information about the measured data. Note that, for example in the case of *Figure 3b,* statistical *t*-test is not able to detect any differences between the POD or PPO values because there are almost total overlaps in their confidence intervals.



3a: Pedunculate oak seedling.

■ - cold shock{-20 °C, 4.5 h}, PPO = 0.0929 POD + 0.4081, $r^2 = 0.9206$;

◆ - control, PPO = 0.0419 POD + 0.3737, $r^2 = 0.9529$;

▲ - lack of illumination{72 h}, PPO = 0.0153 POD + 0.1948, $r^2 = 0.9195$

3b: large white bean plant.

■ - cold shock{2 °C, 4.5 h}, PPO = 0.6043 POD + 0.1415, $r^2 = 0.9258$;

◆ - control, PPO = 0.4074 POD - 0.0766, $r^2 = 0.9477$

Figure 3. Effects of the cold shock and lack of illumination on the PPO versus POD correlations

5 CONCLUSION

Linear correlations between the activities of POD and PPO isoenzymes in leaf samples from oak trees as well as bean plants have been established. The linear relationship independently of the individual character of the species is exactly able to reflect the synchronic regulation of these isoenzymes in leaf metabolism. If there is small POD specific activity in the leaves, then small value of PPO specific activity will be related to it. This correlation has been assumed to reveal some important information characterizing the plant species and to eliminate the individual characteristics of the investigated plant or tree.

Comparing the confidence intervals of the activities the effect of environmental conditions on the metabolism in the leaves could not always be detected. On the contrary, the slope of a linear relationship between the resultant oxidative activities is stress sensitive. The cold shock and the lack of illumination were able to alter the enzyme correlation characterizing a steady state of the metabolism in significant way. The linear character of the regressions obtained after the stress effect can be related to the property of the plant leaf cells that were able to find a new steady state for their metabolism.

Acknowledgements: This work was supported by a grant from the Hungarian Scientific Research Fund (OTKA No. T 046408) and partly by a HAS’s Bolyai scholarship research.

REFERENCES

ARKIN, A. – ROSS, J. – MCADAMS, H.H. (1998): Stochastic kinetic analysis of developmental pathway bifurcation in phage-infected *Escherichia coli* cells. Genetics 149(4): 1633-1648.

BOGDANOVIC, J. – DUCIC, T. – MILOSAVIC, N. – VUJCIC, Z. –SIJACIC, M. –ISAJEV. V. –RADOTIC, K. (2005): Antioxidant enzymes in the needles of different omorika lines. Arch. Biol. Sci . 57(4): 277-282.

BOSS, P. K. – GARDENER, R. C. – JANSSEN, B. J. – ROSS, G. S. (1995): An apple polyphenol oxidase cDNA is up-regulated in wounded tissue. Plant Mol. Biol 27: 429–433.

BRADFORD, M. M. (1976): A rapid and sensitive method for the quantisation of microgram quantities of protein utilising the principle of protein-dye binding. Anal. Biochem. 72: 248-257.

BUCHAN, I.E. (2000): The development of a statistical computer software. Resource for medical resource. MD Thesis, University of Liverpool, Liverpool, UK, 91-92.

CHANDRA, A. – SAXENA, R. – DUBEY, A. – SAXENA, P. (2007): Change in phenylalanine ammonia lyase activity and isozyme patterns of polyphenol oxidase and peroxidase by salicylic acid leading to enhance resistance in cowpea against *Rhizoctonia solani*. Acta Physiol. Plant. 29:361-367. DOI: 10.1007/s11738-007-0045-2

CHEMNITIUS, J-M. – HASELMEYER, K-H. – ZECH, R. (1982): Identification of isoenzymes in cholinesterase preparations using kinetic data of organophosphate inhibition. Anal. Biochem. 125 (2): 442-452.

CHISARI, M. – BARBAGALLo, R. N. – SPAGNA, G. (2008): Characterization and role of Polyphenol oxidase and peroxidase in browning of fresh-cut melon. J. Agric. Food Chem. 56:132-138. DOI: 10.1021/jf0721491

COHEN, E. – ARAD, S. – HEIMER, Y. H. – MIZRAHI, Y. (1984): Polyamine biosynthetic enzymes in the cell cycle of *Chlorella* (Correlation between ornithine decarboxylase and DNA synthesis at different light intensities). Plant Physiol. 74: 385-388.

DUNFORD, H. B. (1999): Heme Peroxidases. Wiley-VCH, New York.

FAIR, P. – TEW, J. – CRESSWELL, C.F. (1974): Enzyme activities associated with carbon dioxide exchange in illuminated leaves of *Hordeum vulgare* L. IV. The effect of light intensity on the carbon dioxide compensation point. Ann. Bot. 38: 45-52.

FLURKEY, W. H. – JEN, J. J. (1978): Peroxidase and polyphenol oxidase activities in developing peaches**.** J. Food Sci. 43 (6): 1826–1828.

HEINRICH, R. – SCHUSTER, S. (1996): The regulation of cellular systems. Chapman and Hall, New York, USA.

JALEEL, C. A. – RIADH, K. – GOPI, R. – MANIVANNAN, P. – INES, J. – AL-JUBURI, H. J. – CHANG-XING, Z. – HONG-BO, S. – PANNEERSELVAM, R. (2009): Antioxidant defense responses: physiological plasticity in higher plants under abiotic constraints. Acta Physiol. Plant. 31:427-436. DOI: 10.1007/s11738-009-0275-6

JALEEL, C.A. – GOPI, R. – KISHOREKUMAR, A. – MANJVANAN, P. – SANKAR, B. – PANNEERSELVAM, R. (2008): Interactive effects of triadimefon and salt stress on antioxidative status and ajmalicine accumulation in *Catharanthus roseus*. Acta Physiol. Plant. 30:287-292. DOI: 10.1007/s11738-007-0119-1

KIM, J. Y. – SEO, Y. S. – KIM, J. E. – SUNG, S-K. – SONG, K. J. – AN, G. – KIM, W. T. (2001): Two polyphenol oxidases are differentially expressed during vegetative and reproductive development and in response to wounding in the Fuji apple. Plant Sci. 161:1145–1152.

LI, H. – JIANG, Y. – LI, J. (2006): Use of Ga(3) to inhibit flesh browning development of plum fruit during storage at low temperature. Eur. J. Hort. Sci .71 (5): 231-235.

LI, L. – STEFFENS, J. C. (2002): Over-expression of polyphenol oxidase in transgenic tomato plants results in enhanced bacterial disease resistance. Planta 215: 239–247.

MASANORI, K. – SHIGEO, A. – YUHEI, M. – HIROSHI, N. – KEITARO, H. (1984): Comparative studies on kinetic behavior of horseradish peroxidase isoenzymes. J. Biochem. 95 (3): 861-870.

MAYER, A.M. (2006): Polyphenol oxidases in plants and fungi: Going places? A review. Phytochemistry 67:2318-2331.; DOI: 10.1016/j.phytochem. 2006.08.006

MCADAMS, H. H. – ARKIN, A. (1999): It is a noisy business! Genetic regulation at the nanomolar scale. Trends Genet. 15(2): 65-69.

NÉMETH, Zs. I. – SÁRDI, É. – STEFANOVITS-BÁNYAI, É. (2009a): State-dependent correlations of biochemical variables in plants. J. Chemometr. 23:197-210. DOI: 10.1002/cem.1226

NÉMETH, Zs. I. –- POZSGAI-HARSÁNYI, M. – STEFANOVITS-BÁNYAI, É. – SÁRDI, É. (2009b): Characterization of plant stress syndrome by some correlation of biochemical variables. Cereal Res. Commun. Suppl S 37:141-144. DOI: 10.1556/CRC.37.2009.Suppl. 2.

NUNES, M. C. N. – BRECHT, J. K. – ALICINA, M. M. – MORAIS, A. M. M. B. – SARGENT, S. A. (2005): Possible influences of water loss and polyphenol oxidase activity on anthocyanin content and discoloration in fresh ripe Strawberry (cv. Oso Grande) during storage at 1 °C. J. Food Sci. 70: S79-S84.

OZTURK, L. – KUFREVIOGLU, O. I. – DEMIR, Y. (2008): In vivo and in vitro effects of ethephon on some oxidative enzymes in spinach leaves. Acta Physiol. Plant. 30:105-110. DOI: 10.1007/s11738-007-0096-4

POLLE, A. (2001): Dissecting the superoxide dismutase-ascorbate-glutathione-pathway in chloroplasts by metabolic modeling. Computer simulations as a step towards flux analysis. Plant Physiol. 126: 445-462.

PRESTANO, G. – PALOMARES, L. – SANZ, P. (2004): Broccoli (*Brasica oleracea*) treated under pressure-shift freezing process. Eur. Food Res. Tech. 219 (6): 598-604.

RAJESWARI, V. – PALIWAL, K. (2008): Peroxidase and catalase changes during in vitro adventitious shoot organogenesis from hypocotyls of *Albizia odoratissima* L.f. (Benth). Acta Physiol. Plant. 30:825–832. DOI 10.1007/s11738-008-0187-x

SAVAGEAU, M. A. (1976): Biochemical systems analysis. Addison-Wesley Publishing Co, Massachusetts, USA

SÁRDI, É. – STEFANOVITS-BÁNYAI, É. (2006): Relationship between peroxidase activity and the amount of fully *N*-methylated compounds in bean plants infected by *Pseudomonas savastanoi* pv. *Phaseolicola*. Acta Physiol. Plant. 28: 95-100.

SHANNON, L.M. – KAY, E. – LEW, J.Y. (1966): Peroxidase izoenzymes from horseradish roots. J. Biol. Chem. 241: 2166-2172.

SHEEN, S.J. – CALVERT, J. (1969): Studies on polyphenol content. activities and isozymes of polyphenol oxidase and peroxidase during air-curing in three Tobacco types. Plant Physiol. 44: 199-204.

SVÁB, J. (1967): Biometriai módszerek a mezőgazdasági kutatásban. (Biometrical methods in agricultural research). Mezőgazda Kiadó. Budapest. 392-403.

THATTAI, M. – VAN QUDENAARDEN, A. (2001): Intrinsic noise in gene regulatory networks. Proc. Natl. Acad. Sci .USA 98(15): 8614-8619.

THIPYAPONG, P. – HUNT, M. D. – STEFFENS, J. C. (2004): Antisense downregulation of polyphenol oxidase results in enhanced disease susceptibility. Planta 220:105–107.

THONGSOOK, T. – BARRETT, D. M. (2005): Heat inactivation and reactivation of Broccoli peroxidase. J. Agric. Food. Chem. 53: 3215-3222.

TORALLES, R. P. – VENDRUSCOLO, J. L. – VENDRUSCOLO, C. T. – DELPINO, F. A. B. – ANTUNE, P. L. (2005): Properties of polyphenoloxidase and peroxidase from Granada clingstone peaches. Braz. J. Food Technol. 8 : 233-242.

WANG, J. – CONSTABEL, C. P. (2004): Polyphenol oxidase overexpression in transgenic Populus enhances resistance to herbivory by forest tent caterpillar (*Malacosoma disstria*). Planta 220: 87–96.

WANG, Y. – HE, W. – HUANG, H. – AN, L. Z. – WANG, D. – ZHANG, F. (2009): Antioxidative responses to different altitudes in leaves of alpine plant *Polygonum viviparum* in summer. Acta Physiol. Plant. 31:839-848. DOI:10.1007/s11738-009-0300-9

WU, S.E. – MARLETTA, M.A. (1988): Carboxylesterase isoenzyme specific deacylation of diacetoxy-scirpenol (anguidine). Chem. Res. Toxicol. 1 (1): 69-73.

SUPPLEMENTAL DATA

I. Equations of covariance analysis (ANCOVA)

Equations (1-12) are necessary to calculate the sums of squares for statistical evaluations. X_{ij} is the POD activity of i^{th} leaf of j^{th} tree shown in the *Table 1*. Y_{ij} is the PPO activity belonging to X_{ij}.

$$(1)\ SST(X) = SS_{Total(X)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(X_{ij} - \overline{\overline{X}}\right)^2$$

$$(4)\ SST(Y) = SS_{Total(Y)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(Y_{ij} - \overline{\overline{Y}}\right)^2$$

$$(2)\ SSB(X) = SS_{Between(X)} = n\sum_{j=1}^{k}\left(\overline{X}_j - \overline{\overline{X}}\right)^2$$

$$(5)\ SSB(Y) = SS_{Between(Y)} = n\sum_{j=1}^{k}\left(\overline{Y}_j - \overline{\overline{Y}}\right)^2$$

$$(3)\ SSW(X) = SS_{Within(X)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(X_{ij} - \overline{X}_j\right)^2$$

$$(6)\ SSW(Y) = SS_{Within(Y)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(Y_{ij} - \overline{Y}_j\right)^2$$

$$(7)\ SW(X)_j = \sum_{i=1}^{n} X_{ij}^2 - \frac{\left(\sum_{i=1}^{n} X_{ij}\right)^2}{n}$$

$$(8)\ SPT(XY) = SP_{Total(XY)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(Y_{ij} - \overline{\overline{Y}}\right)\left(X_{ij} - \overline{\overline{X}}\right)$$

$$(9)\ SW(Y)_j = \sum_{i=1}^{n} Y_{ij}^2 - \frac{\left(\sum_{i=1}^{n} Y_{ij}\right)^2}{n}$$

$$(10)\ SPB(XY) = SP_{Between(XY)} = n\sum_{j=1}^{k}\left(\overline{Y}_j - \overline{\overline{Y}}\right)\left(\overline{X}_j - \overline{\overline{X}}\right)$$

$$(11)\ SPW(XY) = SP_{Within(XY)} = \sum_{j=1}^{k}\sum_{i=1}^{n}\left(Y_{ij} - \overline{Y}_j\right)\left(X_{ij} - \overline{X}_j\right)$$

$$(12)\ PW(XY)_j = \sum_{i=1}^{n} X_{ij}Y_{ij} - \frac{\sum_{i=1}^{n} X_{ij}\sum_{i=1}^{n} Y_{ij}}{n}$$

Deviations (13-16) for ANCOVA analysis in Table 2.

$$(13)\ D_W = SSW(Y) - \frac{SPW(XY)^2}{SSW(X)}$$

$$(14)\ D_B = SSB(Y) - \frac{SPB(XY)^2}{SSB(X)}$$

$$(15)\ D_T = SST(Y) - \frac{SPT(XY)^2}{SST(X)}$$

$$(16)\ D_C = \sum_{j=1}^{k}\left[SW(Y)_j - \frac{PW(XY)_j^2}{SW(X)_j}\right]$$

II. Results of ANCOVA of *Table 4* by Stats Direct v2.6.5 software

Table 4. Resultant oxidative activities (U μg protein-1) of perosidase (POD) and polyphenol oxidase (PPO) in the leaves of Quercus robur L. seedlings under different enviromental conditions (Figure 3a)

j	1.		2.		3.	
j = 1…*k*	Control		Cold shock (-20 ^{o}C)		Lack of illumination	
i = 1…*n*	POD	PPO	POD	PPO	POD	PPO
i	X_{i1}	Y_{i1}	X_{i2}	Y_{i2}	X_{i3}	Y_{i3}
1	4.345	0.559	4.118	0.821	3.587	0.238
2	2.736	0.522	5.543	0.866	2.895	0.259
3	7.631	0.703	2.243	0.676	9.789	0.345
4	5.872	0.585	6.803	0.982	5.487	0.287
5	2.134	**0.441**	7.357	1.178	3.996	0.245
6	9.056	0.737	1.783	0.553	8.235	0.322
7	8.235	0.745	3.667	0.707	4.763	0.259

Grouped linear regression

Source of variation	SSq	DF	MSq	VR	
Common slope	0.229150	1	0.229150	135.240204	P < 0.0001
Between slopes	0.098859	2	0.049430	29.172567	P < 0.0001
Separate residuals	0.025416	15	0.001694		
Within groups	0.353425	18			

Common slope is significant

Difference between slopes is significant

Slope comparisons

Slope 1 (Xi1) versus *Slope* 2 (Xi2) = 0.04189 *versus* 0.092859
Difference (95% CI) = 0.050969 (0.029801 to 0.072137)
t = 2.956198 P = 0.0098

Slope 1 (Xi1) versus *Slope* 3 (Xi3) = 0.04189 *versus* 0.015259
Difference (95% CI) = 0.026631 (0.00743 to 0.045831)
t = -5.132126 P = 0.0001

Slope 2 (Xi2) versus *Slope* 3 (Xi3) = 0.092859 *versus* 0.015259
Difference (95% CI) = 0.077599 (0.055851 to 0.099348)
t = 7.605173 P < 0.0001

Covariance analysis

Source of variation	YY	xY	xx	DF
Uncorrected				
Between groups	1.063725	-1.782643	6.006368	2
Within	0.353425	5.060858	111.770938	18
Total	1.417151	3.278216	117.777305	20

Source of variation	SSq	DF	MSq	VR
Corrected				
Between groups	1.201629	2	0.600815	82.187254
Within	0.124275	17	0.007310	
Total	1.325905	19		

$P < 0.0001$

Corrected Y means ± SE for baseline mean predictor of 5.25119

Y' = 0.592116	± 0.032534
Y' = 0.860065	± 0.032879
Y' = 0.26639	± 0.032398

Line separations (common slope = 0.045279)

Lines not parallel

Line 1 (Xi1) versus *Line* 2 (Xi2) vertical separation = -0.267949
95% CI = -0.36657 to -0.169328
t = -5.732288 (17 df) P < 0.0001

Line 1 (Xi1) versus *Line* 3 (Xi3) vertical separation = 0.325726
95% CI = 0.229255 to 0.422198
t = 7.123604 (17 df) P < 0.0001

Line 2 (Xi2) versus *Line* 3 (Xi3) vertical separation = 0.593675
95% CI = 0.495652 to 0.691699
t = 12.778037 (17 df) P < 0.0001

III. Results of ANCOVA of Table 5 by Stats Direct v2.6.5 software

Table 5. Resultant oxidative activities (U μg protein-1) of peroxidases (POD) and polyphenol oxidases (PPO) in the leaves of Phaseolus vulgaris L. plants under control and cold shock conditions (Figure 3b)

j *j* = 1…*k*	1. Control		2. Cold shock (2 °C)	
i = 1…*n* *i*	POD X_{i1}	PPO Y_{i1}	POD X_{i2}	PPO Y_{i2}
1	2.745	0.906	1.454	0.932
2	2.803	1.110	3.694	2.739
3	0.978	0.435	5.213	3.483
4	5.693	2.012	4.624	2.747
5	6.328	2.660	1.765	1.435
6	3.431	1.562	2.727	1.453
7	1.986	0.542	4.872	2.916

Grouped linear regression

Source of variation	**SSq**	**DF**	**MSq**	**VR**	
Common slope	8.477383	1	8.477383	138.358472	P < 0.0001
Between slopes	0.333158	1	0.333158	5.43743	P = 0.0419
Separate residuals	0.612712	10	0.061271		
Within groups	9.423253	12			

Common slope is significant
Difference between slopes is significant

Slope comparisons

Slope 1 (Xi1) versus *Slope* 2 (Xi2) = 0.407409 *versus* 0.604322
Difference (95% CI) = 0.196912 (0.008756 to 0.385069)
t = -2.33183 P = 0.0419

Covariance analysis

Source of variation	YY	xY	xx	DF
Uncorrected				
Between groups	2.997463	0.178145	0.010587	1
Within	9.423253	17.563323	36.387443	12
Total	12.420716	17.741468	36.398031	13

Source of variation	SSq	DF	MSq	VR
Corrected				
Between groups	2.827135	1	2.827135	32.878208
Within	0.945869	11	0.085988	
Total	3.773004	12		

P = 0.0001

Corrected Y means ± SE for baseline mean predictor of 3.450929	
Y' = 1.331416	± 0.110841
Y' = 2.230298	± 0.110841

Line separations (common slope = 0.482675)

Lines not parallel

Line 1 (Xi1) versus *Line* 2 (Xi2) vertical separation = -0.898881
95% CI = -1.243918 to -0.553845
t = -5.733952 (11 df) P = 0.0001

Acta Silv. Lign. Hung., Vol. 5 (2009) 47-62

Transfer Analysis of Provenance Trials Reveals Macroclimatic Adaptedness of European Beech (*Fagus sylvatica* L.)[1]

Csaba MÁTYÁS[a*] – Gregor BOŽIČ[b] – Dusan GÖMÖRY[c] – Mladen IVANKOVIĆ[d] – Ervin RASZTOVITS[a]

[a]Institute of Environmental and Earth Sciences, Faculty of Forestry, University of West Hungary, Sopron, Hungary
[b]Slovenian Forestry Institute, Ljubljana, Slovenia
[c]Technical University Zvolen, Faculty of Forestry, Zvolen, Slovakia
[d]Croatian Forestry Institute, Jastrebarsko, Croatia

Abstract – The aim of the study was to analyse provenance tests of beech situated close to the Southeastern-continental limits of the species, in order to develop a response model of adaptation and plasticity of populations on evolutionary-ecological basis, following sudden climatic changes as a result of transplanting. Modelling of juvenile height was performed with the help of ecodistance variables. The concept of transfer analysis and ecodistance is based on the hypothesis that phenotypic response to macroclimatic changes depends on the inherited adaptive potential of the population and on the magnitude and direction of experienced environmental change. In common garden experiments, the transfer to the planting site is interpreted as simulation of environmental change. The application of ecodistance of transfer for evaluating common garden experiments provides much needed quantitative information about response of tree populations to predicted climatic changes.

The analysis of three field experiments of European beech in SE Europe invalidate earlier doubts about the existence of macroclimatic adaptation patterns in juvenile growth and justify restrictions of use of reproductive material on the basis of evolutionary ecology. The presented model illustrates that response to climatic change is regionally divergent, depending on testing conditions and on hereditary traits. In particular, climatic warming in the central-northern part of the range may lead to production increase. However, under the stressful and uncertain conditions at the lower (xeric) limit of the species, growth depression and vitality loss are predicted. The deviating behaviour of higher elevation provenances support their separate treatment.

The results may be utilised in climate change adaptation and mitigation policy in forestry and nature conservation, to revise rules for use of reproductive material and also for validating evolutionary and ecological hypotheses related to climate change effects.

genetic adaptation / common gardens / climate change / phenotypic stability / ecodistance

Kivonat – Származási kísérletek áttelepítési elemzése igazolta a bükk makroklimatikus adaptáltságát. A délkelet-európai, alsó (szárazsági) határhoz közeli származási kísérletek elemzésének célja az alkalmazkodás és plaszticitás által meghatározott válaszreakciók modellezése volt. Az evolúció-ökológiai alapon felépített modell az áttelepítés következtében fellépett hirtelen

---

[1] Paper presented at the COST E52 Beech genetics meeting 2009, and also available at *iForest,* Florence

[*] corresponding author: cm@emk.nyme.hu, H-9401 Sopron, POB 132, Hungary

klímaváltozás leírásához az ún. ökológiai távolság elvét alkalmazza. Az áttelepítési elemzés azon a hipotézisen alapszik, hogy a populáció makroklimatikus változásra adott (fenotipikus) válaszreakciója – minden más tényező állandósága mellett – az öröklött adaptív potenciáltól, és az érzékelt klimatikus változás mértékétől függ. A közös tenyészkerti kísérletekbe való áttelepítést a környezet szimulált változásaként értelmezzük. Az áttelepítés ökológiai távolsága a származási kísérletek újszerű értékelését teszi lehetővé, és régóta hiányzó kvantitatív információkat szolgáltat a fás populációk klímaváltozással kapcsolatban várható válaszáról.

Az elemzésbe vont három DK-európai bükk kísérlet eredményei a fiatalkori növekedés tekintetében igazolják a fajon belüli, makroklimatikus alkalmazkodási mintázat eddig kétségbevont létezését, amely indokolttá teszi a szaporítóanyag-használat evolúciós ökológiai alapú szabályozását. A bemutatott modellből látható, hogy a klímaváltozásra adott válaszokban regionális különbségek léteznek, amelyeket a kísérleti környezet és az öröklött tulajdonságok határoznak meg. A faji área középső-északi részén a melegedés produkciónövekedést eredményezhet. Ugyanakkor a szárazsági (alsó) határ szélsőséges és bizonytalan viszonyai növekedés-csökkenést és vitalitás-vesztést prognosztizálnak. A magasabb tszf. magasságú helyszínek származásai eltérően viselkednek, és ez indokolja külön kezelésüket.

Az eredmények felhasználhatók a klímaváltozáshoz alkalmazkodás stratégiájának megfogalmazásához mind az erdészetben, mind a természetvédelemben. Segítségükkel pontosíthatók a szaporítóanyag felhasználási szabályok, és értékelhetők a klímaváltozási hatásokkal kapcsolatos különböző evolúciós és ökológiai hipotézisek is.

genetikai adaptáció / közös tenyészkert / klímaváltozás / fenotípusos stabilitás / ökológiai távolság

1 INTRODUCTION: CLIMATIC SELECTION AND ADAPTATION STRATEGY

Different hypotheses on the adaptation strategy of trees are co-existing in contemporary genetics and ecology. With regard to predicted climate scenarios, scarcity of reliable information on responses to macroclimatic changes is a central problem and obstacle. In order to formulate realistic predictions, both the nature of genetic adaptation to past and current climate, and the level of sensitivity to sudden environmental changes have to be understood and properly interpreted. In the context of large-scale climatic changes, *macroclimatic adaptation* is an important component to study and evaluate. It is *the fraction of within-species adaptive genetic diversity which is attributable to adaptation to macroclimatic factors*.

Although climatic selection might act more reliably on local, microclimatic level, macroclimate is exclusively considered here mainly for three reasons: climatic scenarios utilized for forecasting describe changes on macro-level only, and on the other hand, data on micro- and meso-level climate is in most cases not sufficient for proper analysis. Finally, the extensive sampling pattern of the studied set of populations prohibits a finer-scale approach.

Under selection pressure, genetic resources of populations are adjusted to maintain competitive growth, adapted phenology, reproductivity and tolerance to diseases and pests, i.e. stability and adaptability. Differing direction and intensity of selection pressure within the species' range exert a disruptive selection effect, which may lead to characteristic, stabilised patterns of adaptive genetic variability. Counting on the strong and lasting effects of local selection, a close ("ecotypic") adaptation is implicitly assumed for K-strategist tree species such as beech. This assumption has been generally accepted in practical silviculture; a view which has been nourished by classic field experiments with perennials, starting with Clausen et al. (1940).

However, molecular genetic studies have revealed the effect of strong counteracting forces such as genetic drift and isolation, but first of all the effect of postglacial migration which produced for woody species such as beech characteristic geographic patterns. These patterns follow rather routes of colonisation than ecological conditions (Comps et al. 1998, Comps et al. 2001, Magri et al. 2006). There are a number of other biotic reasons why the genetic system of tree species may robustly counteract climatic selection (Mátyás 2007).

Conflicting approaches and unclear role of different factors determining adaptability keep macroclimatic selection still as an open question, in spite of its importance for practical forest management. Adaptation to macroclimate is the basis for setting the rules of reproductive material use, for concepts to conserve genetic resources of species, and for strategies to adapt to and to mitigate expected effects of environmental changes. This raises the following questions:

- what kind of phenotypic response is expected if macroclimatic environment changes,
- how much of observed response is attributable to macroclimatic adaptation,
- what is the role of phenotypical stability,
- what is the relation of macroclimatic to micro-scale (local) adaptation?

In the present study only a part of these problems are addressed.

2 TRACING MACRO-CLIMATIC SELECTION ON QUANTITATIVE TRAITS

Annual growth and development cycle of beech – as for any other temperate species – is governed besides the photoperiod by the amount of physiologically effective heat sum (Kramer 1994, Chuine et al. 2003) and of course precipitation. As the latter two are unevenly distributed across the range of the species, diverging direction and intensity of climatic selection may be assumed. The consequence of climatic selection, differentiation in phenological behaviour is well reflected by field test results. For example, budbreak of beech shows a clinal East-West pattern: Atlantic coast provenances are late, while Alpine and SE-European continental sources are early flushing (Wühlisch et al. 1995, Führer et al. 2009, Gömöry 2009).

Reports on similar patterns are expectable also for growth traits. However, studies on growth of beech provenances in field tests describe instead of climate-related patterns rather an ecotypic (i.e. unexplained random) type of variation (e.g. Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Jazbec et al. 2007), or explain spatial differentiation in response by the phylogenetic past (e.g. Gömöry 2009). (The term "provenance" is used synonymously in the paper for "transferred population of known origin”.)

2.1 The ecodistance approach of modelling macroclimatic adaptation

For the investigation of macroclimatic adaptation, the concept of ecodistance has been applied. The ecodistance (ecological distance) concept is based on the idea that if populations adapted to certain ecological (climatic) conditions are transferred to a new environment, and all other site factors are kept equal or disregarded, their *phenotypic response to climate depends not only on the climatic conditions where the population is actually grown or tested, but also on the ecodistance of transfer, i.e. on the magnitude and direction of environmental change experienced due to the transplanting to the test site, related to the macroclimate they had been adapted to originally*. Accordingly, the ecodistance value of a locally adapted population in a test takes the value 0. The concept of transfer analysis and ecodistance (Mátyás & Yeatman 1992, Mátyás 1994, 1996, Mátyás et al. 2008b) has been used for the analysis and modelling of data of common garden (provenance) tests. This approach enables a pooled comparison of various test sites and thus increases statistical reliability. Applying ecodistance instead of simple geographic or ecological parameters allows the detection of general patterns of adaptation. An important advantage of the concept is that *responses to transfer into new environments may be interpreted as simulations of future climatic changes:* a realistic validation of prediction models.

In the transfer analysis, the climatic variable (E) selected to best describe macroclimatic adaptation serves as independent variable, expressed as difference between test site (X_t) and location of origin (X_o). It may be a simple or complex variable such as drought or continentality index, or a principal component etc.

The ecodistance (ΔE) is then calculated as

$$\Delta E = X_t - X_o$$

For example, if the variable is mean annual temperature, and $X_t > X_o$, the positive value of ΔE expresses a simulated warming of the environment through transfer to the site.

2.2 Modeling response of populations to transfer

According to the classical additive model of Fisher (1958) and Wright (1950), the phenotypic response of an individual or population (P_i) may be described as the sum of the estimated genetic (γ_i) and the environmental (ε_i) deviations from the experimental mean (μ):

$$P_i = \mu + \gamma_i + \varepsilon_i$$

Both the genetic and the environmental component may be partitioned for our purposes. Regarding the effect of the environment, response strongly depends on the site potential of the test. The site conditions have a powerful influence on differentiation between populations and on interaction effects. It is therefore advisable to separate the test site potential *(T),* expressed usually as the local mean of tested populations, and the interaction effect (see further below).

There are two types of genetic response to transfer which may be calculated from a dataset containing data of numerous populations from a set of experimental sites:

a) General or "species-specific" response *(G)* to macroclimatic change, calculated from pooled data of the observed trait Y from all (*t*) test sites, and all (*p*) provenances, providing the function

$$Y_G = f\,(\Delta E_{tp})$$

The function supplies quantitative information on the pooled response to changing environment, triggered by the transfer of locally adapted populations into a new ambient. (Needless to say that ΔE values for the same provenance are different at every test location.)

b) As the various populations investigated may have a different microevolutionary background and have been exposed to selection effects of different nature and intensity, the general response will conceal much of the between-provenance genetic differentiation. Individual, population-specific response *(P)* of population "*p*" across test sites, defined as response function *per se* in recent literature (e.g. Thomson - Parker 2008). It is indicating individual sensitivity or phenotypic plasticity of the population to changes, in interaction with local site conditions. It is identical with the term "reaction norm" of ecology:

$$Y_P = f\,(\Delta E_p)$$

In case of sufficient data, the function may define the physiological (genetic) optimum for the population in the climatic niche.

The residual of the recorded population mean at a test site, which is left unexplained by the other additive components, is regarded as interaction (I) and error. *Interaction* in genetic sense is the part of response which appears as deviation from the average response regressions established across the test sites, *causing a change in ranking* of populations *(see Figure 3)*. Strong interaction effects indicate narrower plasticity, and responsiveness to certain (usually extreme) conditions.

The unified additive model to comprise all components is then:

$$Y = \mu + G + P + T + I + \varepsilon$$

where the residual error (ε) may include also genetic components unrelated to macroclimatic adaptation.

3 A CASE STUDY: ANALYSIS OF THREE SE-EUROPEAN TRIALS

In the case study the construction of an additive response model is presented, based on the ecodistance concept. The selected variable for ecodistance calculations is one of multiple options. Environmental effects other than macroclimate (e.g. soil characteristics) are not discussed here because these are beyond the interests of this study.

The transfer analysis had been applied since its first formulation (Mátyás - Yeatman 1992) for numerous conifer species. For beech, growth response predictions have not been validated thus far by field tests, rather backed by climatic envelopes (Fang - Lechowicz 2006, Czúcz et al. 2009). The beech provenance test series (Wühlisch 2007) offers an opportunity to obtain results similar to conifers with a "recalcitrant" broadleaved species.

3.1 Selected ecodistance variable

For ecodistance calculation, Ellenberg's climate quotient (*EQ*) has been selected. It is a simple index to express humidity, respectively continentality of climate and has been developed by Ellenberg (1988) first of all for beech. Recent analyses have proven its high distinctive power to predict presence of beech under Central European conditions (Czúcz et al. 2009). Ellenberg's climate quotient is defined as the mean temperature of the warmest month (July, T_{07}) divided by the annual precipitation (P_{ann}):

$$EQ = 1000 \cdot T_{07} \cdot P_{ann}^{-1}$$

The quotient indicates favourable climatic conditions for beech if the *EQ* value lies below approximately 26 for Central Europe. In Hungary, zonal sites with *EQ* values above 28 represent the xeric (lower) limits of the distribution of species (Czúcz et al. 2009). *EQ* values of provenances[2] and test sites are given in *Tables 1 and 2*.

Table 1. Data of analysed beech provenance trials (for geographic locations see Figure 1)

a. Geographic, climatic data

Reg. Nr.	Country	Location	Altitude a.s.l. (m)	July mean temperature (°C)	Annual mean precipitation (mm)	Ellenberg index (*EQ*)
2012	Slovenia	Straza	545	19.3	1260	15.3
2015	Hungary	Bucsuta	200	19.7	747	26.3
2020	Slovakia	Mlacik - Tále	850	16.8	779	21.5
	mean					21.0

b. Statistical data

Reg. Nr.	Aver. height (H)	Site effect (*T*) (cm)	Std. deviation of prov. means	Linear regression slope H' vs. *ΔEQ* of provenances	F value between prov.
2012	228.3	+17.5	17.9	+0.628	14.00***
2015	218.9	+8.1	25.3	-0.690	3.36**
2020	185.2	-25.6	11.3	-1.572	3.40**
	210.8	0			

3.2 Analysed experiments and provenances

On the basis of an unpublished preliminary surveying study (Mátyás et al. 2008a), three experiments of the 1998 series of the all-European beech provenance trials (Wühlisch 2007) have been selected for analysis *(Table 1a and 1b)*. The tests have been chosen within a region of restricted size, to grant a relatively uniform synergy of climatic factors.

---

[2] The term "provenance" is used synonymously for "transferred population of known origin"

The test sites are located in the Carpathian basin, in Hungary, Slovenia and Slovakia, at different elevations *(Figure 1).* All three are under the influence of the more or less humid-continental climate of SE Europe. The mid-elevation site in Slovenia provides climatically optimal conditions, while the two other sites are more continental as shown by their Ellenberg indices *(Table 1a).*

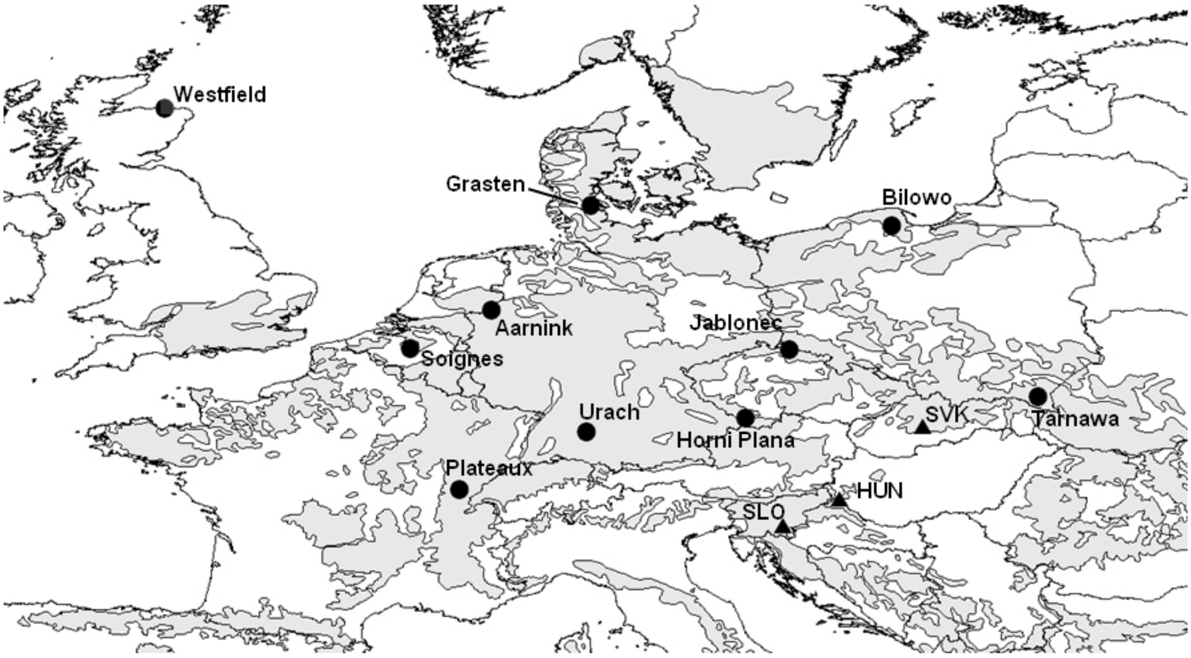


Figure 1. Location of 10 beech populations selected for statistical analysis and of the 3 test sites. The distribution range of beech (grey shade) has been provided by EUFORGEN

Table 2. Data of the 12 maritime (M), continental (C) and Alpine (A) beech provenances common in the 3 tests, ranked by their EQ index (for geographic locations see Figure 1)

Type	Nr.	Location name, country	Altitude a.s.l. (m)	July mean *T* (°C)	Annual mean *P* (mm)	*EQ* of origin	Corrected mean *H'* (cm)	Additive height response (cm)	Average ecodistance (*EQ* index)	Regression *H'* vs. *EQ* across tests
A	35	Hinterstoder AUT	1250	11.8	1380	8.6	216.4	+6.54	12.46	+2.660
A	53	Postojna M. SLO	1000	17.0	1718	9.9	222.5	+12.58	11.20	-1.432
C	51	Horni Plana CZE	990	13.4	1014	13.2	194.8	-15.07	7.73	-3.313
C	6	Plateux FRA	600	17.5	1223	14.3	197.5	-12.37	6.69	-4.239
C	48	Jablonec CZE	760	13.5	944	14.3	203.0	-6.87	6.56	-1.014
C	31	Urach GER	760	16.4	887	18.5	211.7	+1.83	2.43	+2.251
M	17	Westfield GBR	10	14.0	741	18.9	214.1	+4.23	2.03	+2.746
M	21	Grasten DEN	45	16.3	810	20.1	189.3	-20.57	0.96	+1.458
M	14	Aarnink NED	45	17.5	794	22.0	229.3	+19.43	-0.94	+1.258
M	13	Soignes BEL	110	17.9	796	22.5	214.4	+4.53	-1.38	+0.524
C	40	Tarnawa POL	540	17.6	762	23.1	228.1	+18.23	-2.03	-1.440
M	67	Bilowo POL	250	15.5	643	24.1	216.5	+6.63	-2.93	+1.740

The experiments contain 36 provenances, however not exactly the same ones. 12 populations have been selected from the 36 which are represented in all three tests and where available climatic data seemed to be reliable *(Table 2, Figure 1).* Out of the 12 provenances, 5 originate from low elevation sites in maritime climate, with *EQ* indices between 19 and 24. Another 5 populations have been transferred from inland, continental regions where beech is occupying sites at medium elevations. The original sites have generally *EQ* values below 20, except for Tarnawa, Poland (23.1) and are situated in medium mountains (540 to 990 m). Two Alpine populations originate from altitudes at or above 1000 m with *EQ* values below 10.

At the warm-continental site in Hungary (*EQ* = 26.3), all the 12 provenances have been transferred into an environment with increased continentality, higher average temperatures and higher drought stress. On the other hand, in the Slovenian test (*EQ* = 15.3) the majority of the selected populations has been brought into an environment cooler/wetter than their original climate.

For the analysis, 8th year heights measured in winter 2005/2006 have been used. Between-provenance *F* values from variance analysis of the 3 test sites (Mátyás et al. 2008a) are presented in *Table 1b*. In the following analyses only average heights of tests have been used. Obviously damaged or crippled trees have been omitted from the calculation.

3.3 Separating components of the additive model

Effect of test site potential differences

The additive *test site effect (T)* is the difference of test averages from the grand mean of all experiments (210.8 cm, *Table 1b*). Measured average heights of provenances at the three tests were corrected with the test site effect, to make them directly comparable (corrected heights are denoted further as *H’*). A correction for standard deviation differences between tests was omitted because the range of variation of provenance means indicates the differentiating power of the site *(Table 1b).*

The Slovak site has the lowest site potential, first of all due to its relatively harsh conditions. It shows also the lowest standard deviation of means. At the Hungarian site, differentiation between populations is the strongest, presumably also because of higher climatic stress, close to the climatic limit for beech (i.e. the xeric limit, Mátyás et al. 2008b, Jump et al. 2009).

General (“species-specific”) response

Response to transfer has been analysed by two types of regressions: calculating the individual response of provenances to respective ecodistances across sites, and by using means of all three tests for both provenances and ecodistances.

“Mean ecodistance” expresses the general effect of climatic conditions of the tests as experienced by differently adapted provenances. It is calculated from the difference between the average of *EQ* value of tests (21.0, *Table 1a*) and the *EQ* of origin of populations *(Table 2).*

The limited number of observations allowed only the calculation of a linear function instead of the theoretically expected curvilinear one. The data and regression shown in *Figure 2* display a significant decline of height towards increasing warming (R^2 = 0.486**)[3]. The Alpine provenances appear as outliers, maybe partly caused by inaccurate climate interpolation at higher elevations, but more probably due to truly different adaptation, as the context of precipitation vs. temperature is modulated by altitude. The analysis by

---

[3] Throughout the paper, star signs stand for level of significance: * = 0.05, ** = 0.01 and *** = 0.001 probability

Gömöry (2009) also points out the divergent behaviour of populations from higher elevations. Therefore these were excluded from further calculations.

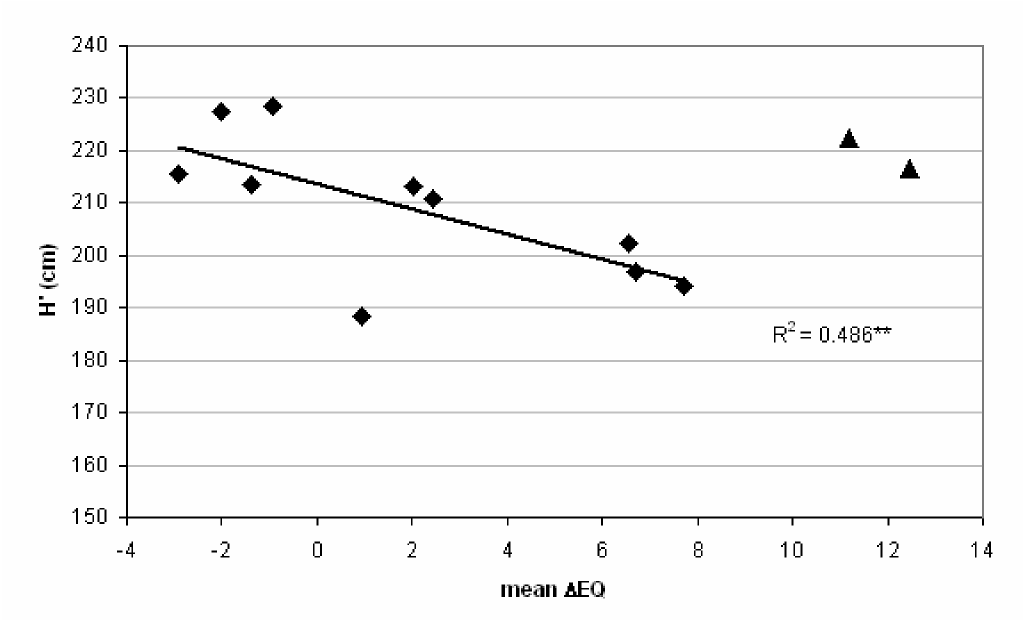


Figure 2. General response regression for corrected mean height (H') vs. mean ecodistance of provenances. Means are averages of all 3 tests. Equation is calculated for 10 maritime and continental provenances only, ▲ indicates the two Alpine outliers

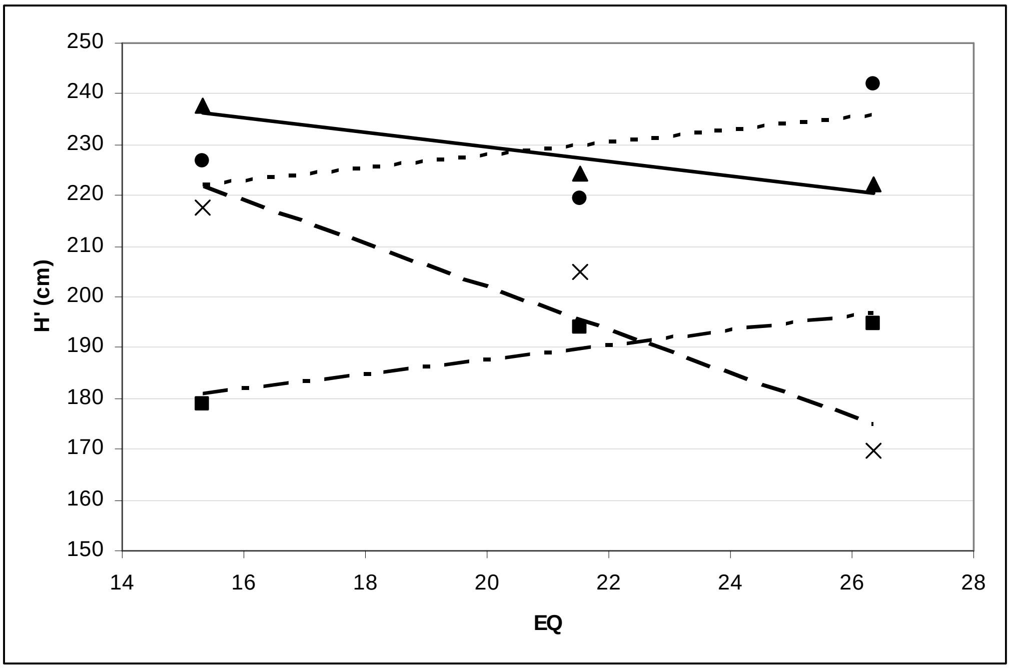


Figure 3. Reaction norm of corrected heights (H') of two maritime provenances Aarnink (•), Grasten (■), and of two continental ones Tarnawa (▲) and Plateaux (×), displaying individual differences in response against EQ values of test sites

Comparing response regressions of different provenances across test sites, the calculated slopes show a marked differentiation. A group of mostly maritime provenances show improving performance with warming and dryer conditions (positive slopes), while continental populations display an opposite trend *(Table 2, Figure 3)*. The results propose a relationship between the (climatic) origin and the character of response to changing climate. The connection, expressed by the slope values of the regressions, is significant (R^2 = 0.383*). This indicates that a *general or "species-specific" response (G)* may be predicted by using ecodistance and site conditions as independent variables (see later for details).

Table 3. Results of analysis of variance of mean heights of 10 provenances at 3 locations (uncorrected height data in cm units)

Effect	SS	DF	MS	F	p
Provenances	4946.00	9	549.6	2.620	0.039
Sites	7110.30	2	3555.1	16.949	0.001
Interaction and error	3775.66	18	209.8		

Individual response of populations

Deviation of the population mean from the grand mean represents the *individual, population-level additive response* (*P*). Population-specific differences of response across sites suggest also divergent sensitivity to climatic change, thus regression statistics characterise phenotypic plasticity. Low regression slope values indicate stable performance across sites *(Table 2, Figure 3).*

Table 3 shows the results of the analysis of variance of (uncorrected) means of 10 provenances at 3 sites. No surprise that the effect of sites is clearly more significant compared to the effect of provenances.

Interactions

In *Figure 4*, response of populations is comparable at two locations, as the horizontal sequence of populations is identical in the graphs. (The sequence is the same as in *Table 2,* as populations are ranked by their original EQ values; at the extreme left: Bilowo, Poland.) A closer observation leaves no doubt that interactions with local climatic conditions exist. Two provenances are marked for interaction: Tarnawa (PL) and Plateaux (FR). Both originate from medium elevations and perform at low elevation in Hungary below average, and the opposite is true for Slovenia.

Interaction was found confounded with microsite inhomogeneity: in the variance analysis by test locations (Mátyás et al. 2008a) replication × provenance interactions were significant (P = 0.01, not shown) in the Slovak and Hungarian trials, but not in Slovenia. Therefore the *interaction component (I)* was not separated from the residual (error) component.

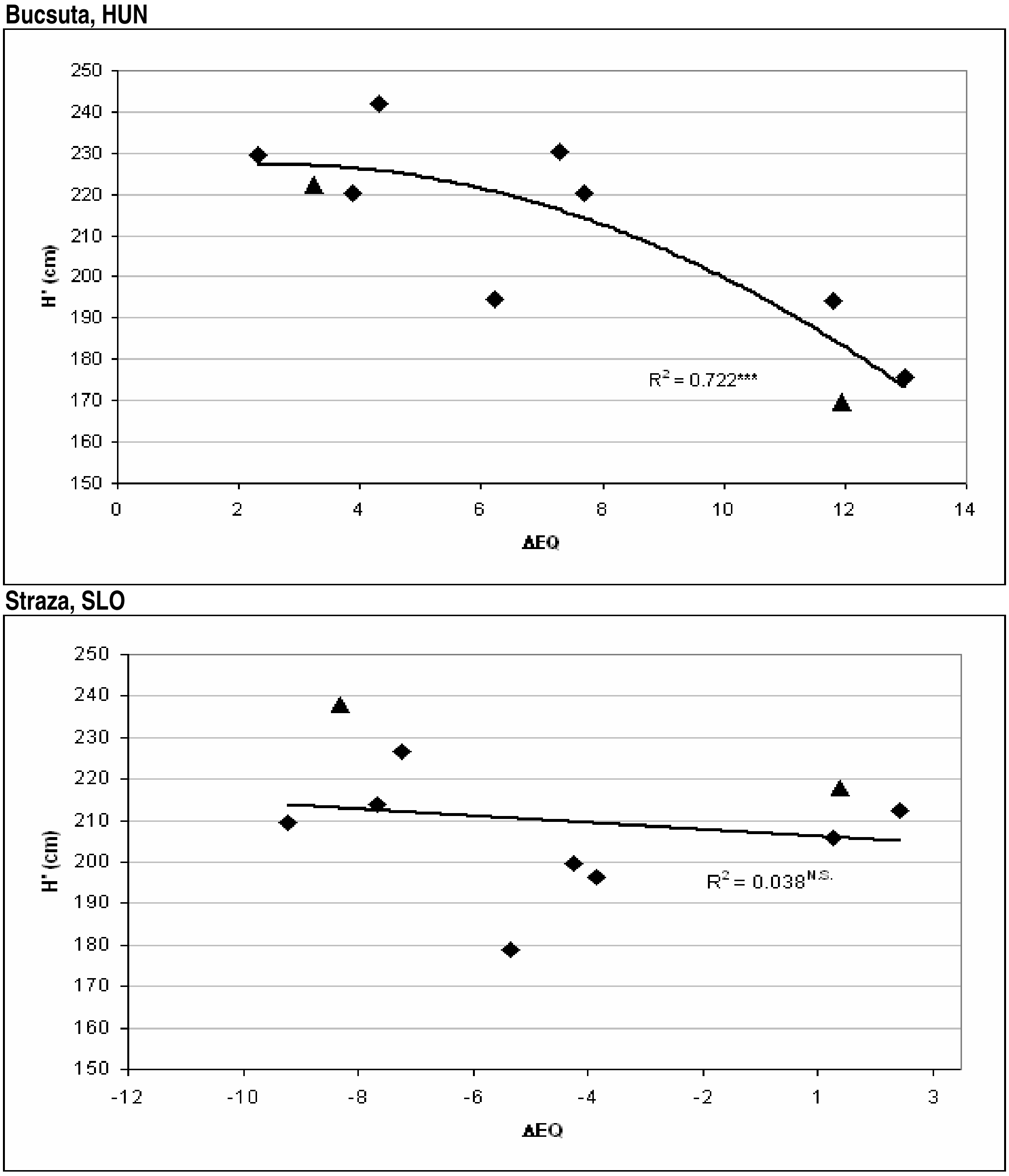


Figure 4. Regression of corrected height (H') of 10 identic provenances with ecodistance, at two sites with strongly differing EQ values (top: Bucsuta, HUN: 26.3, bottom: Straza, SLO: 15.3). The sequence of provenances is the same. Compare the two provenances marked with ▲ for interaction: Tarnawa (POL, left) and Plateaux (FRA, right). Both mountain populations perform much better at higher elevation in Slovenia than in Hungary

Construction of a 3-D response surface model

Based on the previous results, a three-dimensional model is presented which expresses that *height growth response to macroclimatic change depends on the climatic distance by which the adapted populations were moved (ΔEQ), and on the climatic environment where they are tested (siteEQ)*. Corrected height (H') serves as dependent variable. Although the regression is theoretically exponential, due to the low number of tested sites, only a linear response surface has been fitted on the data *(Figure 5)*. Calculated for 10 provenances, the equation of general height response is:

$$H' = 162{,}63 + 2{,}288 * \mathit{\Delta EQ} + 2{,}674 * \mathit{siteEQ} - 0{,}223 * \mathit{\Delta EQ} * \mathit{siteEQ}$$

The proportion of variance accounted for is 35.78%, the coefficient R = 0,598***, the individual differences between provenances left unconsidered. The distribution of residuals is even, indicating a balanced regression. Certain parts of the response surface are not supported by data and are separated by lines in *Figure 5*. The regression surface illustrates and summarises some important conclusions:

- increasing, positive EQ values, i.e. warming and more arid conditions lead to decreasing height growth and vitality;
- the effect of worsening of climatic conditions increases toward the lower (xeric) limit of distribution (EQ = 28)
- the interaction of site and macroclimatic adaptation is significant, an equation excluding the interaction component explains only 27.5% of the variation.

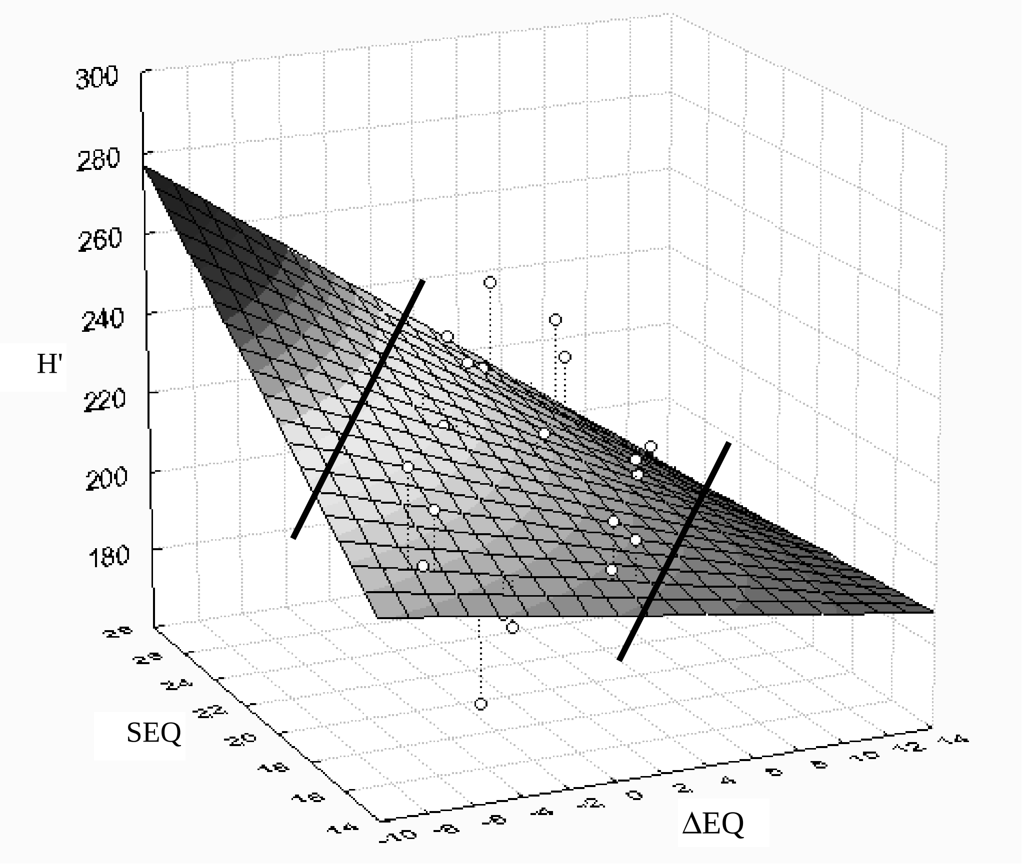


Figure 5. Linear model of height response of tested provenances, with corrected height (H') as dependent, and ecodistance of provenances (ΔEQ), respectively EQ value of sites (SEQ) as independent variables. Positive EQ values of ecodistance (to the right on the X axis) stand for simulated warming effect. Lines separate the part of the surface not supported by data

4 DISCUSSION

4.1 Modelling adaptive response to macroclimatic change

Modelling of expected response has to express that adaptation is an evolutionary-genetic issue. Present ecological models of phenotypic behaviour usually treat temperate tree species, including beech as monolithic, genetically uniform entities (e.g. Kramer 1994, Chuine et al. 2003, Czúcz et al. 2009). Another approach is the application of process-based genetic simulations which describe genetic processes on local level (Kramer et al. 2008). Both approaches necessarily disregard within-species adaptive differentiation: ecological models assume functional properties of species uniform across space. This is a general problem of bioclimatic models (Mátyás et al. 2009, Jeschke – Strayer 2008).

The special feature of the selected set of experiments is, that due to the specific climatic relations between test locations and provenances, it provides a unique opportunity to study adaptive differentiation and responses to climatic warming. Detecting adaptive responses for a species exhibiting a strongly developed plasticity (Wühlisch et al. 1995, Kleinschmidt – Svolba 1995, Gömöry 2009) did not promise easy results. The selected variable *EQ* applied for the ecodistance approach seems to describe, however, macroclimatic conditions sufficiently well, at least for Central Europe and low to medium elevations.

The study was successful in detecting that

- adaptation (and consequently, selection effect) to macroclimate exists in spite of counteracting genetic and evolutionary forces;
- response of provenances strongly depends on the climatic conditions at origin and at the test, i.e. ecological distance is a valid concept for explaining responses;
- site potential and the local climatic conditions decide not only height response and its differentiation, but also interactions;
- a general, species-specific component of genetic response could be identified beside the individual differences of populations;
- interaction was noticeable mainly in relation to altitudinal changes.

The regression surface shown in *Figure 5* summarises the general trend of response to macroclimatic change. At the warm-continental site in Hungary, all provenances had been moved into warmer and drier conditions and the calculated polynomial shows a clear decline of height growth beginning from *ΔEQ* value 4 *(Figure 5)*. Such a strong effect is not visible at the site with lowest *EQ* value, in Slovenia, where most populations came into a cooler and wetter (i.e. less stressful) environment than original. In this case growth depression with growing ecodistance was not detectable.

Regarding the mean performance of individual populations in the average of sites, the Dutch provenance Aarnink was the best, and Grasten from Denmark the worst *(Table 2, Figure 3)*. This had little or nothing to do with the (macroclimatic) distance from the test sites.

The individual response of a population to changing environmental conditions is described by the term *phenotypic plasticity*. Between-provenance differences in plasticity are detected by testing growth response along an ecological gradient, in our case by calculating regression of height vs. *EQ* values of the test sites *(Figure 3)*.

4.2 Caveats and limitations to the analysis

In the case study an attempt was made to quantify and model the genetic effect of macroclimatic selection on juvenile height growth of beech. A trait important for early-stage competition, height is integrating effects of numerous growing seasons, which makes it logically related to climate which represents also an average of annual fluctuations. Climate means hide however year-to-year and local deviations from long term averages, although irregular extreme events may have a decisive selection effect (Berki et al. 2007). Climate means should be therefore regarded rather as surrogates for extremes.

For analysis of climatic adaptation, large-scale international trials seem to be ideal, as they are established with natural populations of known origin, sampled across a large area. It is a pity and a serious fault of international provenance research that sufficiently reliable, detailed climate data are missing in most cases. Ecological characterisation was traditionally confined to description of geographic parameters (coordinates, altitude). The selective role of concrete climatic parameters has been analysed in detail only in recent literature, as interpolated, digital databases are increasingly accessible (e.g. Rehfeldt et al. 2003, 2008, Mátyás et al. 2008b). Interpolations may, however, carry considerable bias especially for higher elevations and regions with complex topography. The relatively low number of test sites and of populations, certainly limit the general validity of results. However, it is suspected, that synergy of climatic components might change across larger regions and therefore an evaluation in an ecologically restricted area might bring better results as pooling all available data without preliminary screening.

The analysed data were measured in juvenile stage. Switches in ranking may be expected up to higher ages in beech, and early age–age correlations are unreliable (Kleinschmidt – Svolba 1995). Also, results refer to the investigated populations and sites and may not be fully applicable in other environments. Therefore the application of the method on extended datasets is absolutely necessary.

Also, modelling the evolutionary-genetic background of adaptive response is still not precise enough for predictions as it fails to regard biotic interactions and migration limitations (Jeschke - Strayer 2008, Jump et al. 2009) or human interference such as planned forest management (Mátyás et al. 2009).

Finally an additional factor causing estimation errors should be mentioned. This lies in the unavoidable contradiction between the conditions of natural regeneration and selection populations are adapted to, and the necessarily different, artificial character of nursery raising and outplanting in comparative tests. In common gardens, populations experience transfer into rather artificial environments. This has little to do with natural conditions of regeneration, but one should remember that the aim of these studies is a) to derive information on use of reproductive material, and b) to forecast effects of man-made climatic changes. Neither of them are typically natural processes.

Understandably, a simulation of the natural ecological demands of a tree species in the field tests would cause a further loss of precision of response identification. Thus, the planned experimentation itself compromises the exact determination of genetic response: an unsolvable contradiction and an unexpected parallel to Heisenberg's uncertainty principle in quantum physics (Mátyás et al. 2008b).

5 CONCLUSIONS

5.1 Implications for the management and conservation of beech

The existence of macroclimatic adaptation patterns in juvenile growth justifies genetically based regulations for use of reproductive material. Regarding the sensitivity of beech to macroclimatic changes, the results show that adaptive pattern and plasticity of the species is fairly comparable to better explored conifer species such as pines, spruces (Mátyás – Yeatman 1992, Rehfeldt et al. 2003, 2008, Mátyás et al. 2008b, Thomson – Parker 2008).

Main conclusions for reproductive material use are:

- it would be more appropriate to use ecologically-based criteria instead of geographic-based ones to define recommended directions and limits of transfer;
- transfer effects are not similar in different part of the distribution area, in particular:
- in the range of the climatic optimum, in the area centre, and towards the thermal limit (northward) transfers are less critical;
- proposed separate treatment of higher elevation populations is supported by the deviating behaviour of provenances from above 1000 m;
- stressful and uncertain conditions at the lower (xeric) limit of the species demand there more rigorous rules for use and conservation.

Observations of mortality events close to the lower (xeric) limit of the species indicate that stability and vitality of populations depends not only on growth rate modelled from test results. Extreme weather events (droughts) may weaken physiological condition of populations relatively fast and may lead to insect and disease outbreaks in regions generally suitable for the species (Berki et al. 2007, Lakatos – Molnár 2009). Therefore, when defining maxima of allowable (ecological) distance of transfer, the principle of precaution should be observed, i.e. limits should be drawn stricter than the results of response regressions suggest.

Regarding climate change, the most important question is how populations react to warming, i.e. to positive ΔEQ values. The test in Hungary did detect sensitivity to EQ differences above the value of 4 *(Figure 4).*

Closer to the xeric/continental limit, already smaller changes are limiting presence (Czúcz et al. 2009). The results support the opinion that predicted climatic changes will not have serious consequences and even lead to production increase in the central-northern part of the range and at higher elevations as shown for conifers (Mátyás et al. 2008b). It is strongly cautioned from overestimating the plasticity potential found in this experiment, for regions close to the lower (xeric) limit of the range, furthermore also because the results obtained at juvenile age may not be maintained in later age.

Differences in growth performance and plasticity of provenances left unexplained by macroclimatic factors sustain earlier assumptions that local genetic adaptation also exists ("ecotypes") and maybe also epigenetic effects; neither of them have been investigated in detail in this analysis. It seems that in beech, a population- (stand-) level differentiation co-exist with large-scale adaptedness and with significant plasticity. This supports the maintenance of selection of stands for reproductive material procurement (seed stands).

5.2 Application and advantages of the proposed approach

The proposed approach provides otherwise inaccessible information on the real-world effects of expected climatic changes. The success of evaluation depends of course on the characteristics of the dataset: number and quality of test sites, number and differentiation of populations and last not least, the reliability of recorded data.

The obtained results may be applied in adaptation and mitigation policy in forestry and related fields such as nature and gene conservation, e.g. for planning human-aided migration (Marris 2009). Typical uses are rules of forest reproductive material use, assessment of local, adapted populations or conservation strategy of marginal populations (Mátyás 2007).

The results may be useful also for testing or validating ecological models, evolutionary and ecological concepts and hypotheses related to climate change effects (see review of Jump – Peñuelas 2005, Mátyás et al. 2008b, Jump et al. 2009). The design and concept of presently existing tests are however unsuitable to elucidate problems such as micro-scale adaptation, ongoing selection in extant populations, or the importance of genetic carryover (epigenetic) effects. These questions need further, very carefully planned experimentation.

Acknowledgments: The financial support of the Hungarian government research fund NKFP 6/047/2005 and of EU-FP6 Program "EVOLTREE" are gratefully acknowledged. Similarly, I am grateful to László Nagy (Sárvár) and to Ervin Rasztovits and collaborators (Sopron) for providing climatic data and support in data processing. Further support was provided by the researcher teams of the projects "EVOLTREE" and "COST E52 Beech genetics", S. Bogdan (Zagreb) and K. Kramer (Wageningen) through fruitful discussions and critics.

REFERENCES

BERKI, I. – MÓRICZ, N. – RASZTOVITS, E. – VIG, P. (2007): [Determination of the drought tolerance limit of beech forests and forecasting their future distribution in Hungary.] Erdő és klíma [Forest and Climate] V: 213-229 (in Hungarian with Engl. summary)

CHUINE, I. – KRAMER, K. – HÄNNINEN, H. (2003): Plant development models. In: Schwartz, M.D.(ed.): Phenology: an integrative environmental science. Kluwer Ac. Publ. pp. 217-235

CLAUSEN, J. – KECK, D.D. – HIESEY, W.W. (1940): Experimental studies on the nature of species. Vol I and II-IV (the additional volumes published in 1945, 1948, 1958) Carnegie Inst. Publ. Nr 520, Washington D.C.

COMPS, B. – Mátyás, Cs. – GEBUREK, T. – LETOUZEY, J. (1998): Genetic variation in beech populations along the Alp chain and in the Hungarian basin. Forest Genetics 5: (1) 1-9

COMPS, B. – GÖMÖRY, D. – LETOUZEY, J. – THIÉBAULT, B. – PETIT, R.J. (2001): Diverging trends between heterozygosity and allelic richness during postglacial colonisation in European beech. Genetics 157: 389-397

CZÚCZ, B. – GÁLHIDY, L. – MÁTYÁS, CS. (2009): Low altitude xeric climatic limit of beech and sessile oak distribution in Central Europe. Annals of Forest Science (submitted)

ELLENBERG, H. (1988): Vegetation ecology of Central Europe. 4th ed., Cambridge University Press

FANG, J. – LECHOWICZ, M.J. (2006): Climatic limits for present distribution of beech species in the world. Journal of Biogeography 33: 1804-1819

FISHER, R.A. (1958): The genetical theory of natural selection. 2nd ed., New York

FÜHRER, E. – RASZTOVITS, E. – CSÓKA, GY. – LAKATOS, F. – BORDÁCS, S. – NAGY, L. – MÁTYÁS CS. (2009): Current status of European beech (*Fagus sylvatica* L.) genetic resources in Hungary. Comm. Inst. Forestalis Bohemicae, Praha (in print)

GÖMÖRY, D. (2009): Geographic patterns in the reactions of beech provenances to transfer. Report for COST E52 meeting, Thessaloniki, Greece (manuscript) 8 p.

JAZBEC, A. – SEGOTIC, K. – IVANKOVIC, M. – MARJANOVIC, H. – PERIC, S. (2007): Ranking of European beech provenances in Croatia using statistical analysis and analytical hierarchy process. Forestry, 80: 2, 151-162

JESCHKE, J. M. – STRAYER, D.L. (2008): Usefulness of bioclimatic models for studying climate change and invasive species. In: Ostfield, R.S. - Schlesinger, W.H. (eds.): The year in Ecology and conservation, 2008. Ann. New York Ac. Sci., Boston 1134: 1-24

JUMP, A.S. – PEÑUELAS, J. (2005): Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8: 1010-1020

JUMP, A. – MÁTYÁS, CS. – PEÑUELAS, J. (2009): The paradox of altitude for latitude comparisons in species range retractions. (Review) Trends in Ecology and Evolution, 1147, doi: 10.1016/j.tree. 2009.06.007

KLEINSCHMIDT, J. – SVOLBA, J. (1995): Results of the Krahl-Urban beech provenance experiments 1951, 1954, and 1959 in Northern Germany. In: Madsen, S. (ed.): Genetics and silviculture of beech. Proc. 5th IUFRO Beech Symp., Danish Forest and Landscape Res. Inst., Forskningsserien 11/1995, 15-34

KRAMER, K. (1994): Selecting a model to predict the onset of growth of *Fagus sylvatica.* Journal of Applied Ecology 31: 172-181.

KRAMER, K. – BUITEVELD, J. – FORSTREUTER, M. and 8 further authors (2008): Bridging the gap between ecophysiological and genetic knowledge to assess adaptive potential of European beech. Ecological Modelling 216: 333-353.

LAKATOS, F. – MOLNÁR, M. (2009): Mass mortality of beech in South-East Hungary. Acta Silvatica et Ligniaria Hung. 5: 75-82

MAGRI, D. – VENDRAMIN, G.G. – COMPS, B. and 11 further authors (2006): A new scenario for the Quaternary history of European beech populations: paleobotanical evidence and genetic consequences. New Phytologist 171: 199-222

MARRIS, E. (2009): Planting the forest of the future. Nature, 459: 906-908, doi 10.1038/459906a

MATYAS, CS. (1994): Modelling climate change effects with provenance test data. Tree Physiology 14: 797-804

MÁTYÁS, CS. (1996): Climatic adaptation of trees: Rediscovering provenance tests. Euphytica 92: 45-54.

MÁTYÁS, CS. (2007): What do field trials tell about the future use of forest reproductive material? In: KOSKELA J. – BUCK A. – TEISSIER DU CROS E. (eds.): Climate change and forest genetic diversity: Implications for sustainable forest management in Europe. Bioversity International, Rome, Italy. 53-69

MÁTYÁS, CS. – YEATMAN, C.W. (1992): Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb) populations. Silvae Genetica 43: (6) 370-376.

MÁTYÁS, CS. – IVANKOVIC, M. – BOGDAN, S. – BOZIC, G. – RASZTOVITS, E. – GÖMÖRY, D. – JAZBEC, A. (2008a): Analysis of height variation in four East European provenance trials of European beech. Manuscript, Zagreb University, 27 p.

MÁTYÁS, CS.– NAGY, L. – UJVÁRI-JÁRMAI, É. (2008b): Genetic background of response of trees to aridification at the xeric forest limit and consequences for bioclimatic modelling. In: Strelcová, K. – Mátyás, Cs. – Kleidon, A. – Lapin, M. – Matejka, F. – Blazenec, M. – Škvarenina, J. – Holecy J. (eds.): Bioclimatology and natural hazards. Springer Verlag, Berlin, 179-196.

MÁTYÁS, CS. – BOROVICS, A. – NAGY, L. – UJVÁRI-JÁRMAY, É. (2009): Genetically set response of trees to climatic change, with special regard to the xeric (retreating) limits. Forstarchiv, Hannover, 80: (accepted, in print)

REHFELDT, G.E. – TCHEBAKOVA, N.M. – MILYUTIN, L.I. – PARFENOVA, E.I. – WYKOFF, W.R. – KOUZMINA, N.A. (2003): Assessing population responses to climate in *Pinus silvestris* and *Larix* spp. of Eurasia with climate transfer models. Eurasian Journal of Forestry Research, 6(2): 83-98

REHFELDT, G.E. – FERGUSON, D.E. – CROOKSTON N.L. (2008): Quantifying the abundance of co-occuring conifers along inland northwest (USA) climate gradients. Ecology, 89 (8): 2127-2139

THOMSON, A.M. – PARKER, W.H. (2008): Boreal forest provenance tests used to predict optimal growth and response to climate change. 1. Jack pine. Canadian Journal of Forest Research 38: 157-170.

WRIGHT, S. (1950): The genetics of quantitative variability. Edinburg.

WÜHLISCH, G. VON (2007): Series of international provenance trials of European beech. In: Improvement and Silviculture of Beech, Proc. the 7th Intern. Beech Symp. IUFRO Res. Gr. 1.10.00, RIFR, Teheran, Iran 135-144

WÜHLISCH, G. VON – KRUSCHE, D. – MUHS, H.J. (1995): Variation in temperature sum requirement for flushing of beech provenances. Silvae Genet. 44: 343-346

Acta Silv. Lign. Hung., Vol. 5 (2009) 63-74

Effect of Thinning on the Diameter Increment in Black Locust (*Robinia pseudoacacia* L.) Stands

Károly RÉDEI[a*] – Henrik MEILBY[b]

[a] Hungarian Forest Research Institute, Budapest, Hungary
[b] Danish Centre for Forest, Landscapes and Planning, University of Copenhagen, Denmark

Abstract – Black locust is one of the most important stand forming tree species in Hungary, covering approximately 23% of the forested land (410 thousand ha) and providing 23% of the annual timber cut of the country. Hence, during the past two decades several experiments with this species have been carried out in the country. This paper investigates the influence of thinning on the diameter increment in an experiment including four plots. One plot was left as an unthinned control plot and three plots were thinned with various thinning intensities at age 22. The experiment was measured at ages 22, 27, 32, and 36. Apparently the thinning intensities applied on two of the plots did not come up to the intensity required to influence the diameter growth of the remaining upper-storey trees. Therefore, for a given tree size the growth of the trees on these two plots did not differ significantly from the growth of similar trees in the unthinned plot. By contrast, significant thinning effects on the diameter increment of individual trees were observed on the most heavily thinned plot. Here the diameter increment was enhanced for trees with diameters of less than 20 cm, whereas the largest trees of the stand exhibited moderately increased growth. Apparently a stand density corresponding to the heavy thinning treatment (F_w values of 22-23) is required to get a significant thinning response. On the other hand, to avoid thinning shocks, it may be recommendable to apply two moderate thinning treatments instead of a single heavy one.

***Robinia pseudoacacia L.* / thinning trial / diameter increment**

Kivonat – A gyérítés hatása a mellmagassági átmérő növedékére akácállományokban. A fehér akác az egyik legfontosabb magyarországi állományalkotó fafaj, amely az erdőterület 23%-át (410 ezer ha) borítja, s az éves fakitermelés 23%-át adja. Ebből következően az elmúlt két évtizedben több, a fafajt érintő kísérlet létesült az országban. A jelen tanulmány a gyérítésnek a mellmagassági átmérő növedékére gyakorolt hatását vizsgálja egy négyparcellás kísérletben. Egy parcella a kontrollt képviselte, három parcella (állományában) pedig különböző erélyű gyérítést viteleztek ki 22 éves korban. A kísérleti faállományokban 22, 27, 32 és 36 éves korban végeztek méréseket. Az értékelésekből következően két parcella faállományában az alkalmazott gyérítés intenzitás mértéke nem volt hatással a visszamaradó, felsőszintben elhelyezkedő fák átmérő-növekedésére. Ebből adódóan, adott méretű fák esetében, azok átmérő növekedése szignifikánsan nem különbözött a kontroll parcellában található, hasonló méretű faegyedek növekedésétől. Ezzel ellentétben, a gyérítésnek a fák átmérő-növedékére történő szignifikáns hatását regisztrálták a legerősebb eréllyel gyérített faállomány parcellájában. Itt az átmérő-növedék fokozódását a 20 cm-nél kisebb átmérőjű fák esetében regisztrálták, míg a faállomány ennek nagyobb átmérőjű egyedeinél mérsékelt növekedés volt megfigyelhető. Mindezekből az következik, hogy erős intenzitású gyérítés (F_w=12-23) szükséges

---

[*] Corresponding author: redei.karoly@t-online.hu, H-1023 Budaepst, Frankel Leó u. 42-44.

a belenyúlás szignifikáns hatásának eléréséhez. Ugyanakkor gyérítési sokk elkerülése érdekében, inkább két mérsékeltebb erélyű gyérítés javasolható, az egy, de erős intenzitású helyett.

Fehér akác / gyérítési kísérlet / átmérő növedék

1 INTRODUCTION

Black locust (*Robinia pseudoacacia* L.) was the first forest tree species to be imported from North America to Europe (to France) some time after 1601. Its rapid spread in Europe and other parts of the world (Asia Minor - Turkey, China, Korea) may be attributed to its adaptability to a wide range of growth conditions, its favourable breeding properties, frequent and abundant seed production, excellent coppicing, fast growth and high yield, as well as its highly valuable timber.

In Hungary black locust is the most widespread tree species, covering approximately 23% of the forested land (410 thousand ha) and providing 25% of the annual timber cut of the country. In Hungary black locust stands have been established on good as well as on medium or partly poor quality sites. However, for high-quality timber producing black locust forests, the site must provide adequate moisture and a well-aerated and loose-structured soil that is rich in nutrients and humus. Implementing good silvicultural plans and models will lead to profitable black locust stands and better acceptance of the species by timber growers (Rédei 2002).

A lot of international papers have published research results on the effect of tending operations on the increment of diameter at breast height and of standing volume.

In experimental thinning trials established, in Douglas-fir stands in Italy with initial stocking varied between 1600 and 3100 trees. ha^{-1}. At age of 23-35 years, for all thinning methods and grades, total production (standing volume plus volume of thinned trees) and current annual volume increment of standing trees were not significantly different from the control plots. Thinnings, regardless of method, favoured increased DBH increment, compared to control plots, but trees of the poorer site classes responded the best (Cutini – Nocentini 1987).

According to the investigations of a *Pinus nigra* thinning trial at age of 35 years, 8 years after the thinning no statistically significant differences arose in total production, but growth rates of basal area and stem volume were significatively higher in the three thinning plots compared with the control (Silvano – Vincenzo 1997).

Seven thinning trials investigations with Norway spruce in southern Sweden showed that diameter class had no effect on response to thinning as indicated by the fact that the smaller trees also responded strongly when thinned from above (Paper 1999).

A precommercial thinning trial, conducted in 1978 in a 20-year old balsam fir stand in Canada was evaluated at 5 years intervals until 1998. The diameter growth during the 20 year period following thinning was inversely related to the residual density. The increase in diameter of trees in thinned plots accumulated mainly during the first 10-year period. Total volume per hectare after 20 years was proportional to residual stand density, white merchantable volume per hectare was similar through the range of densities (Pothier 2002).

The effect of different thinning intensities on growth and yield was studied in *Pinus silvestis* L. stands in Central Spain. The investigations showed that the total volume and volume increment decreased with thinning intensity, this loss being more significant in the case of moderate and heavy thinning. Height increment was not influenced by thinning, whereas dominant and quadratic mean diameter increments increased with the thinning intensity. The response of diameter growth to thinning was greater at younger ages (less than 50 years) and in medium sized trees (Rio et al. 2008).

In order to investigate the influence of various thinning intensities on the diameter increment, several thinning trials were established in Hungary (Rédei 1992, 1995). In this paper, the evaluation of one of these trials is presented.

2 MATERIAL

2.1 Description of the study area

In the past two decades several experimental plots have been established in forest regions of Hungary for investigating the growth, yield, and tending operation techniques of black locust stands. A thinning trial with four plots of 0.10 ha each were established in the subcompartment Pusztavacs 201 E, which is located in the Danube-Tisza Interflow region, in the central lowland part of Hungary.

According to the classification of site types used in Hungary, the main ecological characteristics of the study area are:

- Forest steppe climate zone: the air humidity is less than 50% in July at 2 pm, the annual precipitation is less than 600 mm.
- Hydrology: free draining.
- Genetic soil type: combination of humic sand soils.
- Elevation: < 100 metres

According to the Hungarian yield table for black locust stands (Rédei 1983) the site class of the investigated stand is III, that is the third best out of VI.

2.2 Assessment of stand characteristics

At age 22, 27, 32, and 36 the tree height and the diameter at breast height (d.b.h.) were measured for all trees on the four plots. Based on these measurements the following parameters were calculated: stem number, stand basal area, diameter corresponding to mean basal area, stand height (Lorey's height), stem volume, and stand volume. Stem volume was estimated using the volume function (Sopp 1974):

$$v = 10^{-8}\, d^2\, h^1\, (h/[h-1.3])^{p0}\, (p_1 d\, h + p_2\, d + p_3\, h + p_4)$$

where d is diameter at breast height (cm),
h is tree height (m),
$p_0 = 4.00$,
$p_1 = -0.6326$,
$p_2 = 20.23$,
$p_3 = 0.00$ and
$p_4 = 3034$.

2.3 Thinning intensity

To stimulate the diameter increment a thinning was carried out at age 22 in three of the four plots. Plot 1 was left as an unthinned control plot and the other three plots were thinned from below using a range of different thinning intensities, among which the treatment applied in plot 4 can be considered a heavy treatment. The resulting stem numbers after thinning were:

plot 1: control, stem number = 770 per ha
plot 2: stem number (after thinning) = 700 per ha
plot 3: stem number (after thinning) = 550 per ha
plot 4: stem number (after thinning) = 400 per ha

To provide a description of the thinning intensity the Wilson factor (F_w) was used: $F_w = 100/(H_L\ N^{1/2})$, where H_L is Lorey's height in metres and N is stem number per ha.

2.4 Tree classification

Before the thinning at age 22 all trees on the four plots were classified according to the tree height classification system generally used in Hungarian silvicultural practice: 1 = dominant tree, 2 = codominant tree, 3 = intermediate (partly dominated) tree, 4 = suppressed tree. At the same occasion, all trees were classified using the silvicultural classification system generally applied in Hungarian practice: 1 = superior tree, 2 = subdominant tree, 3 = rejected tree to be removed, 4 = dead or dying tree.

3 STATISTICAL METHODS

The objective of the analysis is to determine the apparent effects of thinning on the diameter growth of black locust. Accordingly, we investigate the variation of growth between plots and height classes for each of the periods 22-27 years, 27-32 years, and 32-36 years. Furthermore, we analyse the relationship between stem diameter and diameter increment and the effect of plot (thinning), height class, silvicultural class, and period on this relationship. This analysis enables us to distinguish the effect of plot (thinning) on diameter growth from the effect of variations in the tree size composition of the strata. Unfortunately, as the experiment does not include replications, it is not possible to distinguish the effect of thinning from the effect of plot (growth conditions).

As our first approach, we test the hypothesis of identical mean increments in each of two specific groups of trees. These tests are carried out as ordinary t-tests using the TTEST procedure of the SAS (v. 6.12) software package. Each individual comparison of two groups of trees can be considered a simple analysis of variance based on the model:

$$\Delta D_{ij} = \mu_i + \varepsilon_{ij}$$

where ΔD_{ij} is the observed increment of tree j in group $i \in [1,2]$, μ_i is the true mean diameter increment in group i, and the ε_{ij}s are normal and independent errors with mean zero and equal variances. In cases where the hypothesis of equal variances is rejected, an approximate t statistics is used. The degrees of freedom associated with the approximate t statistics are calculated using Satterthwaite's approximation.

The analysis of the relationship between diameter and diameter increment was carried out using general linear models. The models were developed using the GLM procedure of the SAS (v. 6.12) software package. Instead of presenting separate models for each of the three periods, it seems more informative to develop all-embracing models describing the relationship between diameter and diameter increment. As both level and slope of this relationship may depend on plot (thinning), height class, silvicultural class, and period the basic formulation of the model is:

$$\Delta D_{hijst} = \alpha + a_{1i} + b_{1h} + c_{1t} + d_{1s} + (\ \beta + a_{2i} + b_{2h} + c_{2t} + d_{2s}\ )\ D_{hijst} + \varepsilon_{hijst}$$

where D_{hijst} is the breast height diameter (cm) of tree j in plot i, height class h, and silvicultural class s at time t; ΔD_{hijst} is the annual diameter increment (cm/year) in the period immediately after time t; α and β are model parameters common to all classes; a_{1i} and a_{2i} are class-specific parameters for plot i; b_{1h} and b_{2h} are specific for height class h, c_{1t} and c_{2t} are specific for the period following time t, and d_{1s} and d_{2s} are specific for silvicultural class s. Finally, the ε_{hijst}s are assumed to be normal and independently distributed random errors with mean zero and equal variances.

The possible interactions between plot (thinning intensity), height class, silvicultural class, and period were also considered in models of the above type.

4 RESULTS AND DISCUSSION

4.1 Stand diameter and diameter increment

The most important stand parameters of the plots are included in *Table 1*. From this table it appears that, before thinning, the mean diameter and stem number of plot 1 were slightly lower than those of plots 2-4. Therefore, after thinning at age 22, the basal area and volume of plot 3 were almost equal to those of the unthinned plot 1, and the basal area and volume of plot 2 were even greater. As for the most heavily thinned plot (4), more than half of the original stem number and one third of the original volume were removed. All thinning treatments were carried out from below and, therefore, the average height and diameter of thinned trees were less than those of the remaining stand. Moreover, after thinning the diameter corresponding to mean basal area increased consistently from 16.7 cm to 20.1 cm with increasing thinning intensity. This should be taken into account when examining the average diameter increments on the four plots. Furthermore, it should be noted that the stand heights of plots 1, 2, and 4 were almost equal before thinning, and that of plot 3 was only slightly higher. Accordingly, we may assume that the growth potential of the four plots was similar. Finally, the mortality during the observation period (age 22-36) decreased with increasing thinning intensity.

Table 1. The most important stand parameters of the four plots (Pusztavacs 201 E)

Plot Number	Age	Remaining stand					Thinning					Before thinning					Mortality		F_w
	Yr.	N /ha	H_L m	D_g cm	G m^2/ha	V m^3/ha	N /ha	H_L m	D_g cm	G m^2/ha	V m^3/ha	N /ha	H_L m	D_g cm	G m^2/ha	V m^3/ha	N /ha	V m^3/ha	
Plot 1. Control	22	770	20.0	16.7	16.84	177.9						770	20.0	16.7	16.84	177.9	60	4.2	
	27	760	21.4	18.3	20.07	221.9						760	21.4	18.3	20.07	221.9	70	5.4	
	32	630	22.8	20.6	21.08	244.7						630	22.8	20.6	21.08	244.7	200	21.6	
	36	630	23.2	22.0	23.62	271.4						630	23.2	22.0	23.62	271.4	200	23.1	
Plot 2.	22	700	20.4	18.9	19.61	211.1	150	16.0	11.5	1.57	14.2	850	20.1	17.8	21.18	225.3			18.5
	27	610	21.0	21.4	21.86	241.1						610	21.0	21.4	21.86	241.1	90	14.7	
	32	510	22.9	23.6	22.40	262.2						510	22.9	23.6	22.40	262.2	190	34.5	
	36	510	23.3	24.9	24.02	282.1						510	23.3	24.9	24.02	282.1	190	22.4	
Plot 3.	22	550	21.7	19.3	16.10	180.3	370	19.1	14.5	6.15	64.0	920	21.2	17.5	22.25	244.3			19.6
	27	550	22.2	21.4	19.44	221.3						550	22.2	21.4	19.44	221.3			
	32	500	23.5	23.2	21.20	252.0						500	23.5	23.2	21.20	252.0	50	11.7	
	36	500	24.9	24.2	23.02	279.0						500	24.9	24.2	23.02	279.0	50	12.3	
Plot 4.	22	400	21.6	20.1	12.71	141.8	500	18.2	14.2	7.88	77.6	900	20.3	17.1	20.59	219.4			23.1
	27	400	22.4	22.3	15.71	179.8						400	22.4	22.3	15.71	179.8			
	32	380	23.8	24.2	17.43	208.8						380	23.8	24.2	17.43	208.8	20	6.0	
	36	380	24.3	25.3	19.16	228.8						380	24.3	25.3	19.16	228.8	20	6.3	

F_w (Wilson factor):= $100/(H_L N^{1/2})$

The average periodic annual diameter increments are summarised in *Table 2* for each plot and height class. From this table it appears that the average diameter increment increased consistently from plot 1 to plot 4 in all three periods. On the other hand, as for the individual height classes, this increase is not reflected clearly. For most plots and periods the average diameter increment increased consistently from height class 4 to height class 1, as the variation between height classes within plots is considerably greater than between plots for a given height class. The general increase in average diameter increment from plot 1 to 4 is most pronounced in the first period (22-27 years) where the difference between plot 1 and 4 amounts to 0.15 cm/year. For comparison, the difference between plot 1 and 4 in the third period (32-36 years) only amounts to 0.05 cm/year.

Table 2. Average periodic annual increment (cm/year) for various periods, plots and height classes

Period (age)	Plot	Height class				
		1	2	3	4	All
22-27	1	0.488 (0.03)	0.388 (0.01)	0.231 (0.02)	0.141 (0.02)	0.300 (0.02)
	2	0.591 (0.04)	0.433 (0.02)	0.305 (0.04)	0.167 (0.02)	0.361 (0.02)
	3	0.543 (0.06)	0.429 (0.03)	0.300 (0.04)	0.128 (0.03)	0.394 (0.03)
	4	0.513 (0.02)	0.440 (0.02)	0.364 (0.06)	0.160 (-)	0.446 (0.02)
27-32	1	0.383 (0.04)	0.260 (0.01)	0.180 (0.01)	0.082 (0.01)	0.213 (0.02)
	2	0.363 (0.03)	0.287 (0.02)	0.142 (0.02)	0.081 (0.02)	0.219 (0.02)
	3	0.358 (0.04)	0.261 (0.02)	0.227 (0.03)	0.148 (0.04)	0.263 (0.02)
	4	0.335 (0.04)	0.333 (0.02)	0.204 (0.03)	0.100 (-)	0.312 (0.02)
32-36	1	0.377 (0.04)	0.311 (0.03)	0.168 (0.02)	0.112 (0.02)	0.234 (0.02)
	2	0.296 (0.05)	0.297 (0.02)	0.165 (0.03)	0.160 (0.03)	0.240 (0.02)
	3	0.423 (0.04)	0.268 (0.04)	0.196 (0.04)	0.190 (0.04)	0.276 (0.02)
	4	0.292 (0.04)	0.302 (0.02)	0.225 (0.07)	0.075 (-)	0.284 (0.02)

Standard errors are given in parentheses.

From *Table 2* it also appears that the average annual diameter increment within a given height class quite often reaches its maximum value (for a given period) in plot 4, but maximum values occur in plot 3 with a similar frequency, and the occurrence of maximum values in plots 1 and 2 is not uncommon either. Accordingly, if it were not for the reduced proportion of lower-storey trees with increasing thinning intensity, it is not likely that the highest average increment (all trees on a plot) would generally be found in plot 4.

In Figure 1 the diameter distributions are shown after thinning for all plots and stand ages. For plots 1 and 2 it appears that the distribution at age 22 is slightly skewed. It also appears that the unthinned plot 1 tends to develop a bimodal diameter distribution. In fact, this would not be surprising, as bimodality is a frequently reported property of diameter distributions in unthinned stands (e.g. Mohler et al. 1978). Development of a bimodal diameter distribution implies that the stand must consist of two well-defined storeys with distinguishable levels of diameter increment. Moreover, the mortality rate of the lower storey must be so low that it does not offset the effect of the faster growth of the upper storey on the bimodality of the diameter distribution. Inspection of the developmental paths (not shown) of trees in plot 1 yields the impression that distinct levels of growth in the two storeys can actually be observed. In addition, it turns out that a diameter of 16 cm at age 22 constitutes a reasonable boundary between the two storeys.

A remarkable property of the diameter distributions in Fig. 1 is that the distributions of plots 1-3 all increase their spread over time, whereas the spread of the distribution in plot 4 is almost constant. This seems to indicate that the diameter increment on this plot is not as size dependent as on the other plots, i.e. compared with plots 1-3 the growth of small trees on plot 4 is enhanced, or that of large trees is reduced, or both.

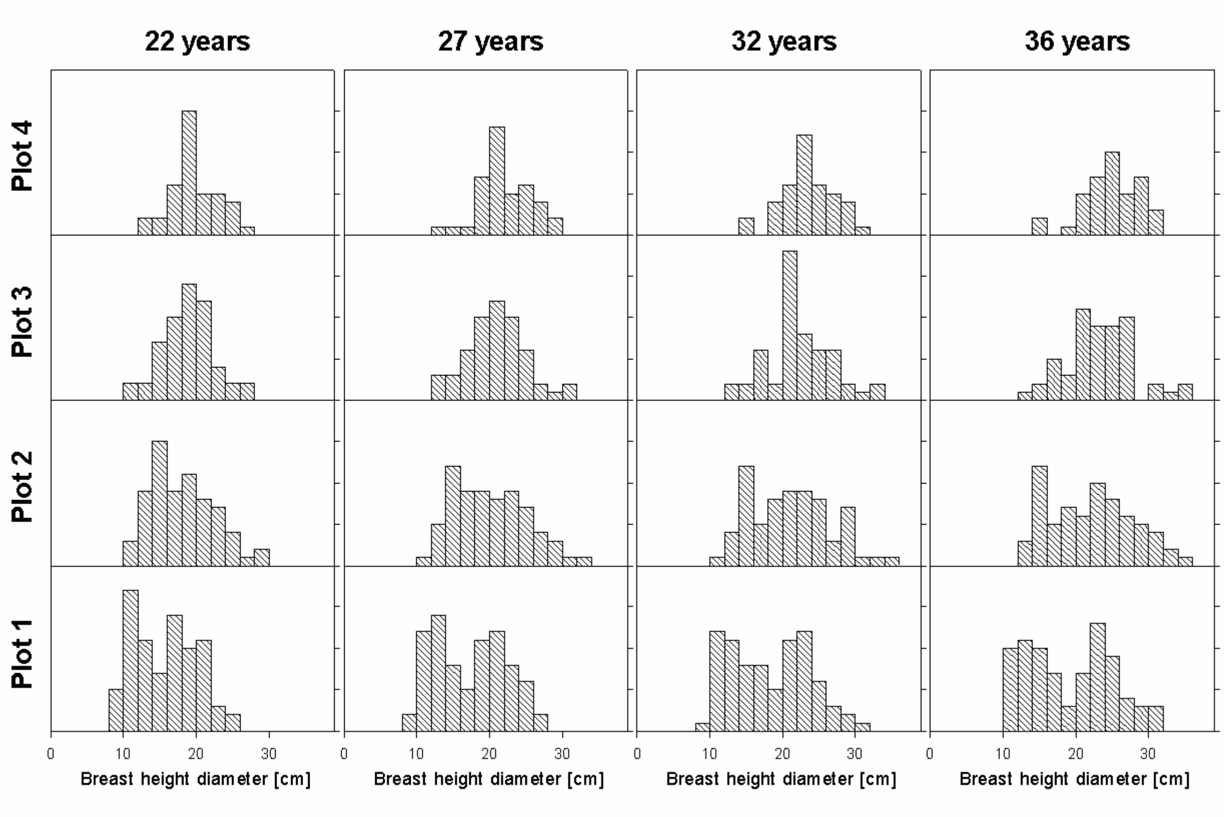


Figure 1. Diameter distributions in the four plots at ages 22, 27, 32, and 36 years

4.2 Testing the differences between average diameter increments

In *Table 3* the differences between the average diameter increments of the four plots have been tested for each of the three periods. Using 5% significance levels we find that in the first period (22-27 years) plot 1 differs significantly from all the other plots, whereas in the second period (27-32 years) it only differs significantly from plots 3 and 4. The diameter increment in plot 2 differs significantly from plot 4 in the first two periods. No significant differences are found between any of the plots in the third period (32-36 years). As will appear below, most of the difference between plots is caused by the dissimilarities of their tree size compositions, rather than by marked differences as regards the growth of trees in a given size class.

Table 3. Tests of equal mean diameter increment for plots within periods

Plot	Period (age)	Plot 1	2	3
2	22-27	*		
	27-32	NS		
	32-36	NS		
3	22-27	**	NS	
	27-32	*	NS	
	32-36	NS	NS	
4	22-27	***	**	NS
	27-32	***	***	NS
	32-36	NS	NS	NS

Significance levels: ’NS’: not significant; ’*’: 5%, ’**’: 1%, ’***’: 0.1%.

In *Table 4* the effect of increased thinning intensity on the average diameter increment has been tested for each of the height classes in each of the three periods. The table shows whether the observed effect of increased thinning intensity is positive, negative, or insignificant for a given height class. As the number of trees per height class and plot is less than 30 in all cases except one, the t-tests are generally weak. Accordingly, the significance levels applied in *Table 4* are 5, 10, and 20%. As it appears from the table the highest frequency of significant differences are found in height classes 2 and 3. The total number of differences that are found to be significant at the 20% level is 22 and, out of these, only 4 are negative, so the effect of increased thinning intensity is positive in most cases. However, three of the significant negative effects are found in height class 1 when plots 1, 2, and 3 are compared with plot 4. Thus, it appears that the highest trees respond negatively to the strong thinning in plot 4. By contrast, when plots 1, 2, and 3 are compared with plot 4 for height classes 2 and 3, all significant differences are positive, indicating that increased thinning intensity generally influences the diameter increment of height classes 2 and 3 positively. On plot 4 the number of trees in height class 4 is only 1 and, therefore, in this height class no significant thinning effects are found in comparisons with plot 4. However, in comparisons between plots 1, 2, and 3 it appears that trees in height class 4 are also influenced positively by thinning.

Table 4. Tests of equal mean diameter increment for plots within periods and height classes.

		Height class 1			**Height class 2**		
Plot	Period	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
2	22-27	+ +			+ +		
	27-32	NS			NS		
	32-36	NS			NS		
3	22-27	NS	NS		+	NS	
	27-32	NS	NS		NS	NS	
	32-36	NS	+ +		NS	NS	
4	22-27	NS	- -	NS	+ +	NS	NS
	27-32	NS	NS	NS	+ + +	+	+ + +
	32-36	-	NS	- - -	NS	NS	NS
		Height class 3			**Height class 4**		
Plot	Period	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
2	22-27	+ +			NS		
	27-32	-			NS		
	32-36	NS			+		
3	22-27	+	NS		NS	NS	
	27-32	+	+ + +		+ +	+	
	32-36	NS	NS		+	NS	
4	22-27	+ + +	NS	NS	NS	NS	NS
	27-32	NS	+	NS	NS	NS	NS
	32-36	NS	NS	NS	NS	NS	NS

Signs indicate the effect of increased thinning intensity on average diameter increment.
Significance levels: ’NS’: not significant; ’+’/’-’: 20%, ’+ +’/’- -’: 10%, ’+ + +’/’- - -’: 5%.

The tests in *Table 4* indicate that the relatively strong thinning on plot 4 leads to reduced diameter increment in height class 1, whereas height classes 2 and 3 respond positively. As for the moderate thinning of plot 3 the thinning effects are generally positive (or insignificant) as compared with plots 1 and 2, and the majority of the significant differences occur for height classes 3 and 4. Finally, the effect of the light thinning applied in plot 2 only seems to last for the first period where the differences between plots 1 and 2 are significant at the 10% level for height classes 1, 2, and 3.

In *Table 5* the differences in average annual diameter increments have been tested between periods for each of the four plots. Accordingly, this table yields an impression of the combined effect of stand age, climate, and the gradually decreasing effect of the thinning treatment for various thinning intensities. It emerges that, for all four plots, the mean annual increments differed significantly between period 1 (22-27 years) and the two other periods, whereas no significant differences are found between periods 2 and 3. Clearly, as similar results are obtained for the thinned plots 2-4 and for the unthinned plot 1, most of the difference observed between period 1 and the two other periods must be ascribed to age and climate, rather than to effects of thinning.

Table 5. Tests of equal mean diameter increment for periods within plots.

Period	Plot	Period (stand age)	
		22-27	27-32
27-32	1	***	
	2	***	
	3	***	
	4	***	
32-36	1	*	NS
	2	***	NS
	3	**	NS
	4	***	NS

Significance levels: ’NS’: not significant, ’*’: 5%, ’**’: 1%, ’***’: 0.1%

4.3 Relationship between diameter and diameter increment

A wide range of models were tested, some of them including interactions between the class variables: plot, height class, silvicultural class, and period. It turned out that the lowest possible root mean squared error (RMSE) was 0.117 cm, which was reached by a model that included interactions between plot and silvicultural class and between height class and silvicultural class. However, in this model there was no significant effect of plot, and the total number of non-zero parameters was 26. By comparison, models without interactions between class variables obtained RMSE values that were only slightly higher (0.119-0.120 cm) with only 13-16 non-zero parameters. Accordingly, the final models do not include interactions between class variables.

In the final model the effect of silvicultural class is statistically significant. However, the influence of silvicultural class on the annual diameter growth is small (much less than that of height class) and, as the height and silvicultural classifications are closely related it has been decided to present two models, one with and one without silvicultural class. Apart from this, the models both include the effect of current diameter, separate levels of increment for each plot (thinning), separate levels for each height class, separate slopes for each plot, and separate slopes for each period. The two models are summarised in *Tables 6 and 7*. It should be noted that the RMSE and R^2 of the two models are almost equal; so – from a practical point of view – we may choose quite freely among them. For both models we tested whether the residuals could actually be assumed to originate from a normal distribution (using the

Shapiro-Wilk test statistic). In both cases the test statistics were outside the significance region and we may therefore confidently assume that the residuals are actually normal.

As for the model in *Table 6* the a_{1i}s are negative and the a_{2i}s are positive for plots 1-3, and it appears that the relationship between diameter and diameter increment moves to a higher level and becomes more flat with increasing thinning intensity. The height class turns out mainly to influence the level of the relationship and it appears that the level becomes approximately 0.17 cm/year higher for height class 1 than for height class 4. The isolated effect of silvicultural class is smaller and accounts for a maximum of 0.08 cm/year. It should be noted that for silvicultural class 2 the growth apparently does not differ significantly from class 4, as its d_{1s}-parameter is not significantly different from zero. Finally, the period mainly influences the slope of the relationship and, as was also observed in *Table 5*, a significant difference is observed between period 1 and the two other periods, whereas these two periods do not differ significantly from each other.

Table 6. Linear model with class-specific levels and slopes, including silvicultural class

Model: $\Delta D_{hijst} = \alpha + a_{1i} + b_{1h} + d_{1s} + (\beta + a_{2i} + c_{2t}) D_{hijst} + \varepsilon_{hijst}$
RMSE = 0.1188 cm $R^2 = 0.505$

Parameter estimates										
α	β	**Plot**	a_{1i}	a_{2i}	**Height class**	b_{1h}	**Silv. class**	d_{1s}	**Period**	c_{2t}
0.2743	-0.0065	**1**	-0.2789	0.0127	**1**	0.1651	**1**	0.0795	**22-27**	0.0067
		2	-0.2321	0.0103	**2**	0.1334	**2**	0.0313^{NS}	**27-32**	-0.0003^{NS}
		3	-0.2282	0.0102	**3**	0.0360^{NS}	**3**	0.0500	**32-36**	0
		4	0	0	**4**	0	**4**	0		

All class-specific parameters are calculated under the condition that the parameter of the highest numbered class is restricted to zero. Symbols: see text.
NS-marked parameter estimates are not significantly different from zero (at the 5% level).
Units of measurement: D_{hijst}: cm, ΔD_{hijst}: cm/year.

In *Table 7* the model not including silvicultural class is presented. The table shows that the effects of plot (a_{1i} and a_{2i}) and period (c_{2t}) are almost unchanged as compared with the model in *Table 6*, whereas the effect of height class has increased as a consequence of the removal of silvicultural class from the model. This is due to the mentioned positive relationship between height class and silvicultural class.

Table 7. Linear model with class-specific levels and slopes, not including silvicultural class

Model: $\Delta D_{hijt} = \alpha + a_{1i} + b_{1h} + (\beta + a_{2i} + c_{2t}) D_{hijt} + \varepsilon_{hijt}$
RMSE = 0.1197 cm $R^2 = 0.495$

Parameter estimates								
α	β	**Plot**	a_{1i}	a_{2i}	**Height class**	b_{1h}	**Period**	c_{2t}
0.2609	-0.0054^{NS}	**1**	-0.2374	0.0106	**1**	0.2242	**22-27**	0.0067
		2	-0.1956	0.0084	**2**	0.1587	**27-32**	-0.0003^{NS}
		3	-0.2091	0.0095	**3**	0.0669	**32-36**	0
		4	0	0	**4**	0		

Explanation: see *Table 6*.

In *Figure 2 the* predicted values of annual diameter increment in the first period (22-27 years) are presented for various combinations of diameter and height class. As will appear from the figure, the overall difference between the diameter increments of various height classes is considerable. Furthermore, for height class 2 in plots 1-3 the predicted annual increment in this period varies from 0.3 cm to 0.55 cm over the 10-30 cm diameter range. However, for plot 4 the variation is less than 0.05 cm and, compared with the other three plots, trees with a diameter of less than approximately 20 cm exhibit increased diameter increment whereas thicker trees respond to the increased thinning intensity by decreasing diameter growth.

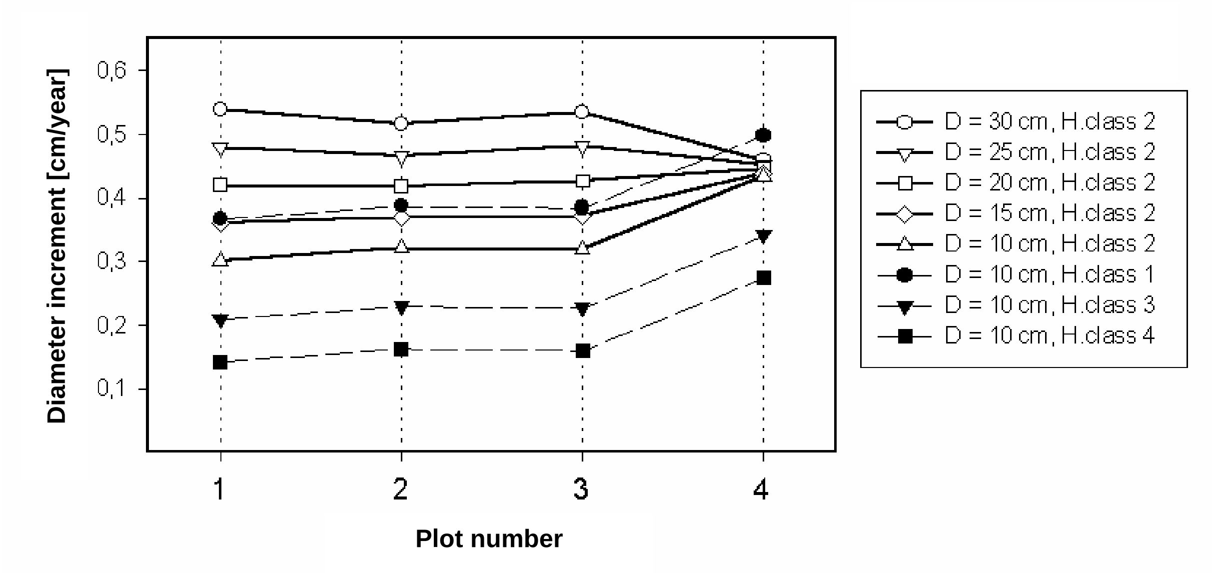


Figure 2. Predicted annual increment in the first period (22-27 years) as depending on plot (thinning), diameter (D), and height class (H.class). All predictions are calculated using the model in Table 7.

In the following two periods (27-32 and 32-36 years; not shown) the considerable difference between the growth of small and large diameter trees has almost disappeared on plots 1-3, and on plot 4 the relationship between diameter and diameter increment has been reversed, meaning that the predicted increment of small diameter trees exceeds that of large diameter trees. However, small diameter trees (d.b.h. < 20 cm) on plot 4 still exhibit faster growth than on plots 1-3, so the thinning response persists. On the other hand, the reduced growth of large diameter trees seems to indicate that the dominant trees experienced a thinning shock, whereas the smaller trees benefited from the thinning. Clearly, this is in agreement with the results in *Table 4.*

The predicted increments of trees on plots 1, 2, and 3 are almost similar and, provided that the growth conditions on these plots are also similar, this implies that within the range of thinning intensities applied on plots 2 and 3 almost no thinning response occurs. Thus, as for these plots the differences observed in *Table 4* are mainly caused by the varying diameter composition of each height class on the three plots. In fact, it turns out that the average diameter of trees in a given height class on plot 1 is generally 1-3 cm smaller at age 22 as compared with trees in the same height class on plots 2 and 3. Similarly, the thinning effects observed in *Table 3* are mainly caused by the varying tree size composition on the four plots.

5 CONCLUSION

In this experiment the stands were thinned from below. This implies that most of the thinned trees are in the lower part of the canopy (height classes 3 and 4) and, therefore, effects of thinning on the diameter increment of the remaining upper-storey trees cannot be observed at low thinning intensities. Apparently, the thinning intensities applied on plots 2 and 3 did not quite come up to the intensity required to influence the diameter growth of the remaining trees. Thus, on these plots the differences in diameter increment reported in *Tables 3 and 4* are basically consequences of unequal tree size compositions. By contrast, significant thinning effects on diameter increment are observed on plot 4. In this case, the diameter increment is enhanced for trees with diameters of less than 20 cm, whereas larger trees exhibit reduced growth.

Many thinning experiments have consistently reported increasing diameter growth with decreasing stand density (Clutter et al., 1983). Stands thinned in time develop larger average diameters than comparable unthinned stands. This is also observed in the current experiment. From a tending operations point of view one of the most important tasks is to create suitable growing space for superior trees that exhibit the greatest diameter growth and volume increment. However, in the present experiment, it appears that the thinning intensity required to obtain a significant thinning response among medium-sized trees also implied that the largest trees of the stand experienced a thinning shock. Nevertheless, we conclude that when increment thinnings are carried out, an F_w value of 22-23 may be preferable. This corresponds to the stand density obtained in plot 4. However, to prevent thinning shocks on certain sites it may be considered to carry out two moderate thinning treatments instead of a single heavy one.

REFERENCES

CLUTTER, J.L. – FORTSON, J.C. – PIENAAR, L.V. – BRISTAR, G.H. – BAILEY, R.L. (1983): Timber management: A quantitative approach. John Wiley and Sons, p. 66-81.

CUTINI, A. – NOCENTINI, S. (1989): Experimental thinning trials in Douglas-fir stands in Tuscany. Annali dell'Istituto Sperimentale per la Selvicoltura, 20:73-152.

MOHLER, C.L. – MARKS, P.L. – SPRUGEL, D.G. (1978): Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology, Vol. 66: 599-614.

PAPER, R. (1999): Influence of thinning and tree diameter class on the development of basic density and annual ring width in Picea abies stands. Scandinavian Journal of Forest Research, 14:27-37.

PINKARD, E. A. – NEILSEN, W.A. (2003): Crown and stand characteristics of Eucaliptus nitens in response to initial spacing: implications for thinning. Forest Ecology and Management, 172: 215-337.

POTHIER, D. (2002): Twenty-year results of pre commercial thinning in a balsam fir stand. Forest Ecology and Management, 168: 177-186.

RÉDEI, K. (1983): Akácosok fatermése. [Yield of black locust stands.] Erdészeti Kutatások, Vol. 77: 195-203. (in Hungarian).

RÉDEI, K.(1992): Növedékvizsgálatok akácállományokban. [Increment investigations in black locust stands] Erdészeti Lapok, CXXVII. 3: 72-73. (in Hungarian).

RÉDEI, K. (1995): A növedékfokozó gyérítések hatása az akácosok hozamára és értékére. [The effect of increment thinning on the yield and timber value of black locust] Erdészeti Kutatások, Vol. 85: 79-90. (in Hungarian).

RÉDEI, K. (2002): Management of black locust (Robinia pseudoacacia 2) stands in Hungary. Journal of Forestry Research, 13: 260-264.

RIO, D. – CALAMA, M. – CANELLAS, I. (2008): Thinning intensity and growth response in SW - European Scots pine stands. Annals of Forest Science, 65: 308 (Article Number).

SILVANO, A. – VINCENZO, B. (1997): Thinning trials based on the choice of final crop trees for artificial stands of calabrian pine. Annali dell' Istituto Sperimentale per la Selvicoltura, 28: 9-37.

SOPP, L. (1974): Fatömegtáblák. [Volume tables.] Mezőgazdasági Kiadó, Budapest. (in Hungarian).

Acta Silv. Lign. Hung., Vol. 5 (2009) 75-82

Mass Mortality of Beech (*Fagus sylvatica* L.) in South-West Hungary

Ferenc LAKATOS[*] – Miklós MOLNÁR

Institute of Sylviculture and Forest Protection, Faculty of Forestry, University of West Hungary, Sopron, Hungary

Abstract – The mass mortality of beech (*Fagus sylvatica* L.) in Hungary, which started in 2003 and went on through 2004, is the result of a typical damage chain. Mortality appeared first of all in beech forests close or outside of its native distribution area. The most significant reason was the drought period from 2000 to 2004, which weakened the trees, and favoured the development of different pests and pathogens. Characteristic symptoms were frequent at stand margins and in stands thinned for regeneration. The direct causes of the mortality were insects, the green jewel beetle (*Agrilus viridis*) and the beech bark beetle (*Taphrorychus bicolor*) as well as the fungus species *Biscogniauxia nummularia*. With the improvement of weather conditions a continuous recovery of the stands has been observed since 2005.

Fagus sylvatica* / *Agrilus viridis* /*Taphrorychus bicolor* / *Biscogniauxia nummularia

Kivonat – A bükk (*Fagus sylvatica* L.) tömeges pusztulása Délnyugat-Magyarországon. A zalai bükkösökben 2003-ban kezdődött, majd 2004 során jelentős mértékben jelentkező pusztulás egy tipikus kárláncolat eredménye. A megjelenő tünetek jellegzetesek, különösen a napsütötte állományszegélyeken és a bontóvágással érintett faállományokban gyakoriak.

A pusztulás elsősorban az extrazonális bükkösökben jelent meg. A legfőbb kiváltó ok a 2000-ben kezdődött, öt évig tartó aszályos időszak, melynek következtében az állományok legyengültek, különböző kártevő és kórokozó fajok elszaporodtak. A pusztulás közvetlen kiváltó tényezői a zöld karcsúdíszbogár (*Agrilus viridis*) és a bóbitás bükkszú (*Taphrorychus bicolor*) rovarfajok valamint a *Biscogniauxia nummularia* gombafaj voltak.

Az időjárási tényezők javulásával 2005-óta az erdőállományok egészségi állapotának fokozatos javulása figyelhető meg.

Fagus sylvatica* / *Agrilus viridis* /*Taphrorychus bicolor* / *Biscogniauxia nummularia

1 INTRODUCTION

Starting from 2003 mass mortality of beech was observed in several parts of Hungary. Health conditions of beech stands were objectives of several investigations in Hungary (Tuzson 1931, Szántó 1948, Szontagh 1989, Leskó 1993, Tóth et al. 1995, Molnár – Lakatos 2007). However, similar symptoms were recorded only once in the eastern part of the Carpatian basin (Máramaros county) in the 1880s. A short description of the event was published at that

---

[*] Corresponding author: flakatos@emk.nyme.hu; H-9401 Sopron, POB 132, Hungary

time, however no detailed investigation was made (Piso, 1886). Similar decay of beech has been recently reported from the southern part Germany too (Delb 2005).

The recent mortality appeared with different intensity in beech forests of several parts of Hungary. Symptoms were first observed in Balaton highlands and Bakony mountains, but the most serious damage occurred in the south-western part of Hungary (Zala county). In this area approximately 120,000 cubic meter of damaged or dead timber had to be cut between 2003-2006, which caused approximately 400 million HUF (1.6M EUR) direct loss (Góber 2005) for the forest owner.

The effect of change in the climatic conditions on forest stands have been studied intensively in the recent years (for review see Strelcova et al (2009) and Mátyás (2006)). The aim of our investigation in the present study was to determine the role and importance of the biotic factors, like insects and fungi in these processes.

2 MATERIALS AND METHODS

Field studies were carried out in order to assess the correlations between the climatic characteristics of the affected area and the damages & symptoms. The investigation sites were at the eastern border of Zalaegerszeg, where the heaviest mortality was observed.

2.1 Site characteristics/features

The elevation of the study sites were between 196-302 m above see level. Due to the hilly terrain, shallow and deep tilths alternate with each other in short distances. Soils are of medium and at some places very good fertility.

The macroclimate of the area is typical for the hornbeam-sessile oak zone (*Querco petreae-Carpinetum*). Owing to the prevailing wind direction and the features of the terrain, this area is characterized by cooler and rainier conditions than expected based on the general climatic data.

2.2 Field observations

We established a network of 92 study plots with different terrain and age (60-122 years) in mixed forest subcompartments on an area of 102.6 hectares. Each plot was marked by a sample point. We evaluated the condition of the five beech-trunks closest to each point (altogether 460 individuals) every year at the end of the vegetation period from 2003 to 2007. During the experiment, besides the characteristic symptoms of the damage and disease-causing agents like insect and pathogens, we also evaluated the crown conditions.

The following categories were used:

1. The crown of the tree died, epicormic branches may be seen.
2. Several side-branches are infected or died.
3. One side-branch is infected or died.
4. Branch-ends, small branches died, but side-branches are healthy.
5. Totally healthy specimen.

The following criteria were considered for attack and/or infection: blackish chromatism, the existence or lack of bark-loss and the possible drying of the foliage. Other symptoms, like bark beetle attack or early stage fungal infections were not eye-catching at the time of the investigation. Due to the dieback of the trees and the continuous sanitary cuttings, the number of the investigated trunks decreased from year to year.

Xylo- and phloeophagous insects were assessed by felled trees in 2004 and 2006-2007 respectively. We selected trees in the health categories 4 and 3 during autumn and cut them next

February. Altogether 13 trees were cut (3-5-5 in the years 2004, 2006 and 2007 respectively). A total number of 37 cylinders of 35-40 cm length (from the stump, the trunk and the crown each, except two trees, where the crown was missing at the time of cutting). Cylinders were taken after cutting into our lab for insect rearing. Samples from one tree (stump, trunk and crown) were placed into one eclector, and this – unfortunately – does not allow any further differentiation of the tree parts. Hatched insects were collected every week for determination.

Four discs from trunks attacked by insects were cut in October 2005, and were put into a wet incubator to determine the fungi in the early phase of the infection.

We used the last past 46 years' temperature and precipitation data of a meteorological station closest to the examined area. (Zalaegerszeg-Andráshida; courtesy of P. Vig). We analysed the longest available data-set in order to receive the most complete overview about the changes of the climatic factors in the area.

3 RESULTS, STATEMENTS

3.1 Health conditions

The first symptoms of insect attack and fungal infection appeared in 2003 in forest subcompartments relatively far from one another: in old understocked stands on hilltops and in open forest edges exposed to the south. In the following year the mortality increased rapidly and many trees died. We did not find correlation between the social status of the specimens, the exposure of the stands, the site parameters and the health condition of the trees. The mortality was mostly initiated by insolation to the tree trunks.

From the year 2005 fresh symptoms have been observed only on specimens with dying or broken crowns. The spread of the mortality has stopped. Side-branches, which were previously infected, have broken down from the trunks. This was the main reason, why the canopy closure of the stands was still incomplete. A number of trees, having symptoms earlier, have regenerated and developed new crown. Only those side-branches and trunks have broken down where bark became blackish during the years of the decay.

The number of trees in the critical health categories 1-2-3 decreased continuously (*Figure 1*). This shows the loss of side-branches with symptoms as well. A tree classified previously into categories 2 or 3 got into categories 3 or 4 after the loss of certain infected side-branches.

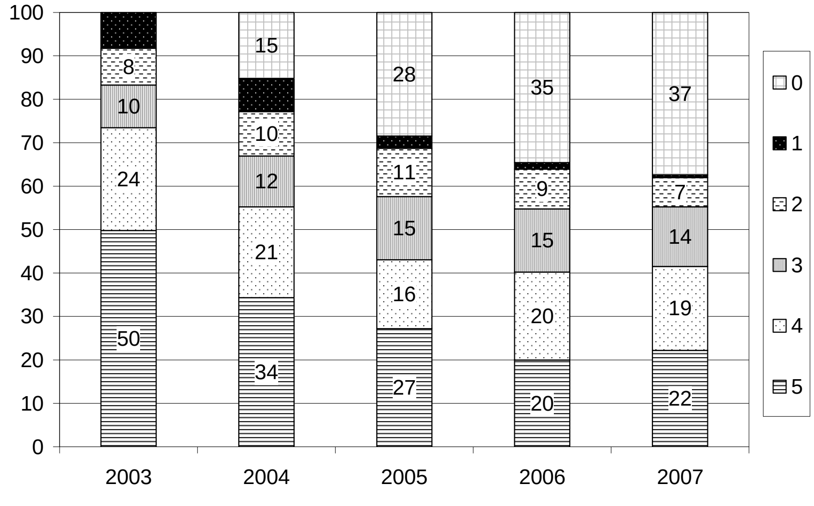


Figure 1. The change of health condition between 2003-2007 (%)
(0: cut/disappeared, 1: dead crown, 2: several dead side-branches,
3: one dead side-branch, 4: dead small branches or branch-ends, 5: healthy)

3.2 Insects and pathogens

Table 1. Insect species emerged from the samples collected in 2004-2007

Family	Species	Number of insect individuals 2004 N of logs: 21	 2006 N of logs: 8	 2007 N of logs: 8
Staphylinidae	*Staphylinidae*	12	1	
Buprestidae	*Agrilus viridis*	73	3	13
Lymexylidae	*Hylecoetus flabellicornis*		50	
Lymexylidae	*Lymexylon navale*		1	
Cleridae	*Thanasimus formicarius*	3		1
Cucujidae	*Monotoma* sp.	8		
Cucujidae	*Laemophloeus* sp.	6		
Cucujidae	*Laemophloeus testaceus*	5	1	1
Cucujidae	*Silvanus unidentatus*	2	1	2
Bostrichidae	*Lichenophanes varius*	4	2	11
Anobiidae	*Ptilinus pectinicornis*			14
Tenebrionidae	*Tenebrionidae* sp.	49		1
Mycetophagidae	*Litargus connexus*	1		3
Colydiidae	*Cerylon* sp.	434	6	
Cerambycidae	*Cerambyx scopolii*		1	
Cerambycidae	*Xylotrechus antilope*			1
Scolytidae	*Crypturgus* sp.	74	186	26
Scolytidae	*Taphrorychus bicolor*	34	1136	707

Altogether 2,873 individuals of 18 beetle species emerged from the collected wood samples. From every collected trap tree sample we were able to rear the specimens of *Agrilus viridis* and *Taphrorychus bicolor*. However, their ratio has changed during the years. In the intensive dieback phase (2004) *A. viridis*, but in the recovery (2006-07) phase *T. bicolor* prevailed. This might be connected with the different health status of the cut trees in the different years. During the second period the number of emerging insect species hatching from dead or dying trees has increased (*Table 1*). Most of them are connected to dead, discoloured wood (e.g. *Hylecoetus flabellicornis*), or to insects (*Thanasimus formicarius*) and fungi (*Litargus connexus*) living on this wood material. Some of them are even considered as a rare species to Hungary (e.g. *Lichenophanes varius*). We have found insect galleries in the bark usually just around the trunk part with fungal attack. In the bark with healthy xylem we could detect only a few insect galleries. Only the two beetle species *A. viridis*, and *T. bicolor* can be considered as important in the sense of forest protection. While *A. viridis* seems to be able to attack healthy trees and cause tree death, *T. bicolor* attacks felled logs, fallen branches, stressed trees and in some cases healthy looking (but very probably already stressed) trees. Even the pupal chamber of *A. viridis* was different in the different years. While during the intensive mortality phase L-type (one hole) pupation chamber was typical, during the recovery phase the U-type (two holes) pupation chambers.

Fungal species involved in the process couldn’t be identified from the sample disks, therefore we did not repeat this examination on the recovering stand. The fungus causing characteristic blackish chromatism on side-branches, was identified as *Biscogniauxia nummularia* (Bull) Kuntze (earlier name: *Hypoxylon nummularium* (Bulliard ex Fries)).

3.3 Climate conditions

The macroclimate of the area is typical for the hornbeam-sessile oak zone (*Querco petreae-Carpinetum*) (*Figure 2*). The values of the Pálfai drought index (*Figure 3*) show, that the mass mortality have been initiated by an unusually heavy and long drought period from 2001 to 2003. Especially the value of 2003 (6.71) is an extreme. The drought period lasted for five years (*Figure 4-7*). Even the average precipitation of the years 2005 and 2006 yet fell behind the average of the previous decades (1961-2007). 2007 showed an average precipitation again (*Table 2*).

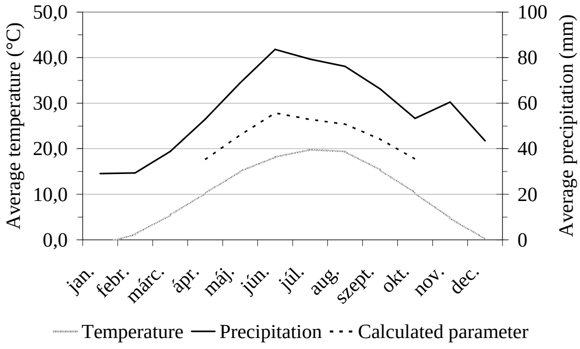


Figure 2. Walter climate diagram of the investigated area (Zalaegerszeg, 1961-2007)

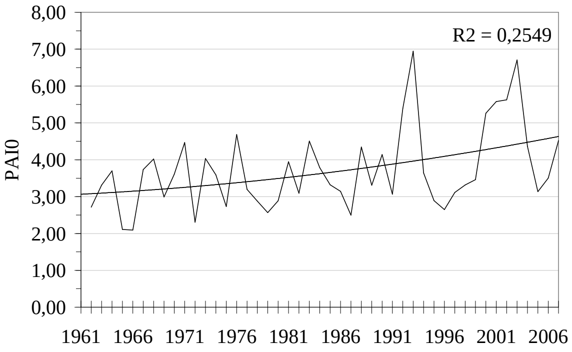


Figure 3. Pálfai drought index and trend for the investigated area (Zalaegerszeg, 1961-2007)

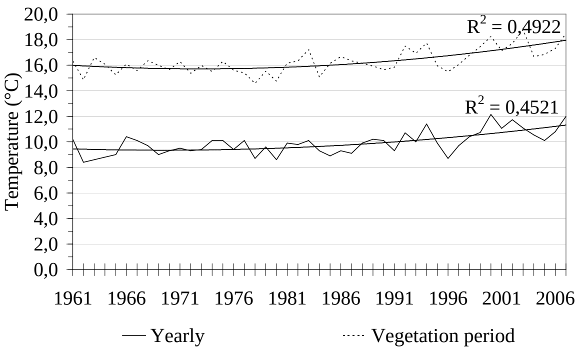


Figure 4. Average temperatures (annual and vegetation period; Zalaegerszeg, 1961-2007)

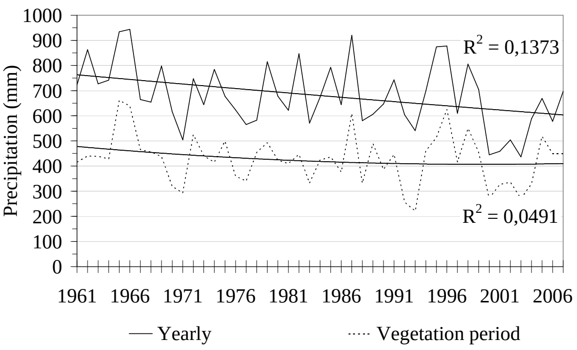


Figure 5. Precipitation (annual and vegetation period; Zalaegerszeg, 1961-2007)

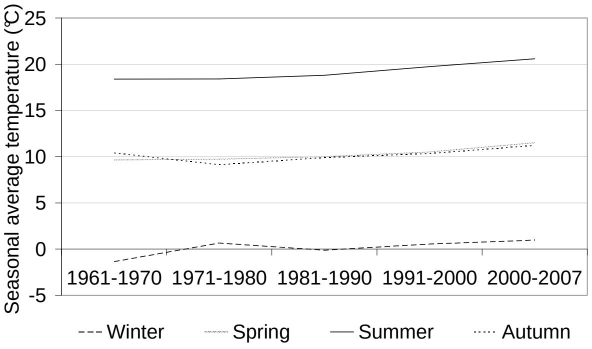


Figure 6. Seasonal average temperature (Zalaegerszeg, 1961-2007))

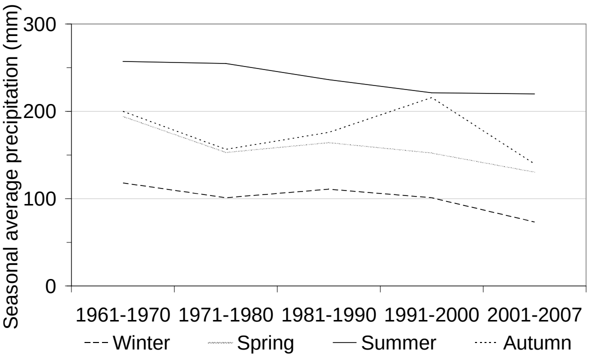


Figure 7. Seasonal precipitation (Zalaegerszeg, 1961-2007)

Table 2. Amount of precipitation and average temperature, and values of the drought index between 1961 and 2007 (Meteorological station, Zalaegerszeg; courtesy of P. Vig)

	Amount of precipitation (mm)			Average temperature (C°)			Pálfai drought index
	Annual	Apr - Sep	Oct - Mar	Annual	Apr - Sep	Oct - Mar	
2000							5,26
2001	459	327	132	11,1	17,1	5,0	5,58
2002	504	336	168	11,7	17,7	5,8	5,63
2003	436	270	166	11,1	18,8	3,4	6,71
2004	588	329	259	10,5	16,7	4,4	4,36
2005	669	518	151	10,1	16,8	3,4	3,13
2006	578	449	129	10,8	17,3	4,2	3,50
2007	697	449	248	12,0	18,5	5,5	4,52
1961-2007	681	427	254	9,9	16,3	3,5	3,71

4 CONCLUSIONS

During the last 50 years there have been unfavourable changes in the weather conditions for the beech forests both in Europe (Jump et al. 2006) and in Hungary (Mátyás et al. 2007). During this period the temperature was increasing while the amount of precipitation was decreasing. Also its dispersion was changing in the unfavourable direction: the relatively abundant rainfall of late autumn can hardly compensate the lack of summer precipitation (Szalai – Mika 2007). To assume, the tendency is ongoing, the natural range of beech will be definitely reduced in Hungary (Berki et al. 2007). The weakened trees are ideal places for mass reproduction of different pests and heavy infestation of pathogens (Csóka et al. 2007, Lakatos – Molnár, 2008).

The analysis of the climatic data showed that there had been dry years earlier, too (*Figure 3*), however without remarkable damage symptoms. This unfavourable periods, however, lasted only for short period, followed by more favourable (humid) years. Although the drought, which started in 2000 and lasted for five years, gave pests and pathogenes the chance to attack the weakened trees. Two beetle species, *A. viridis* and *T. bicolor*, were the major biotic factors. *Agrilus viridis* can be considered as the main pest species in this case, while *T. bicolor* attacks only weakened trees even if they look rather healthy based on our categories (e.g. 4 and 5). The population size of the two insects differs strongly in the intensive and the recovery phase of the dieback. *A. viridis* prefers the still living phloem with sap circulation disorders, mainly in higher altitude of the trunk. Imagines developed in a drying trunk part often do not have the capacity to create exit holes, and they die in the pupation chamber or in the exit hole. Bark beetle adults could be found under the bark of stumps, assortments and side-branches on the ground as well. The importance of *T. bicolor* in the mortality of beech was highlighted in two recent publications from Austria (Steyrer 2008) and Bavaria (Muck 2008). Delb (2005) reported the same insect species involved in the beech mortality in Baden-Württemberg. Other xylo- and phloeophagous species emerged from the trees have no significance in the damage chain. Their presence can be explained by the large amount of dying and dry trees suitable for their development.

We presume that there is a strong relation between insects and fungal damage. Larval galleries and exit holes were found above trunk parts with fungal infection. At the present stage it is hard to give an unambiguous explanation and description of the process. It is very likely, that entrance holes of the different insect species offer a unique opportunity for the fungal attack. However, the phloem, having weakened by the fungal attack, provides optimum conditions for the insect development too. On trunk parts without fungal attack insect galleries and exit holes are rare and the mortality of the larvae is higher too. We can assure, that there is a strong correlation between insects and pathogens, nevertheless their exact role needs further explanation.

The role of the pathogene fungus species, *Biscogniauxia nummularia* is not completely clarified either, however its presence or absence is crucial in the damage chain. The fruiting bodies appear in the first year of the decay. Later the tree loses almost all of the infected branches. If the fruiting bodies appear also on the trunk, the entire crown will die. None of the other symptoms can give an unambiguous forecast about the process of the decline, since spontaneous regeneration was often observed. In the recovery phase the beech stands are losing side-branches infected by *Biscogniauxia nummularia*.

Acknowledgements: Our work was supported by the research grant OTKA K-68618 and by the Zalaerdő Zrt. We appreciate the courtesy of Péter Vig, who provided the meteorological data. We thank Ilona Szabó for the identification of *Biscogniauxia nummularia* in the area.

REFERENCES

BERKI, I. – MÓRICZ, N. – RASZTOVITS, E. – VIG, P. (2007): A bükk szárazság tolerancia határának meghatározása. [Determination of the drought tolerance limit of beech.] In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. Nyugat-Magyarországi Egyetem, Sopron. 213-228. (in Hungarian)

CSÓKA, GY. – KOLTAY, A. – HIRKA, A. – JANIK, G. (2007): Az aszályosság hatása kocsánytalan tölgyeseink és bükköseink egészségi állapotára. [Influence of drought on health of sessile oak and beech stand in Hungary.] In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. Nyugat-Magyarországi Egyetem, Sopron. 229-240. (in Hungarian)

DELB, H. (2005): Rindenbrüter an Buchen nach der trocken-heißen Witterung im Sommer 2003. In: Dujesiefken, D. – Kockerbeck, P. (eds.): Jahrbuch der Baumpflege 2005. Thalacker Verlag, Braunschweig. 203-207.

GÓBER, Z. (2005): A Zalaerdő Rt. kezelésében lévő területeken 2004-ben végbement erdőpusztulás értékelése. [Evaluation of forest dieback on the territory of Zalaerdő in 2004.] Erdészeti Lapok 140 (5): 156-159. (in Hungarian)

JUMP, A.S. – HUNT, J.M. – PENUELAS, J. (2006): Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Global Change Biology 12. (11): 2163-2174.

LAKATOS, F. – MOLNÁR, M. (2008): Mass dieback of beech (*Fagus sylvatica*) in Zala County. In: Proceedings of the Workshop „IUFRO Working Party 7.03.10“. Gmunden/Austria. Sept 2006. 142-149.

LESKÓ, K. (1993): A mecseki és Zselici bükkösök egészségi állapota. [Health conditions of beech stands in Mecsek and Zselic] In: WoodTech Erdészeti Szakmai Konferencia. 1993.05.05-1993.05.07. EFE, Sopron, 59-63. (in Hungarian)

MUCK, M. (2008): Verstärktes Auftreten des Kleinen Buchenborkenkäfers in Bayern – Aktuelle Erkenntnisse zur Schwärmaktivität und zum Befallsverhalten in Abhängigkeit von Lufttemperatur und Holzfeuchte. Forstschutz Aktuell 45. (12): 6-8.

MOLNÁR, M. – LAKATOS, F. (2007): Bükkpusztulás Zala megyében – klímaváltozás? [Beech decline in county Zala: triggered by climate change?] In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. Nyugat-Magyarországi Egyetem, Sopron. 257-267. (in Hungarian with English summary)

MÁTYÁS, CS. (2006): Migratory, genetic and phenetic response potential of forest tree populations facing climate change. Acta Silvatica et Lignaria Hungarica 2: 33-46.

MÁTYÁS, CS. – NAGY, L. – UJVÁRINÉ, J.É. (2007): Klimatikus stressz és a fafajok genetikai válaszreakciója az elterjedés szárazsági határán: elemzés és előrejelzés. [Climatic stress and the genetically determined response of tree species at the aridity limit of distribution: analysis and predictions.] In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. Nyugat-Magyarországi Egyetem, Sopron. 241-256. (in Hungarian with English summary)

PISO, K. (1886): A Máramaros megyében 1885. évben előfordult káros rovarokról. [Forest pests in Máramaros County in 1885.] Erdészeti Lapok 25 (11): 795-798. (in Hungarian)

STEYRER, G. (2008): Buchenborkenkäfer: Projekt im Biosphärenpark Wienerwald. Forstschutz Aktuell 45. (12): 9-11.

STRELCOVÁ, K. – MATYAS, CS. – KLEIDON, A. – LAPIN, M. – MATEJKA, F. – BLAZENEC, M. – ŠKVARENINA, J. – HOLECY, J. (Eds.) (2009): Bioclimatology and Natural Hazards. Springer Verlag, 298 p.

SZALAI, S. – MIKA, J. (2007): A klímaváltozás és az időjárási anomáliák előrejelzése az erdőtakaró szempontjából fontos tényezőkre. [Analysis and prediction of climate change and weather anomaly parameters important for forest cover.] In: Mátyás, Cs. – Vig, P. (eds.): Erdő és Klíma V. Nyugat-Magyarországi Egyetem, Sopron. 133-144. (in Hungarian with English summary)

SZÁNTÓ, I. (1948): A bükkfa rákja mint éghajlati betegség. [The cancer of the beech as a climatic illness.] Erdészeti Kísérletek 48. (1-2): 10-31. (in Hungarian)

SZONTAGH, P. (1989): Rovarok okozta károk bükköseinkben. [Insect damages in beech stands.] Állattani Közlemények 75. (1-4): 107-112. (in Hungarian)

TÓTH, J. – PAGONY, H. – SZONTAGH, P. (1995): A magyarországi bükkösök egészségi állapota. [Health conditions of Hungarian beech stands.] In: Az erdők egészségi állapotának változása. MTA Erdészeti Bizottság, Budapest, 77–81. (in Hungarian)

TUZSON, J. (1931): A zalamegyei bükkösök pusztulása. [Dieback of beech in Zala county.] Erdészeti Kísérletek 33. (3-4): 127-137. (in Hungarian)

Acta Silv. Lign. Hung., Vol. 5 (2009) 83-107

Population Trend, Phenology and Dispersion of Common Waterfowl Species in Hungary Based on aTen Year Long Time Series of the Hungarian Waterfowl Monitoring

Sándor FARAGÓ[*] – Lívia GOSZTONYI

Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry,
University of West Hungary, Sopron, Hungary

Abstract – The HUNGARIAN WATERFOWL MONITORING (HWM) takes place at 48 observation units. The current study shows the 25 common waterfowl species, their trend, phenology, and dispersion in Hungary using the data of a ten-year period between the 1996/1997 and 2005/2006 seasons. The six commonest species were: *Anas platyrhynchos, Anser albifrons, Anser fabalis, Anser anser, Anas crecca* and *Fulica atra*. During the ten-year period there were 8 species with about 1000 individuals or less *(Anser erythropus, Mergus albellus, Tachybaptus ruficollis, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Cygnus olor, Mergus merganser)*. We report a heavy increase of *Aythya nyroca, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Anas clypeata, Cygnus olor, Anser albifrons, Podiceps cristatus, Anser anser, Anas strepera* and a slight increase of *Phalacrocorax pygmeus* and *Tachybaptus ruficollis.* A strong decrease can be seen in *Anser erythropus, Aythya fuligula, Anser fabalis, Anas querquedula, Aythya ferina, Anas crecca, Mergus albellus, Anas penelope, Mergus merganser,* a slight decrease in the case of *Anas platyrhynchos* and *Bucephala clangula.* The 25 species were put into six different groups based on their types of phenology: late summer migrating species, species migrating dominantly in autumn, over wintering species, species passing through Hungary dominantly in spring, spring and late summer migrants, species with a stable population. Eco-geographical differences between Transdanubia and the Great Hungarian Plain explain the differences in the dispersion of species: distribution dominance in Transdanubia, dispersion dominance in the Great Hungarian Plain, even distribution. Our conclusions confirmed some of the earlier results, but in some cases we made conclusions different from the earlier suggestions. It is obvious that changing environmental conditions affect the changes in population parameters of waterfowl species.

Hungarian Waterfowl Monitoring (HWM) / common waterfowl species / population trend / penology / dispersion / Hungary

Kivonat – Gyakoribb vízivadfajok állománytrendje, fenológiája és diszperziója Magyarországon a Magyar Vízivad Monitoring 10 éves adatsorainak tükrében. A MAGYAR VÍZIVAD MONITORING megfigyelései 48 megfigyelési egységben folynak. Jelen munka az 1996/1997-2005/2006 között vizsgált 10 év adatai alapján mutatja be 25 rendszeresen előforduló vízivad faj állománydinamikáját, fenológiáját és diszperzióját Magyarországon. A hat leggyakoribb faj az *Anas platyrhynchos, Anser albifrons, Anser fabalis, Anser anser, Anas crecca* és *Fulica atra* volt. 10 év alatt 1000 példány közeli,

---

[*] Corresponding author: farago@emk.nyme.hu; H-9401 Sopron, POB 132, Hungary

vagy az alatti abszolút maximuma 8 fajnak volt (*Anser erythropus, Mergus albellus, Tachybaptus ruficollis, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Cygnus olor, Mergus merganser*). Vízivad állományaink nagy részénél sikerült állománynövekedést kimutatni; erőteljesen növekedett: *Aythya nyroca, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Anas clypeata, Cygnus olor, Anser albifrons, Podiceps cristatus, Anser anser, Anas strepera*. Enyhén gyarapodott: *Phalacrocorax carbo* és *Tachybaptus ruficollis*. Aggasztó jelenség az *Anser erythropus, Aythya fuligula, Anser fabalis, Anas querquedula, Aythya ferina, Anas crecca, Mergus albellus, Anas penelope, Mergus merganser* erőteljes, az *Anas platyrhynchos* és a *Bucephala clangula* enyhe mértékű állománycsökkenése. A fenológiai jellemzők alapján rendezve, a vizsgált 25 fajt hat csoportba sorolhattuk, amelyek az alábbiak: nyárvégi vonuló fajok, dominánsan ősszel vonuló fajok, áttelelő fajok, dominánsan tavasszal vonuló fajok, nyárvégi és tavaszi vonulók, állandó állományú fajok. A diszperziót tekintve több faj előfordulását befolyásolják a Dunántúl és az Alföld közötti ökogeográfiai különbségek, így létezik: dunántúli diszperziós dominancia, alföldi diszperziós dominancia és egyenletes diszperzió. A korábbi megfigyelések alapján született ismereteinket kutatásaink részben megerősítették, ám sok esetben azoktól eltérő megállapításokat tehettünk. A változó környezeti állapotváltozásokat idézhet elő a vonuló vízivadfajok állományjellemzőiben.

Magyar Vízivad Monitoring (MVvM) / gyakoribb vízivadfajok / állománytrend / fenológia / diszperzió / Magyarország

1 INTRODUCTION

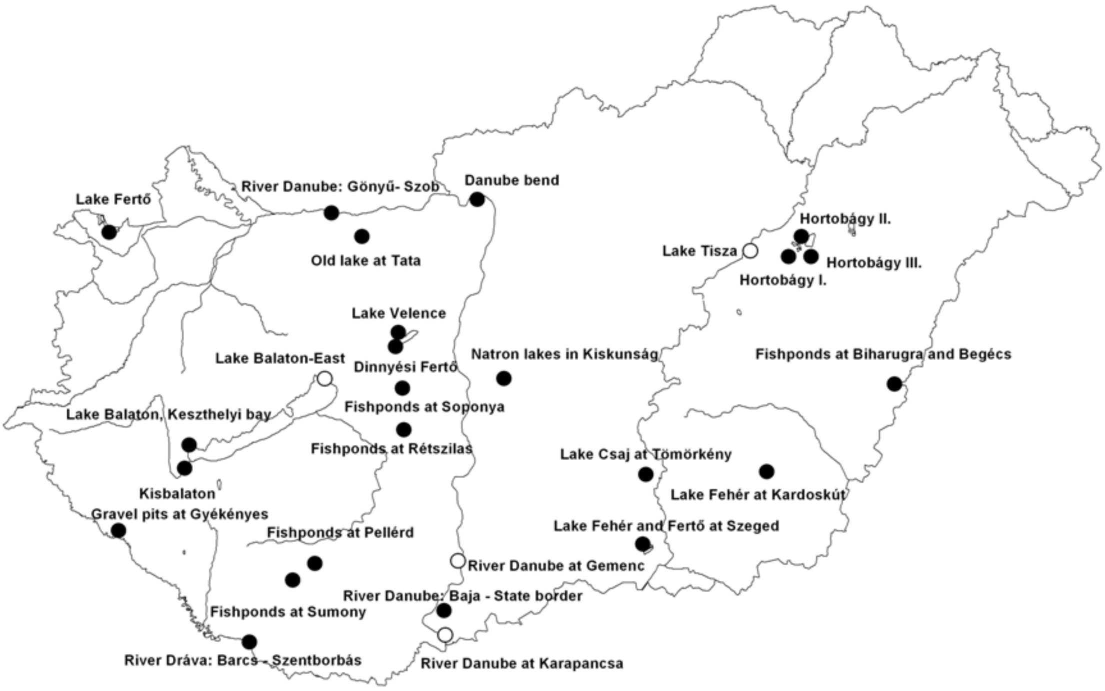
The Hungarian waterfowl information system contributes to fulfilling the requirements of AEWA and, more widely, it serves the purposes of nature protection and sustainable use. It provides necessary information for nature conservation and game management, taking into consideration the unity of the natural systems. An observational sub-system of the Waterfowl Database focuses on the size of the waterfowl population, their current dispersion and the structure of the waterfowl communities. All these refer to the on-going Hungarian Waterfowl Monitoring (Faragó 1998a). The operation of the monitoring provides information on the trend of waterfowl species within individual years and over a period of years, referring to certain sites, regions, and the entire country. It also helps us define the habitat use and selection of certain species within a year and over a period of several years.

2 MATERIAL AND METHODS

The observations of the Hungarian Waterfowl Monitoring (HWM) take place in 23 districts, which are divided into 2 to 6 sub-districts each. It means that HWM takes place in 48 observation units (*Table 1, Map 1*). The censuses were carried out between October, 1996 and March, 1997, in connection with an international census day in each month. Since the 1997/1998 seasons, a nine-month-long period between August and April was used. The observations expanded to the following tax: all species of Anseriformes, Gaviiformes, Podicipediformes, and Pelecaniformes; Great White Egret (*Ardea alba*), Grey Heron (*Ardea cinerea*), Eurasian Coot (*Fulica atra*), Eurasian Crane (*Grus grus*) and White-tailed Eagle (*Haliaaetus albicilla*) totaling **63** species. We have first chosen natatorial birds from this list, but we took into consideration the information needs of fish management, and the Authority for Nature Conservation. That is the reason for including the Grey Heron, the Great White Egret, the Eurasian Crane and the White-tailed Eagle in the survey.

Table 1. Size and geographic coordinates of the observation units of the Hungarian Waterfowl Monitoring (HWM)

	Site	Area ha	Degree of latitude		Degree of longitude	
01	Lake Fertő	1,918	47.6639	47.7389	16.6869	16.8484
02	Danube between Gyönyű and Szob	4,842	47.7279	47.8229	17.8240	18.8414
03	Old Lake at Tata	230	47.6303	47.6499	18.3187	18.3405
04	Lake Velence	2,600	47.1776	47.2383	18.5322	18.6620
05	Dinnyési Fertő	545	47.1378	47.1767	18.5230	18.5639
06	Fishponds at Soponya	520	46.9855	47.0715	18.4197	18.4931
07	Fishponds at Rétszilas	840	46.7950	46.8687	18.5556	18.6009
08	Lake Balaton. Keszthelyi-bay	2,930	46.7062	46.7644	17.2434	17.3177
09.01	Kis-Balaton I.	1,630	46.5899	46.6749	17.1189	17.1738
09.02	Kis-Balaton II.	1,820	46.6127	46.6923	17.1761	17.2379
10	River Dráva between Barcs and Szentborbás	465	45.8623	45.9515	17.4280	17.6501
11	Gravel pits at Gyékényes	170	46.2377	46.2513	16.9718	17.0014
12	Fishponds at Sumony	207	45.9573	45.9745	17.8736	17.8974
13	Fishponds at Pellérd	116	46.0436	46.0525	18.1358	18.1630
14	Danube bend	2,977	47.8219	47.5608	18.8483	19.1358
15	Danube between Baja and state border	2,554	45.9170	46.1875	18.6803	18.9278
16.01	Natron lake Kelemen-szék at Fülöpszállás	430	46.7832	46.8047	19.1678	19.2022
16.02	Natron lake Zab-szék at Szabadszállás	370	46.8126	46.8466	19.1568	19.1813
17.01	Jusztus-Feketerét (marsh)	690	47.5460	47.5777	20.8751	20.9164
17.02	Fishponds at Hortobágy	1,700	47.6040	47.6631	21.0501	21.1140
17.03	Fishponds at Virágoskút	1,500	47.6516	47.7045	21.3235	21.3713
18.01	Fishpond Fényes	258	47.5716	47.5880	21.0019	21.0287
18.02	Fishponds at Csécs and Parajos	554	47.5382	47.5648	20.9984	21.0420
18.03	Fishponds Akadémia and Kungyörgy	248	47.5640	47.5913	21.0631	21.0957
18.04	Pentezug pusza and marshes	4,300	47.4849	47.5879	21.0536	21.1535
18.05	Zámi pusza and marshes	2,880	47.4767	47.5378	20.9843	21.0725
18.06	Borzas	1,600	47.4473	47.4900	21.0377	21.1075
18.07	Nagyiván and Kunmadaras puszta	1,350	47.4883	47.5376	20.9308	20.9944
18.08	Kunkápolnás marshes	4,000	47.4080	47.4959	20.9292	21.0118
19.01	Angyalháza and Szelencés	6,250	47.4403	47.5495	21.0885	21.2076
19.02	Fishponds at Borsós and Malomház	2,230	47.5392	47.5815	21.1336	21.2215
19.03	Borsós. Ökörföld. Görbehát	1,390	47.5395	47.5777	21.2078	21.2886
19.04	Magdolna. Nyírő-lapos. Nyári-járás	3,700	47.5521	47.6152	21.2143	21.3385
19.05	Álomzug. Köselyszeg	4,600	47.4571	47.5443	21.1650	21.2931
19.06	Fishpond at Elep	552	47.5289	47.5589	21.2654	21.2981
20	Lake Fehér at Kardoskút	100	46.4660	46.4762	20.6054	20.6482
21.01	Fishponds at Biharugra	773	46.9370	46.9723	21.6013	21.6423
21.02	Fishponds at Begécs	1,212	46.9074	46.9401	21.5252	21.5979
22	Lake Csaj at Tömörkény	860	46.6044	46.5581	20.0458	20.0950
23.01	Lake Fehér at Szeged	1,506	46.3033	46.3499	20.0666	20.1346
23.02	Szegedi Fertő	628	46.3177	46.3560	20.1367	20.1792
	Total	68,045				



Map 1. Observation units of the Hungarian Waterfowl Monitoring (HWM)

The current study presents information on the **following 25 common waterfowl species**, their trend, phenology, and dispersion in Hungary using the data of a **ten-year-long period between the 1996/1997 and 2005/2006** seasons (Faragó 1998b; 1998c; 1999a; 1999b; 2001a; 2001b; 2002a; Faragó – Gosztonyi, 2002; Faragó, 2002b; 2002c; Faragó – Gosztonyi, 2003a; 2003b; Faragó, 2005a; 2005b; 2006a; 2006b; 2007a; 2007b; 2007c; 2007d):

Mute Swan – *Cygnus olor* (Gmeliin 1789)
Bean Goose – *Anser fabalis* (Latham 1787)
White-fronted Goose – *Anser albifrons* (Scopoli 1769)
Lesser White-fronted Goose – *Anser erythropus* (Linnaeus 1758)
Greylag Goose – *Anser anser* (Linnaeus 1758)
Wigeon – *Anas penelope* Linnaeus 1758
Gadwall – *Anas strepera* Linnaeus 1758
Teal – *Anas crecca* Linnaeus 1758
Mallard – *Anas platyrhynchos* Linnaeus 1758
Pintail – *Anas acuta* Linnaeus 1758
Garganey – *Anas querquedula* Linnaeus 1758
Northern Shoveler – *Anas clypeata* Linnaeus 1758
Red-crested Pochard – *Netta rufina* (Pallas 1773)
Pochard – *Aythya ferina* (Linnaeus 1758)
Ferruginous Duck – *Aythya nyroca* (Güldenstädt 1770)
Tufted Duck – *Aythya fuligula* (Linnaeus 1758)
Common Goldeneye – *Bucephala clangula* (Linnaeus 1758)
Smew – *Mergus albellus* Linnaeus 1758
Goosander – *Mergus merganser* Linnaeus 1758
Little Grebe – *Tachybaptus ruficollis* (Pallas 1764)
Great Crested Grebe – *Podiceps cristatus* (Linnaeus 1758)
Black-necked Grebe – *Podiceps nigricollis* (C.L. Brehm 1831)
Great Cormorant – *Phalacrocorax carbo* (Linnaeus 1758)
Pygmy Cormorant – *Phalacrocorax pygmeus* (Pallas 1773)
Eurasian Coot – *Fulica atra* (Linnaeus 1758)

When investigating the species, we analyzed the following factors:

- Population trends (1) and trends in relation to the examined sites, regions and Hungary in the investigation period. In the current study we show the trends (*Figure 1*) defined on the basis of the annual national **season maximums** (*Table 2*). When qualifying trends, we named the population changes using the method applied by Tucker – Heath (1994). Trend indices characterized the measure of stability of population between 1970 and 1990 with a range of 20%. They showed small changes (increase-decrease) in the 20-49% range, and the larger ones with at least a 50% change. If the direction of the trend was not clear and the change of values exceeded 20%, they classified it as *fluctuating*. While Tucker and Heath (1994) used a twenty-year-long period we studied only a ten-year-long period. Therefore we used the following evaluation:

– Large decrease	at least 25%
– Small decrease	11-24%
– **Stable**	plus or minus 0-10%
– Small increase	11-24%
– Large increase	at least 25%
– **Fluctuating**	over 10% but with no clear trend

- Population trend (2) – **phenology**: minimum, average and maximum number of birds in each month (*Figure 2*).
- We are showing maps based on the **dispersion** in each month. In the current study we are showing the maps of peak seasons (month) of certain species (*Map 2*).

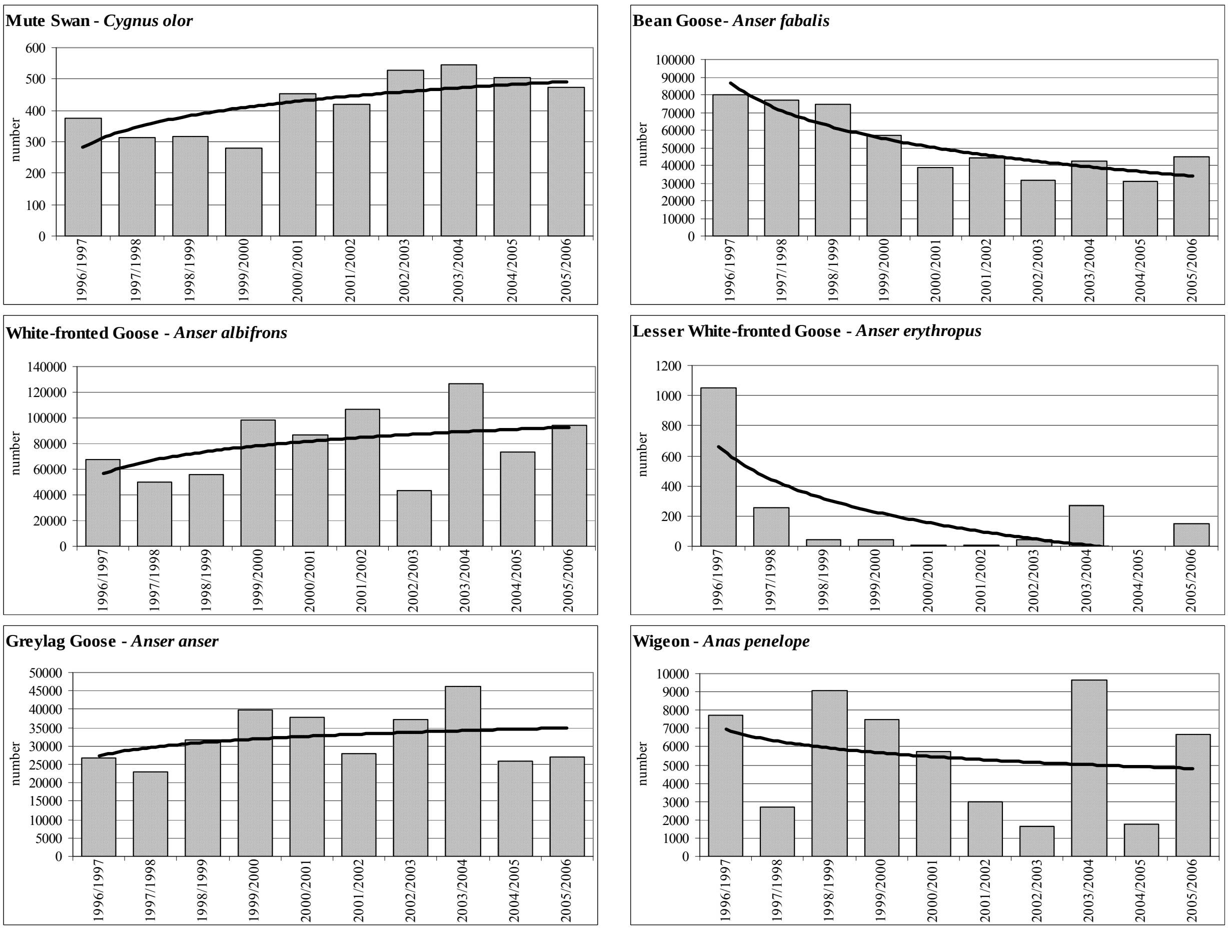


Figure 1: Dynamic and trend calculated on the basis of seasonal maxima in the case of the 25 most frequent waterfowl species

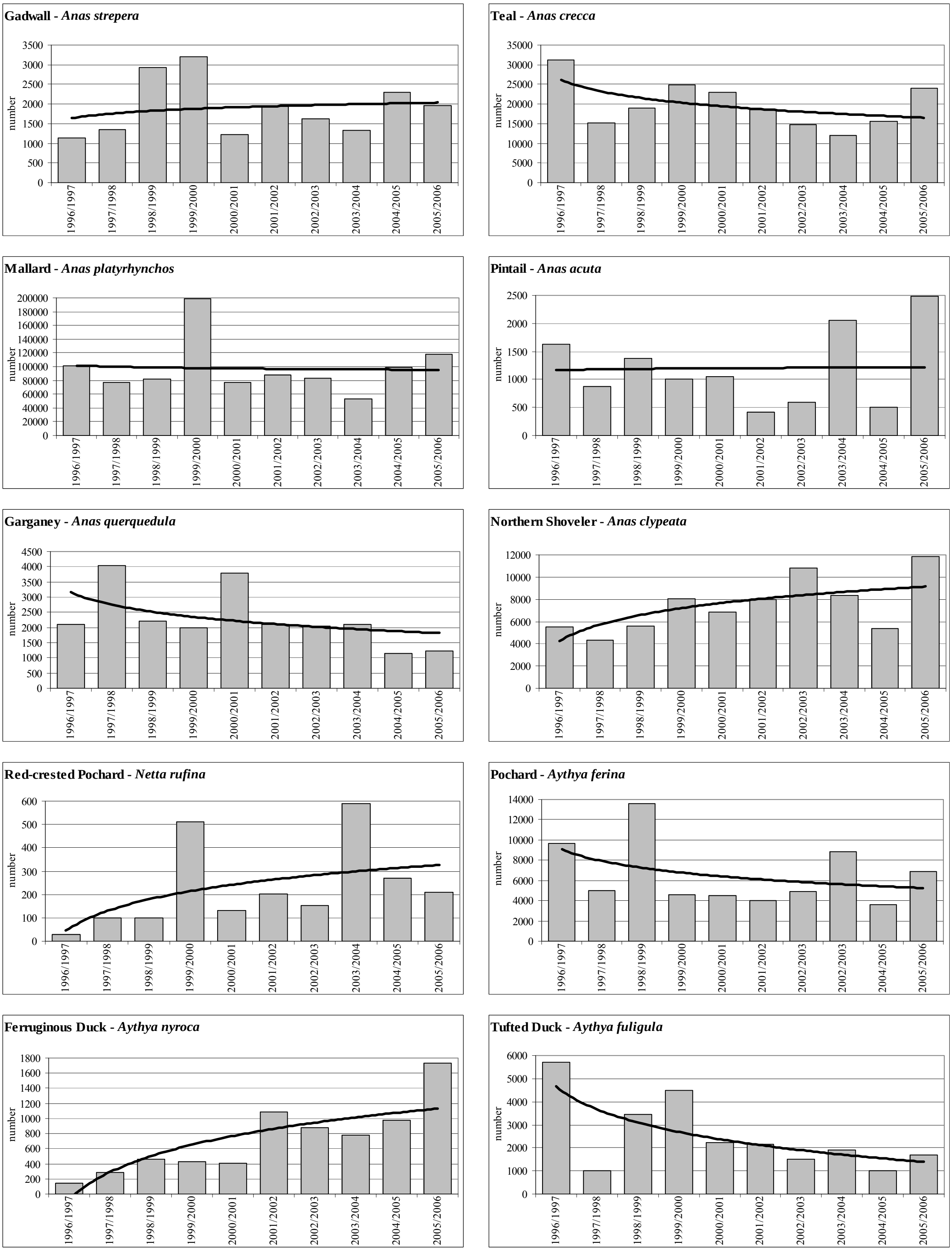


Figure 1 (cont.): Dynamic and trend calculated on the basis of seasonal maxima in the case of the 25 most frequent waterfowl species

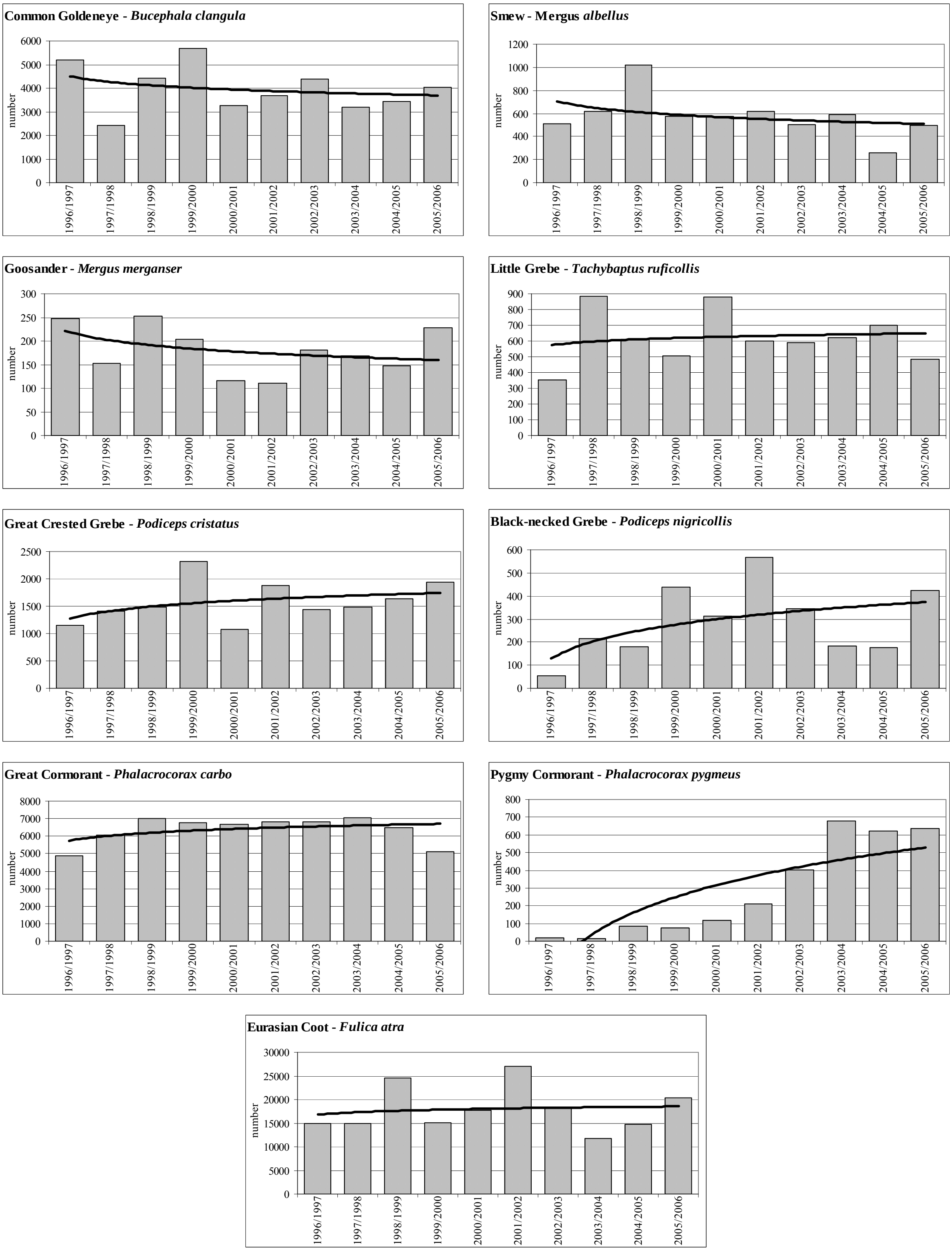


Figure 1 (cont.): Dynamic and trend calculated on the basis of seasonal maxima in the case of the 25 most frequent waterfowl species

Table 2. Seasonal peak values of the 25 most frequent waterfowl species, their 10-year maxima, average values, SD and trends

Species	1996/97	1997/98	1998/99	1999/2000	2000/01	2001/02	2002/03	20003/04	2004/05	2005/06	Max	Average	SD	Trend %
Cygnus olor	374	314	317	278	454	418	529	545	503	474	545	420.6	95.8	75
Anser fabalis	80,247	76,851	74,490	57,099	38,995	44,395	31,589	42,623	30,750	44,756	80,247	52,179.5	18,804.5	-61
Anser albifrons	67,521	49,792	56,048	98,132	86,289	107,011	43,170	126,811	73,668	94,219	126,811	80,266.1	26,934.4	73
Anser erythropus	1,054	256	40	40	6	6	40	270	3	150	1,054	186.5	321.3	-86
Anser anser	26,700	23,020	31,750	39,716	37,766	27,948	37,093	46,184	25,949	26,910	46,184	32,303.6	7,503.5	30
Anas penelope	7,733	2,718	9,063	7,474	5,752	3,003	1,638	9,620	1,743	6,651	9,620	5,539.5	3,035.5	-30
Anas strepera	1,133	1,351	2,934	3,209	1,214	1,945	1,620	1,323	2,299	1,961	3,209	1,898.9	724.1	30
Anas crecca	31,171	15,278	18,986	24,825	23,010	18,604	14,659	12,085	15,521	24,031	31,171	19,817.0	5,864.7	-39
Anas platyrhynchos	100,763	76,573	81,779	198,659	77,702	88,067	83,064	52,583	98,788	117,934	198,659	97,591.2	39,517.8	-14
Anas acuta	1,626	872	1,369	1,007	1,049	407	592	2,059	509	2,483	2,483	1,197.3	686.2	8
Anas querquedula	2,091	4,040	2,220	1,990	3,796	2,108	2,034	2,094	1,139	1,239	4,040	2,275.1	944.5	-44
Anas clypeata	5,524	4,321	5,559	8,086	6,832	7,967	10,831	8,316	5,381	11,829	11,829	7,464.6	2,444.2	113
Netta rufina	29	100	,101	513	130	202	151	589	271	209	589	229.5	183.2	540
Aythya ferina	9,633	4,966	13,580	4,617	4,479	4,020	4,950	8,832	3,642	6,889	13,580	6,560.8	3,200.7	-42
Aythya nyroca	141	,287	459	425	405	1,082	880	776	980	1,735	1,735	717	475.5	1000
Aythya fuligula	5,723	1,023	3,435	4,488	2,212	2,158	1,519	1,904	1,011	1,680	5,723	2,515.3	1,556.4	-68
Bucephala clangula	5,182	2,432	4,429	5,693	3,262	3,692	4,382	3,181	3,433	4,045	5,693	3,973.1	982.0	-18
Mergus albellus	512	616	1,020	578	573	619	506	587	257	497	1,020	576.5	187.9	-31
Mergus merganser	247	153	253	204	116	110	181	168	147	228	253	180.7	51.3	-29
Tachybaptus ruficollis	354	886	612	505	880	598	589	622	700	483	886	622.9	166.3	14
Podiceps cristatus	1,145	1,405	1,481	2,322	1,082	1,879	1,445	1,490	1,629	1,933	2,322	1,581.1	375.8	40
Podiceps nigricollis	54	217	179	437	313	567	345	182	175	424	567	289.3	155.7	192
Phalacrocorax carbo	4,876	6,038	7,029	6,791	6,681	6,794	6,826	7,052	6,497	5,119	7,052	6,370.3	780.6	19
Phalacrocorax pygmeus	18	16	83	75	115	211	402	680	623	638	680	286.1	273.1	940
Fulica atra	14,879	14,941	24,508	15,111	17,662	27,013	18,278	11,737	14,807	20,425	27,013	17,936.1	4,789.9	10

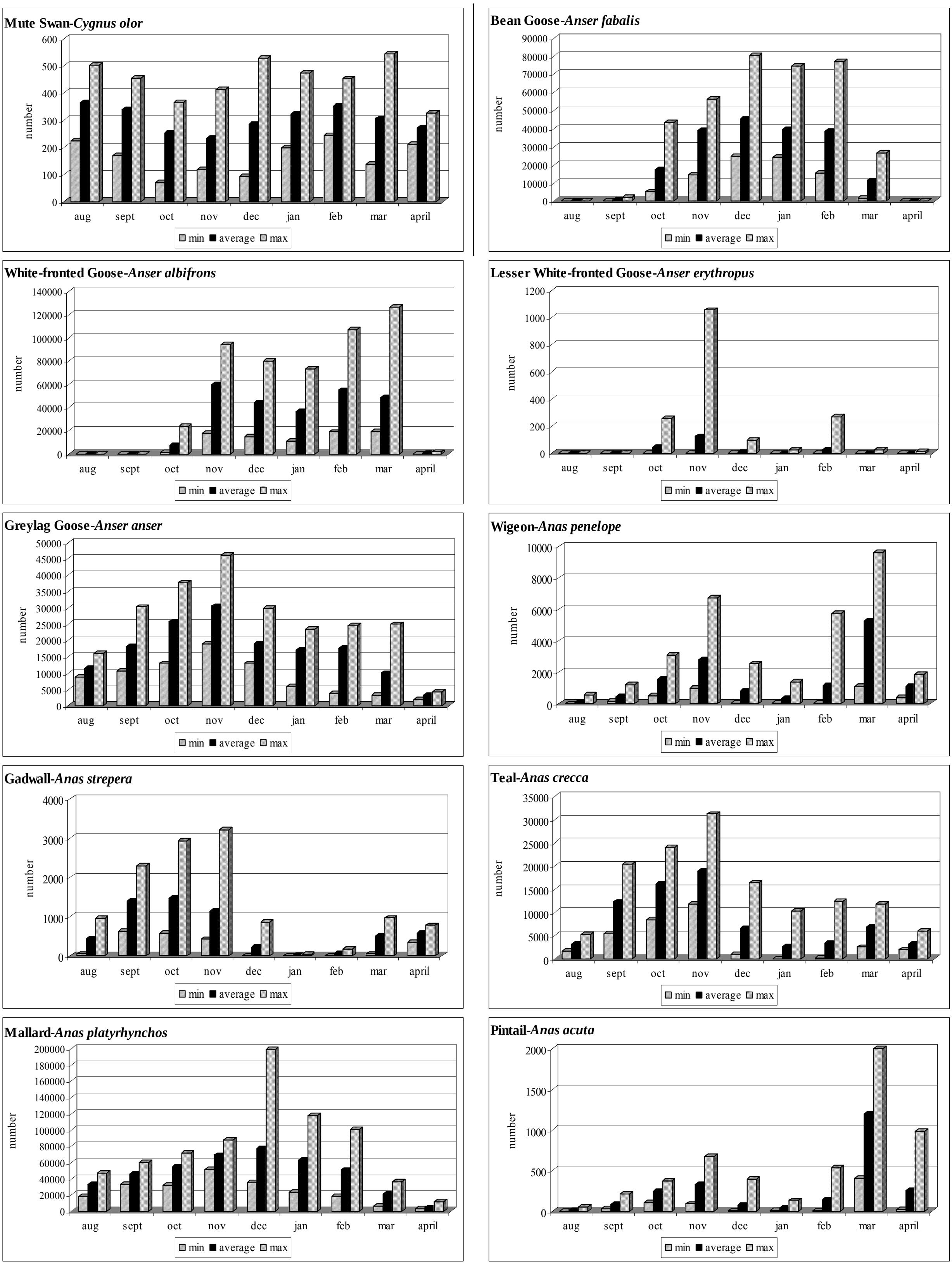


Figure 2. The phenology of the 25 most frequent waterfowl species in Hungary: During the 10-year period the observed minimum, average and maximum number of individuals in each month

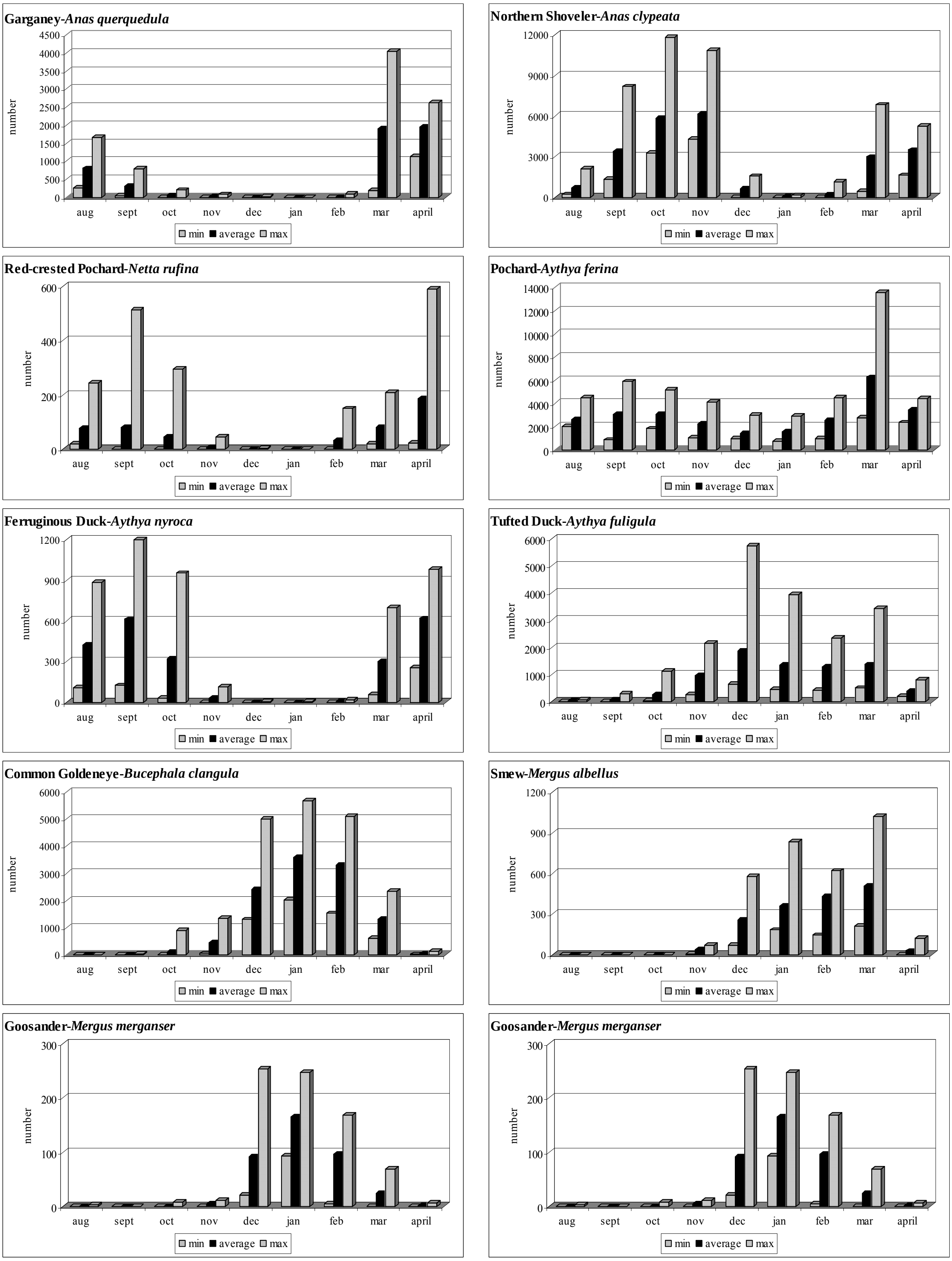


Figure 2 (cont.). The phenology of the 25 most frequent waterfowl species in Hungary: During the 10-year period the observed minimum, average and maximum number of individuals in each month

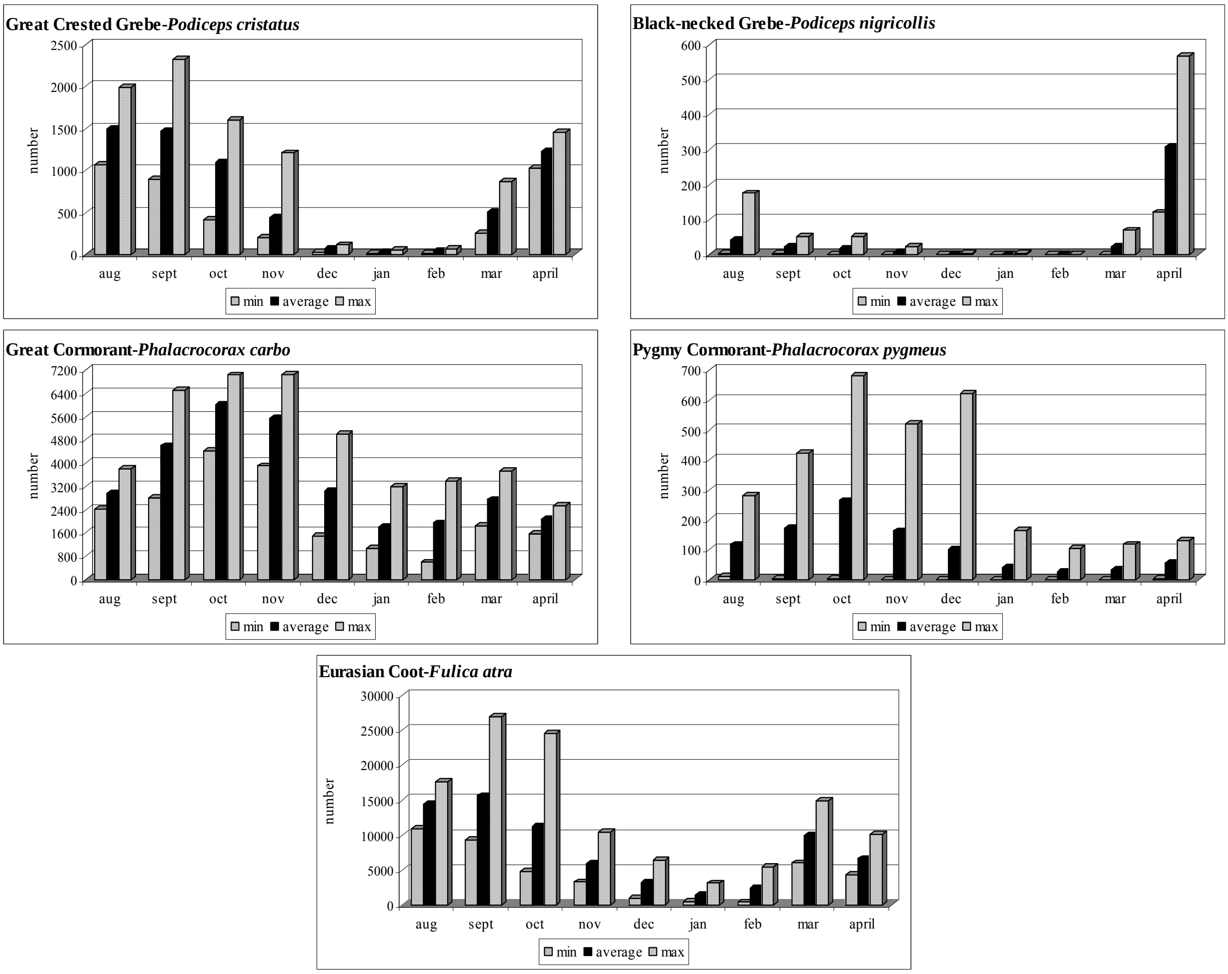
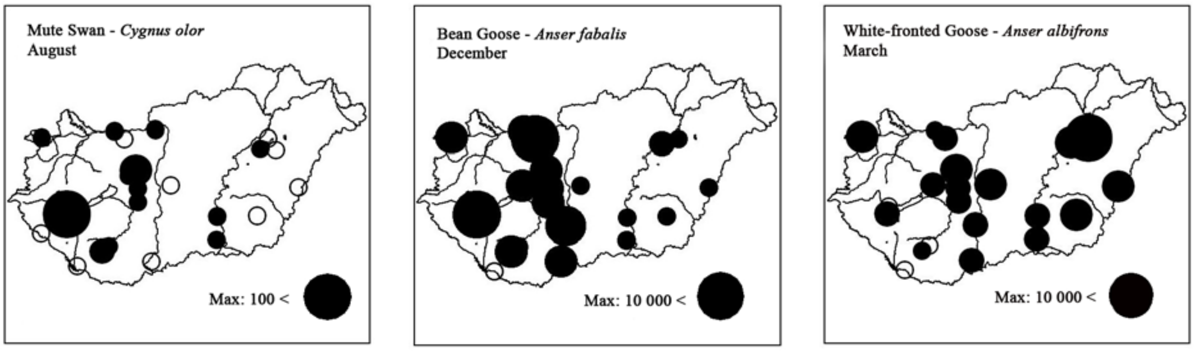
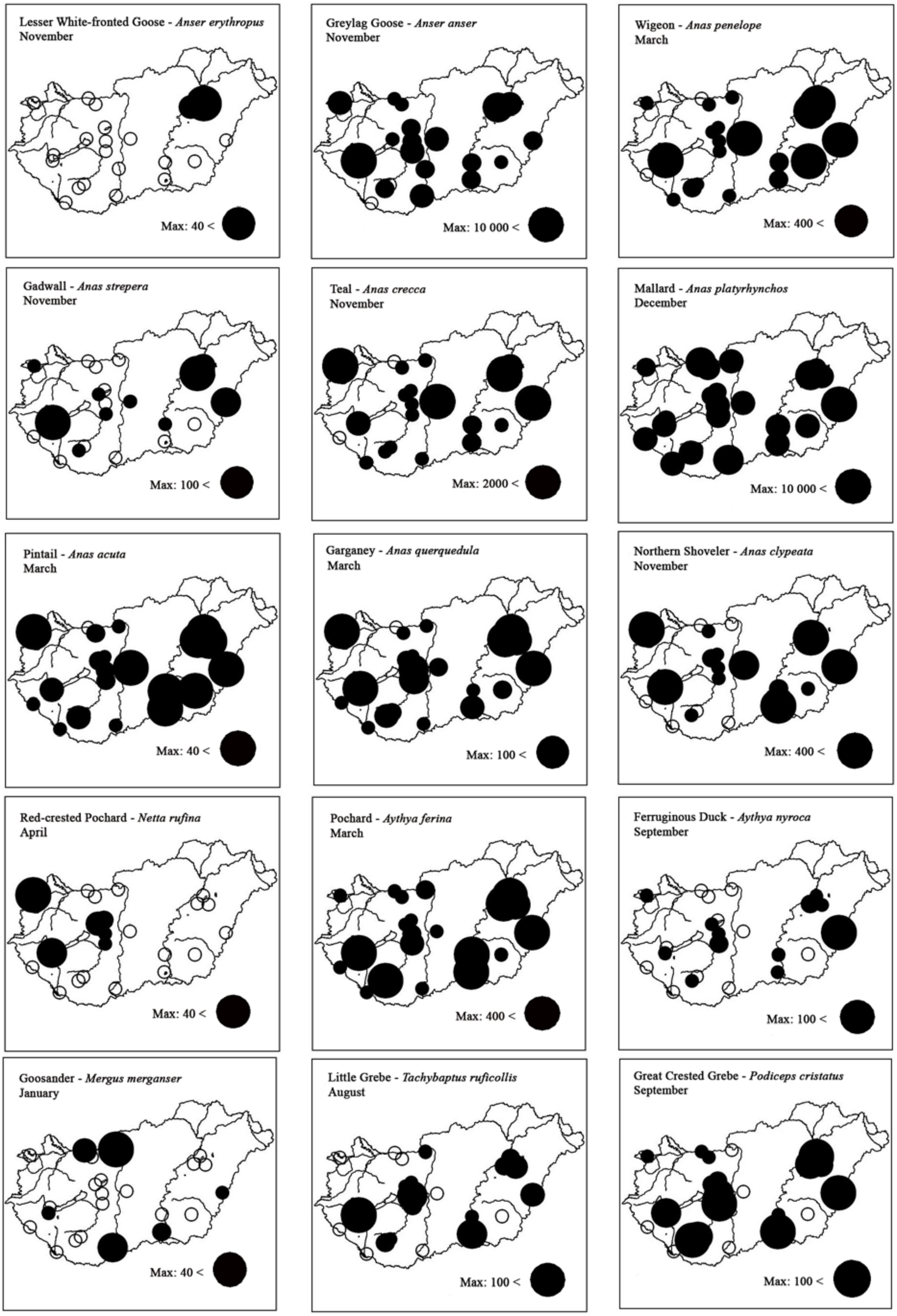


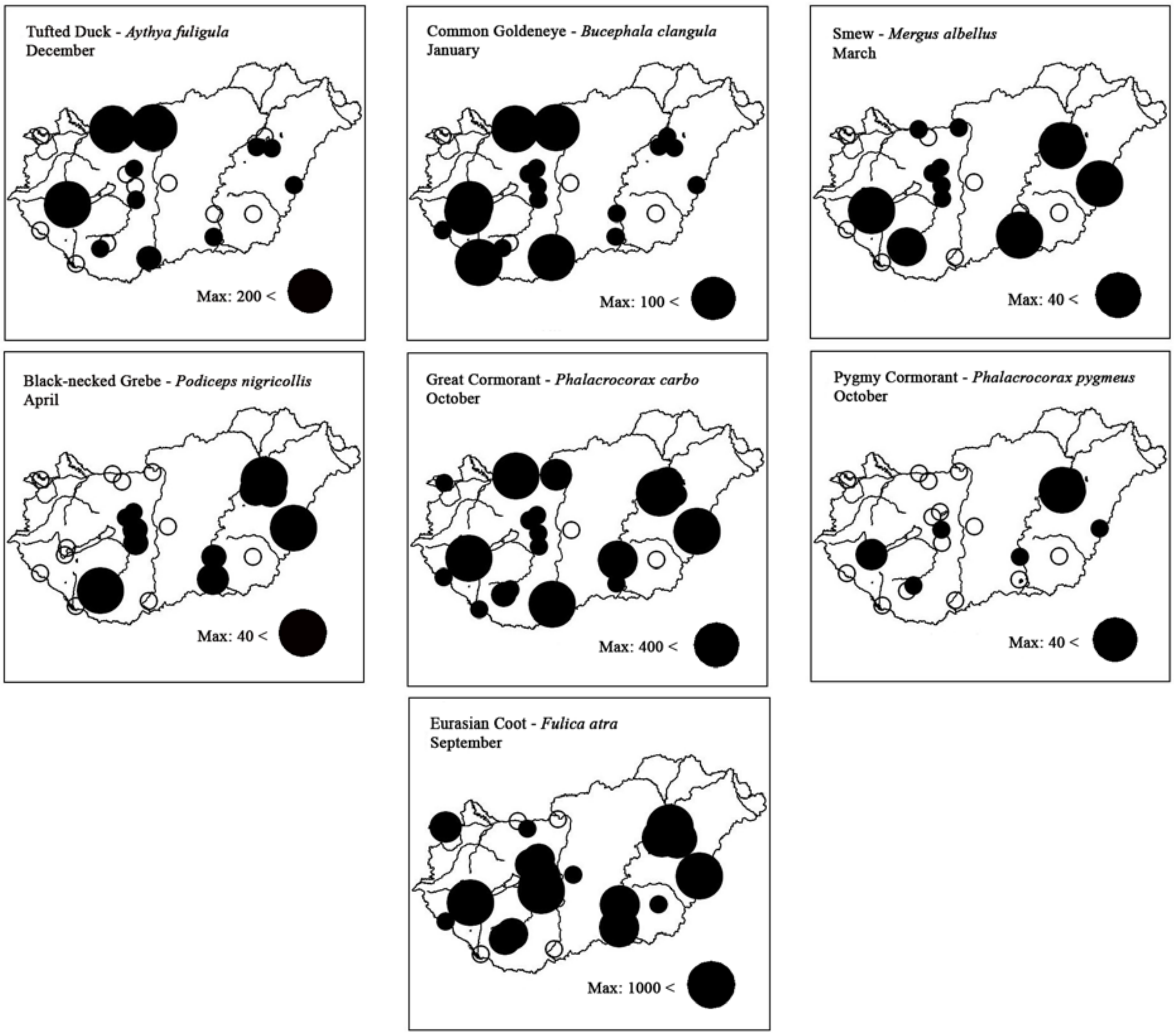
Figure 2 (cont.). The phenology of the 25 most frequent waterfowl species in Hungary: During the 10-year period the observed minimum, average and maximum number of individuals in each month



Map 2. Spatial pattern of the 25 most frequent waterfowl species in their peak month of occurrence



Map 2 (cont.). Spatial pattern of the 25 most frequent waterfowl species in their peak month of occurrence



Map 2 (cont.). Spatial pattern of the 25 most frequent waterfowl species in their peak month of occurrence

3 RESULTS

In an earlier paper we published a detailed regional analysis of all 42 waterfowl species (Faragó, 2008). We defined the phenology of the population of all those waterfowl species migrating through Hungary or overwintering here. We also defined the areal dispersion and its trend (shown on maps) the national, regional and local population trends in this period of examination. We defined the spatial pattern of local population trends (shown on maps) in relation to the season(s) of maximum population (peak period). We gave a comprehensive review for **25 species**. In an additional 17 rare species, no classification was possible because of their small numbers.

We had no or only single records of the following 17 rare vagrant species in the area of the HWM: *Cygnus columbianus, Anser indicus, Branta canadensis, Alopochen aegyptiaca, Anas americana, Anas carolinensis, Anas discors, Marmaronetta angustirostris, Aythya collaris, Aythya affinis, Somateria spectabilis, Polysticta stelleri, Oxyura jamaicensis, Oxyura leucocephala, Gavia immer, Pelecanus onocrotalus, Pelecanus crispus.*

3.1 Analysis by species

Mute Swan – *Cygnus olor* – Migrating species, breeding in small numbers (MME Nomenclator Bizottság, 2008). Within the framework of the HWM its national maximum was **545** individuals (the average of annual maximum was **420.6** individuals). Its phenology had the maximum at late summer and early autumn with a similar maximum in February and at late winter and this was characteristic. In October and November part of the population migrated to the south and its minimum is also in this period. This species is concentrated predominantly in Transdanubia. There were only a few migrating and overwintering observations in the Great Hungarian Plain. We determined a *large increase* in its population trend (+75 %).

Bean Goose – *Anser fabalis* – is a common migrating and overwintering species. Within the framework of the HWM its national maximum was **80,245** individuals, (average: **52 179.5** individuals**).** Its dynamics had a maximum in November/December, which is characteristic. A particular winter minimum (January) and spring maximum (February) can only be shown in certain years. Since Hungary is one of it's overwintering territories (Faragó 1995), after its November (December) peak its quantity continuously decreases until its passage. Departure accelerates in March, and by April only insignificant numbers can be detected. Our investigations supported an earlier finding (Faragó 1995): Bean Goose in Hungary dominantly appears in Transdanubia. Its population trend showed a *large decrease* (–61%).

White-fronted Goose – *Anser albifrons* – is a common as migrating and overwintering species. Within the framework of HWM its national maximum is **126,811** individuals, (average: **80,266.1** individuals). Its phenology had a maximum in autumn (November), a stronger one in February and a weaker one in March, which was very typical for this species. The winter minimum is in January. The remaining April population is only several hundred individuals. The earlier studies had stated (Sterbetz 1967; 1983) and confirmed (Faragó 1995) that the White-fronted Goose mostly appears in the Great Hungarian Plain. Our results have also shown their appearance in a more significant quantity in Transdanubia. Its national population trend showed a *large increase* (+73%).

Lesser White-fronted Goose – *Anser erythropus* – is rare on passage and even rarer as an overwintering species. Within the framework of HWM its absolute national maximum was **1,054** individuals, (average: **186.5** individuals).The top value must be the result of a one-time probably eastern migration, which is not unprecedented in the case of this species. The same phenomenon was shown in Bulgaria in 1991/1992 (Nankinov 1993; Lorentsen *et al.* 1999; Michev – Profirov 2003). It must be known that the European breeding population of this species was under this value in the given period. This is why, regarding the protecting situation of the species, considerable conclusions cannot be drawn. A maximum in November and a weaker one at the end of the winter in February characterize its phenology. The winter minimum is in January. On the basis of our results we achieved similar consequences just as in earlier studies (Sterbetz 1982, 1983): When migrating and overwintering, Lesser White-fronted Geese pay a visit to territories of the Great Hungarian Plain (Tiszántúl); however there are occasional but frequent visits to Transdanubia, too. Its national population trend showed *a large, dramatic decrease* (–86%).

Greylag Goose – *Anser anser* – This waterfowl species of large quantity breeds in increasing population and common migrant (MME Nomenclator Bizottság 2008). Within the framework its national, absolute maximum is **46,187** individuals, (average: **32,303** individuals). A maximum in autumn (November) and a weaker one at the end of winter, in February is characteristic of its phenology. The winter minimum falls in January. According to former enumerations (Sterbetz 1976, 1983) the Greylag Goose paid a visit to areas in the Great Hungarian Plain when migrating and overwintering. Our own examinations (Faragó 1995) demonstrated that up to the 1988/1989 season, a significant part of the observations also came from the Great Hungarian Plain. Since then, however, we have been witnessing a continuous increasing dominance in Transdanubia. Its national population trend showed a *large increase* (+30%) in the period of the survey.

Wigeon – *Anas penelope* – is a common migrant and non-nesting species. Within the framework of HWM its national, absolute maximum was **9,620** individuals (average: **5,539.5** individuals). An autumn (November) weak maximum, and a stronger spring one in March characterized its phenology. The winter minimum fell to January. According to former knowledge (Bankovics 1990) Wigeons visited the eastern parts of the Great Hungarian Plain. Our own investigations highlighted the role of Transdanubia during autumn migration, and they justified the significance of the Great Hungarian Plain in springtime. Its national population trend showed a *large decrease* (–30 %) in the period of the survey.

Gadwall – *Anas strepera* – rare breeding species and frequent migrant (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **3,209** individuals (average: **1,898.9** individuals). Its characteristic phenology has an autumn maximum in October and one weaker, longer lasting spring maximum in March and April. The winter minimum is in January, when it disappears from our wetlands. The former data concerning its regional dispersion were contradictory. Our own investigations showed, besides the presence on the Great Hungarian Plain, their presence in Transdanubia during autumn. Besides their Transdanubian dominance, in certain years we have also recorded their prevalence. Their population trend showed a *large increase* (+30 %) in the examined period.

Teal – *Anas crecca* – This species is rare, occasional breeder in Hungary; but it is a very common migrant, observed in great numbers (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **31,171** individuals, (average: **19,817.0** birds). Its phenology has an autumn maximum in November, and a weaker one in March in the spring. The winter minimum is in January. Even in April it is found in great quantities. According to earlier counts (Schmidt 1977, 1982; Bankovics 1990), Teals appeared, during spring and autumn migrations and overwintering, mostly on regions of the Great Hungarian Plain. Our own investigations showed that recently they showed up in large numbers at the wetlands of Transdanubia. The population trend has showed a *large decrease* (–39 %) in the examined period.

Mallard – *Anas platyrhynchos* – is the commonest nesting and migrating waterfowl species in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM, its national, absolute maximum is **198,659** individuals, (average**: 97,591.2** individuals). Its dynamics showed only one December maximum. Although, every year in February there is a slight increase, but its size hardly differs from the January values. In March, after start of nesting, its population diminishes significantly. Earlier data (Schmidt 1975) on Mallards showed that this species visited sites of the Great Hungarian Plain during the autumn migration. In spring their dispersion was steady in the different parts of the country. Our monitoring showed that during the past few years they appeared in a larger number at important wetlands of Transdanubia, as opposed to the years before. As a result it became a lot more evenly distributed, but there were some places with prominent values, in Fishponds at Biharugra and Begécs, Hortobágy, and parts of the river Danube. The national population trend showed a *small decline* (–14 %) in the period of the survey.

Pintail – *Anas acuta* – is a common migrant in Hungary but nests in small numbers (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **2,483** individuals (average: **1,197.3** individuals). Its characteristic population dynamics is one modest maximum in autumn, in November, and a stronger maximum in spring, in March. The winter minimum fell to January. According to former data, (Schmidt 1959; 1961) the migration of the Pintail may be connected to the areas of sodic soils of the

Great Hungarian Plain. Our investigations have reconfirmed that earlier findings are still valid nowadays. This species' national population trend indicated *stability* but a strong *fluctuation* (+ 8 %) in the examined period.

Garganey – *Anas querquedula* – is a fairly common nesting and migrating species in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum was **4,040** individuals (average: **2,275.1** individuals). Its population dynamics showed a late summer/early autumn maximum, and a somewhat heavier one in March. The winter minimum fell to December and January. According to earlier surveys (Faragó – Zomerdijk 1997a) Garganey preferred the sites of Transdanubia, both during the autumn and the spring migration. As for our recent investigations, the dominance of the western part of the country during migration is still valid, but during spring they appear at certain wetlands of the Great Hungarian Plain in a larger number than on regions of Transdanubia. Its national population trend showed a *large decrease* (– 44 %) in the period of the survey.

Northern Shoveler – *Anas clypeata* – is a regular nesting species and common migrant in some places in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **11,829** individuals (average: **7,464.6** individuals). Its characteristic population dynamics is an autumn, and has a peak in November, and a weaker but longer spring one in March and April. The winter minimum is in January. According to former data (Faragó – Zomerdijk 1997a) the spring migration of the Northern Shoveler may be connected to the Great Hungarian Plain. The autumn migration was steadier, but when a large number of individuals showed up, they were bound always to the regions of the Great Hungarian Plain. Our examinations showed that recently, Northern Shoveler have appeared at certain wetlands of Transdanubia in great quantities, which exceeded their numbers on the plain. This phenomenon can probably be related to the attraction of the habitat restoration of a large area at Kisbalaton and Lake Fertő. The species' population trend showed a *large increase* (+113 %).

Red-crested Pochard – *Netta rufina* – is a rare nesting species, during the past few years its range has expanded eastwards, regular on passage, in some places in Hungary in large numbers (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum was **589** individuals (average**: 229.5** individuals). Its population dynamics is characterized in autumn with a maximum in September and a more definite spring one in April. The winter minimum is in January when it disappears from our wetlands. Up to 1975 there were only 23 observations, and between 1975-1983 there were only 33 observations in Hungary. Later in the course of both the autumn and the spring migration period, it was become commoner in some parts of Transdanubia, where this species was observed in greater quantities. Some individuals were even later observed on the Great Hungarian Plain. Our investigations have recorded its appearance at an increasing number of sites. Its centre of occurrence in terms of migration and nesting has been in Transdanubia since 1983. Its national population trend has shown a *large increase* (+540 %).

Pochard *Aythya ferina* – is a common nesting and migrating species in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **13,580** individuals, (average: **6,560.8** individuals). Its population dynamics shows an autumn maximum in September and October and a stronger spring one, in March. The winter minimum falls to December. According to former appraisals (Keve et al. 1959; Schmidt 1959, 1961) during the autumn migration Pochard only appeared in great quantities either at Transdanubia or in the Great Hungarian Plain, but never at the same time in both parts of the country. According to our investigations a modest dominance of the western part of the country was recorded during the wintering period. In other periods they appear in larger numbers at certain wetlands of the Great

Hungarian Plain than those of Transdanubia. Its national population trend has shown a *significant decline* (-42%) during the period of the survey.

Ferruginous Duck – *Aythya nyroca* – is a regular nesting and common migrant in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum was **1,735** individuals (average: **717.0** individuals). Its population dynamics can be characterized by an early maximum in September and a stronger spring one in April. Its winter minimum is in January. According to former records (Keve et al. 1959; SCHMIDT, 1982) the autumn and spring migration of Ferruginous Ducks was connected to Transdanubia, and they became plentiful in the Great Hungarian Plain regions only during their autumn migration. Our observations showed that in recent times during their autumn migration there has been a slight shift in the focal point towards the Great Hungarian Plain and during the spring migration towards Transdanubia. In the course of the investigated period their population trend showed a *large increase* (+1000%!).

Tufted Duck – *Aythya fuligula* – is a scarce breeder, but a common migrant in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum was **5,723** individuals (average: **2,515.3** individuals). Its population dynamics is characterized by a winter maximum in December. According to earlier data (Keve et al. 1959; Schmidt 1959; 1961) the autumn and spring migration of Tufted Ducks can be related to large lakes of Transdanubia. This phenomenon is not attributable to geography, rather to food supply and ecological reasons (the presence of the *Lythoglyphus* and *Dreissena* as food species). Up to 1980, only 3 nests were found in Hungary. Since then both in Transdanubia and sometimes in the Great Hungarian Plain, it has been nesting and spreading continuously (Sterbetz *in* Haraszthy, 1998). Our investigations showed that certain parts of Transdanubia are of particular importance, even in wintertime. Its national population trend showed a *large decrease* (–68 %) during the period of the survey.

Common Goldeneye – *Bucephala clangula* – Only one Hungarian breeding pair is known, but it is a common migrant and winter visitor in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum was **5,693** individuals, (average: **3,973.1** individuals). The first birds arrive in early autumn, but their multitudinous influx is typical during the autumn season. Their winter maximum is in January. The January quantity remains constant in February, but in March their number diminishes considerably. According to the former counts in autumn and spring, the migration of Common Goldeneye mostly took place in Transdanubia. In winter it appeared nearly exclusively in the Transdanubian sites (Lake Balaton, and the river Danube). There were some observations at the Great Hungarian Plain, mostly at Hortobágy and the River Tisza, (Faragó *in* Haraszthy, 1998). In our examinations their large numbers are unchanged in Transdanubia. Its national population trend in the past decade has shown a *small decrease* (–18%).

Smew – *Mergus albellus* – is a common migrant and winter guest in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national, absolute maximum is **1,020** individuals (average: **576.5** individuals). It appears at our wetlands in greater numbers during November. Following this period its numbers grew continuously. There is a characteristic population culmination in spring, in March. According to former data (Bod *in* Haraszthy 1998) Smew appears at Lake Balaton, fishponds and rivers, during the autumn and spring migration. They overwinter on non-freezing wetlands. During the past decade, when migrating in autumn and spring, they appeared on the Great Hungarian Plain, while their wintering concentrated on Kisbalaton, the River Danube and the wetlands of south-east Hungary. Its national population trend showed a *large decline* (– 31 %).

Goosander – *Mergus merganser* – is an occasional nesting species in Hungary, but a common migrant and winter guest (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum is **253** individuals, (average: **180.7** individuals). During

November it appears in our wetlands in large numbers. After this its numbers increase continuously. Its population dynamics showed a single winter maximum in January. Following this period it decreases steadily. According to earlier data (Bod *in* Haraszthy 1998) Goosanders appear during their autumn and spring migrations adjacent to our lakes and rivers which are rich in fish. They generally overwinter on our non-freezing wetlands. Our investigations have shown that this species concentrates on the river Danube and in the southeast of Hungary during their autumn and spring migrations and wintering is concentrated on the river Danube and the south-east of Hungary. Its national population trend showed a *large decline* in the past decade (–29 %).

Little Grebe – *Tachybaptus ruficollis* – is a common nesting species in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its absolute national maximum was **886** individuals (average: **622.9** individuals). Its phenology showed a late summer maximum in August, and a weaker spring one in April. The winter minimum falls to February. According to earlier estimations (Schmidt 1959, 1961) the migration of Little Grebes concentrated in Transdanubia, both in autumn and spring. In the course of our monitoring we have showed that their appearance has become equalized in terms of the eastern and western parts of the country. All this has been valid with the hegemony of certain parts of Transdanubia (e.g. Kisbalaton). The species' national population trend showed a *small increase* (+14 %).

Great Crested Grebe – *Podiceps cristatus* – is a common nesting species, migrating, and wintering occasionally (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum was **2,322** individuals, (average: **1,581.1** individuals). There is an early autumn population peak in September and a smaller peak in early spring, in April. The winter minimum is in January, but by December there are few individuals, and some birds also appear in February. It starts migrating from its winter territory in March. According to earlier investigations (Keve et al. 1959; Schmidt 1959, 1961), the autumn and spring migration of the Great Crested Grebe is mostly concentrated in Western Hungary, because the species requires big lakes. On the contrary, between 1986 and 1992 these birds stopped on the Great Hungarian Plain during their autumn and spring migrations. Our most recent investigations have proved that they appear on the wetlands of Transdanubia in larger numbers than on the Great Hungarian Plain. Its national population trend has shown a *large increase* (+40%).

Black-necked Grebe – *Podiceps nigricollis* – breeds and migrates in smaller numbers (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum was **567** individuals (average: **289.3** individuals). Its population continuously decreases during late summer. Between December and February it does not appear in our wetlands. It begins to return in March. This is the reason for the slight, characteristic population peak in late summer in August, and a somewhat stronger one during spring, in April. According to earlier investigations (Keve et al. 1959; Schmidt 1959; 1961) Black-necked Grebes mostly concentrate in Western Hungary during their autumn and partially spring migration. This is so because they are attracted to large lakes. In certain years the role of the Great Hungarian Plain increased in migration. Our studies have shown that in recent times they have appeared in great quantities in certain wetlands of the Great Hungarian Plain. Its national population trend has shown a *large increase* (+192 %).

Great Cormorant – *Phalacrocorax carbo* – is a common nesting species and increasing both in population and range in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum was **7,052** individuals (average**: 6,370.3** individuals). It has a characteristic autumn population peak and a slightly stronger one in spring (March). After the autumn cooling down, they depart from the frozen lakes to ice-free rivers. In the winter the larger part of the population, including northern visitors, migrate to the south. At the same time some of the nesting and visiting individuals stay in place. The minimum falls to January. According to the waterfowl census between 1986 and 1992 Great Cormorants mostly visited areas of the Great Hungarian Plain during their autumn migration. In the examined period the dominance of the Plain became more pronounced. In Transdanubia the River Danube, Lake Balaton and the area of Kisbalaton plus certain territories of Baranya County played an important role in their migration. In spring this dispersion changed owing to the predominantly Transdanubian location of nesting places. Because of the latter phenomenon our investigations have shown the increase of the role of Transdanubia. The national population trend showed a *small increase* (+19 %).

Pygmy Cormorant – *Phalacrocorax pygmeus* – is an increasing nesting species and a migrant in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum was **680** individuals (average: **286.1** individuals). Its population dynamics had one autumn maximum in October and one spring maximum in April. It's nesting population leaves continuously until February. In March overwintering species come back from the Mediterranean region or the large European rivers. It has been a regular nesting species in Hungary only since 1988 on the Great Hungarian Plain, before that there were only some occasional observations. Our investigations have shown that apart from the nearly ten-fold increase (+940 %), Pygmy Cormorants also appeared on the wetlands in the regions of Transdanubia, particularly at the Kisbalaton.

Eurasian Coot – *Fulica atra* – is a common nesting, migrating and wintering species in Hungary (MME Nomenclator Bizottság 2008). Within the framework of HWM its national absolute maximum was **27,013** individuals, (average: **17,936.1** individuals). There is a population peak with one strong autumn maximum in September and a weaker spring maximum in March. After its autumn peak, the number of Coots continuously decreases up to the winter minimum in January. Following this its population is gradually increasing up to the above mentioned peak in March. Earlier this species migrated on the Great Hungarian Plain both in autumn and in spring, although Lake Balaton and Kisbalaton also played an important role in its migration. The newest investigations have shown the even distribution of the Eurasian Coot; however, in winter it appears in large numbers on the ice-free wetlands of Transdanubia. Its national population trend showed *stability* and a strong *fluctuation* in the period of the survey.

3.2 Comparative Analysis

In comparative analyses, the first task is to record **species in their largest numbers**, and to make an order for each species**.** These analyses reflect the potential importance of Hungary for migration and overwintering for these species. Mallards had the biggest numbers on the territories of HWM, followed by three species of geese: the White-fronted Goose, the Bean Goose and the Greylag Goose (only latter one is breeding in Hungary). The fifth species—the second commonest duck after Mallard—is the Teal (it is a rare, occasional nesting species). The sixth most abundant waterfowl is the Eurasian Coot.

During the ten-year period there were 8 species with about 1000 individuals or less *(Anser erythropus, Mergus albellus, Tachybaptus ruficollis, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Cygnus olor, Mergus merganser).* These species appeared regularly but the numbers of individuals were small. Since some of the species are migrants, or their winter population decreased markedly during the ten-year period, the ***average maximum numbers*** of the last eight species showed changes, which put them to the end of the list of the commonest species. *Anser erythropus* became second last on the list. Average values for other species were near the end of the list which had very low annual peaks in the first part of the decade, e. g. *Aythya nyroca*. The average number of individuals recorded is unchanged at the top of the list. The position of the first six species is the same as the rank order of their absolute maximums.

Population changes i.e. ***trends*** over ten years provided the most important information for conservation practice**.** We have listed the following species in different trend categories:

- **Species with a heavily increasing population**: *Aythya nyroca, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Anas clypeata, Cygnus olor, Anser albifrons, Podiceps cristatus, Anser anser, Anas strepera.*
- **Species with an increasing population**: *Phalacrocorax carbo, Tachybaptus ruficollis.*
- **Species with a stable population:** –
- **Species with a fluctuating population:** *Fulica atra*
- **Species with a decreasing population**: *Anas platyrhynchos, Bucephala clangula*
- **Species with a heavily decreasing population**: *Anser erythropus, Aythya fuligula, Anser fabalis, Anas querquedula, Aythya ferina, Anas crecca, Mergus albellus, Anas penelope, Mergus merganser.*

To the real evaluation we have to add that even species showing definite changes showed the significance of fluctuations. The irregular variations of climatic (too cold or too mild winters) might change the speed and size of migration and the number of those birds overwintering. Principles of energetic explain why species migrating from the north to overwinter here in the Carpathian Basin are found in smaller numbers in mild winters than during average winters. When winters are unusually harsh, a larger proportion of these birds migrate to the Mediterranean region. In both cases it is the regional realignment of the populations of the species, but that is detected as a fluctuation in the Pannon region. This uncertainty becomes larger in small populations and for those species in areal expansion (*Netta rufina* e.g.). Those species—e.g. *Netta rufina, Aythya nyroca, Tachybaptus ruficollis* and *Podiceps cristatus*—where the number of breeding birds and nesting success at the end of summer results the population peaks, the fluctuation is caused by climate anomalies, since in dry years, the nesting success is reduced. Populations in August are smaller in dry years than in optimal wetland conditions.

25 species were put into six different groups based on **types of phenology.** These are as follows:

- **Species passing through in late summer:** *Tachybaptus ruficollis, Podiceps cristatus.*
- **Species passing through dominantly in autumn:** *Anser erythropus, Anser anser, Anas strepera, Anas crecca, Anas clypeata, Phalacrocorax carbo, Phalacrocorax pygmeus, Fulica atra.*
- **Wintering species:** *Anser fabalis, Anser albifrons, Anas platyrhynchos, Aythya fuligula, Bucephala clangula, Mergus albellus* and *Mergus merganser.*
- **Species passing through dominantly in spring:** *Anas penelope, Anas acuta, Anas querquedula, Aythya ferina, Podiceps nigricollis.*
- **Species passing through in spring and late summer:** *Netta rufina, Aythya nyroca.*
- **Residents:** *Cygnus olor.*

The ranking of two species needs explanation. Our wetlands, which are generally shallow and when they do not freeze in winter, provide good wintering opportunities for those Mallards *(Anas platyrhynchos)* coming southward from the north. This can lead to over-population. There is a population swap when part of the nesting population of *Cygnus olor* migrates south (to the Balkan) and their places are taken over by individuals of the same species arriving from other parts of Central Europe. They equalize the number of the species throughout the whole season.

Eco-geographical differences between Transdanubia and the Great Hungarian Plain explain the differences in the **dispersion** of species.

Dispersion dominance in Transdanubia: *Cygnus olor, Anser fabalis, Anas strepera, Netta rufina, Aythya fuligula, Bucephala clangula, Mergus merganser, Podiceps cristatus.*

Dispersion dominance in the Great Hungarian Plain: *Anser erythropus, Anas penelope, Anas acuta, Anas querquedula, Aythya ferina, Aythya nyroca, Mergus albellus, Podiceps nigricollis, Phalacrocorax carbo, Phalacrocorax pygmeus.*

Equal distribution: *Anser albifrons, Anas crecca, Anas platyrhynchos, Anas clypeata, Tachybaptus ruficollis, Fulica atra.*

These conclusions are only valid for the periods of maximum populations. In other times, both during migration and wintering, different values were obtained periodically.

4 DISCUSSION

Conclusions of the census on the Hungarian population trend, phenology and dispersion of 25 common waterfowl species reconfirmed some of the earlier results, but in some cases different conclusions were drawn from earlier presumptions. It is evident that changing environmental conditions affect population size, phenology and dispersion of migrating waterfowl species.

These current investigations show the status after the change of the political system in 1989. There was a change of property ownership, a certain decrease of intensive agriculture, and change in land use (Báldi – Faragó 2007), unfavorable impacts caused by global climate change on nesting and migrating species and to their habitats (nesting, roosting, and feeding sites) (Faragó 2005c). At the same time there were positive influences from nature conservation efforts and habitat reconstruction. This created a special wetland system in Hungary (Tardy 2007), and the effort is still continuing. This produces a steady positive impact on the status of our waterfowl species. It helps compensate for the negative effects of climate change in certain regions. Because of the large habitat restoration in Transdanubia, there is now more balance in the dispersion of certain species instead of their earlier dominance on the Great Hungarian Plain. This could be evaluated as a positive development. Some conservation measures were taken in this period: closed season for waterfowl shooting in certain wetlands in Hungary (Faragó 1997), designation of wetlands with international importance (IBA) (Nagy in Heath – Evans 2002) and designation of special protection areas (SPA) for birds and establishment of the entire NATURA 2000 ecological network.

Because of this system of changes we were able to increase the population of most migrating and wintering species. We are glad to report a strong increase in some waterfowl species: *Aythya nyroca, Phalacrocorax pygmeus, Netta rufina, Podiceps nigricollis, Anas clypeata, Cygnus olor, Anser albifrons, Podiceps cristatus, Anser anser, Anas strepera* and a slight increase of *Phalacrocorax pygmeus* and *Tachybaptus ruficollis.*

At the same time it is distressing to witness the decline of some other species. A strong decrease can be seen in *Anser erythropus, Aythya fuligula, Anser fabalis, Anas querquedula, Aythya ferina, Anas crecca, Mergus albellus, Anas penelope, Mergus merganser.* There is a slight decrease in the case of *Anas platyrhynchos* and *Bucephala clangula.*

The globally threatened *Anser erythropus* is the most alarming. The focus of this problem is outside of the Carpathian Basin. We can contribute very little to the solution of the problem (Tar 2001), the key tools are not in our hands. Because of the realignment of wintering sites in mild winters, we are witnessing the population decrease of the following waterfowl species: *Aythya fuligula, Anser fabalis, Anas crecca, Mergus albellus, Anas penelope, Mergus merganser, Bucephala clangula.* On the species level there is not much disturbance, since the populations are stable, it is even increasing in the case of *Mergus merganser* (Wetlands International 2006). Although in the case of *Anas querquedula, Aythya ferina* and *Anas platyrhynchos* we are witnesses of a general population decrease (Wetlands International

2006). The causes are not well understood. The decrease might be explained for Garganey by desertification in their wintering territories in Africa. This is similar to the unfavorable climate effects on nesting areas. Harsh winters, the instability of food sources (e.g. *Dreissena polymorpha*) and some unknown processes, which are affecting breeding areas in Russia all account for the decrease of Pochard. Mallards are decreasing for similar reasons.

Eleven species had a declining trend. Some of these species were hunted in the investigation period: *Anser fabalis, Anas platyrhynchos, Anas querquedula, Aythya ferina, Anas crecca, Bucephala clangula.* In the case of three species—*Anas querquedula, Aythya ferina* and *Anas platyrhynchos*—for a positive change of the unfavorable population trend termination of hunting should take responsibility.

Mallard was the commonest species. Large numbers occur in the Central European Region and in the west Mediterranean region where one million individuals winter. There is no direct danger, so no interference is needed (even though there is a slight uncertainty in the trend).

In 2008 the Hungarian hunting authorities decided to remove Garganey and Pochard from the list of quarry species. We know that this is only a supporting measure and not enough to reverse the negative population trend of the species. To achieve success quickly, we will need protecting measures with an array of different methods of active intervention and a variety of sites as locations of species conservation plans.

Last but not least, the importance of the role of long term monitoring systems must be underlined, which are part of waterfowl research and conservation. Only the HUNGARIAN WATERFOWL MONITORING makes it possible in Hungary to detect changes in the population trends of our waterfowl species. This also applies to phenology and dispersion. We should also draw conclusions for the sake of protection and use (hunting), since this has an effect on our national interest.

Acknowledgements: The necessary sources were supplied by Ministry of Agriculture and Country Development, Ministry for Environment and Water and in the case of Fertő Region it was the ERFARET Knowledge Centre, who supplied the operation of the HUNGARIAN WATERFOWL MONITORING in 2005 and 2006. We are thankful for the observers, and all the workers who took part in data processing:

Pellinger, Attila (Lake Fertő), Mogyorósi, Sándor (Lake Fertő), Molnár, Balázs (Lake Fertő), Dr. Jánoska, Ferenc (River Danube between Gyönyű and Szob), Musicz, László (Old Lake at Tata, River Danube at, Nyergesújfalu), Fenyvesi, László (Lake Velence and Dinnyési Fertő), Staudinger, István (Fishponds at Soponya and Fishponds at Rétszilas), Szépe, Attila (Fishponds at Rétszilas), Lelkes, András (Lake Balaton, Keszthelyi-bay and Kisbalaton), Dr. Nagy, Lajos (Lake Balaton, Keszthelyi-bay and Kisbalaton), Fenyősi, László (River Dráva between Barcs and Szentborbás), Mezei, Ervin (Gravel pits at Gyékényes), †Molnár, István (Fishponds at Sumony, Fishponds at Pellérd), Ónodi, Miklós (Fishponds at Sumony), Madas, Katalin (Fishponds at Pellérd), Kókay, Szabolcs (Danube bend), Selmeczi Kovács, Ádám (Danube bend), Kalocsa, Béla (River Danube between Baja and state border), Boros, Emil (Natron lake Kelemen-szék at Fülöpszállás and Natron lake Zab-szék at Szabadszállás), Pigniczki, Csaba (Natron lake Kelemen-szék at Fülöpszállás and Natron lake Zab-szék at Szabadszállás), Nyúl, Mihály (Natron lake Kelemen-szék at Fülöpszállás and Natron lake Zab-szék at Szabadszállás), Gőri, Szilvia (Hortobágy), Tar, János (Hortobágy), Gyüre, Péter (Hortobágy), Dr. Kovács, Gábor (Hortobágy), Végvári, Zsolt (Hortobágy), Barabás, Lilla (Hortobágy), Szilágyi, Attila (Hortobágy), Spakovszky Péter (Hortobágy), Faludi, Csaba (Hortobágy, Lake Tisza), Gál, Lajos (Hortobágy, Lake Tisza), Konyhás, Sándor (Hortobágy), Széll, Antal (Lake Fehér at Kardoskút), Vasas, András (Fishponds at Biharugra and Begécs), Tőgye, János (Fishponds at Biharugra and Begécs), Dr. Bod, Péter (Lake Csaj at Tömörkény), Domján, András (Lake Csaj at Tömörkény), Nagy, Tamás (Lake Fehér at Szeged and Fertő), Dr. Tokody, Béla (Lake Fehér at Szeged and Fertő), Jakus, László (Balaton East), Fodermayer, Vilmos (River Danube at Gemenc and River Danube at Béda-Karapancsa), Sipos, Sándor (River Danube at Béda-Karapancsa), Janács, Gergely (River Danube at Béda-Karapancsa), Hóber Balázs (NymE Sopron), Dr. László, Richárd (NymE Sopron), Vörös, Ákos (NymE, Sopron).

REFERENCES

BANKOVICS, A. (1990): Átvonuló és telelő vadrécék állományviszonyai Magyarországon az 1982-1984-es években. [Population size of migratory and overwintering ducks in Hungary in the period of 1982 and 1984.] A Magyar Madártani Egyesület II. Tudományos Ülése, Szeged 1986: 223-228. (in Hungarian)

BÁLDI, A. – FARAGÓ, S. (2007): Long-term changes of farmland game populations in a post-socialist country (Hungary). Agriculture, Ecosystems & Environment 118: 307-311.

FARAGÓ, S. (1995): Geese in Hungary 1986-1991. Numbers, Migration and Hunting Bags. Slimbridge, UK. IWRB Publication 36.

FARAGÓ, S. (1997): The Hungarian Waterfowl Management Plan. Gibier Faune Sauvage – Game and Wildlife 13: 1023-1038.

FARAGÓ, S. (1998a): A Magyar Vízivad Információs Rendszer. [The Hungarian Waterfowl Information System.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 4: 3-16. (in Hungarian)

FARAGÓ, S. (1998b): A vadlúd monitoring eredményei az 1996/1997-es idényben. Magyarországon. [Results of Geese Monitoring in Hungary in the season 1996/1997.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 4: 17-59. (in Hungarian)

FARAGÓ, S. (1998c): A Magyar Vízivad Monitoring eredményei az 1996/1997-es idényben. [Results of Hungarian Waterfowl Monitoring in Hungary in the season 1996/1997.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 4: 61-263. (in Hungarian)

FARAGÓ, S. (1999a): A vadlúd monitoring eredményei az 1997/1998-as idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 1997/1998.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 5: 3-62. (in Hungarian)

FARAGÓ, S. (1999b): A Magyar Vízivad Monitoring eredményei az 1997/1998-as idényben. [Results of Hungarian Waterfowl Monitoring in the season 1997/1998.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 5: 63-328. (in Hungarian)

FARAGÓ, S. (2001a): A Vadlúd Monitoring eredményei az 1998/1999-es idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 1998/1999.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 7: 3-40. (in Hungarian)

FARAGÓ, S. (2001b): A Magyar Vízivad Monitoring eredményei az 1998/1999-es idényben. [Results of Hungarian Waterfowl Monitoring in the season 1998/1999.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 7: 41-212. (in Hungarian)

FARAGÓ, S. (2002a): A Vadlúd Monitoring eredményei az 1999/2000-es idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 1999/2000.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 8: 3-43. (in Hungarian)

FARAGÓ, S. (2002b): A Vadlúd Monitoring eredményei a 2000/2001-es idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 2000/2001.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 9: 3-45. (in Hungarian)

FARAGÓ, S. (2002c): A Magyar Vízivad Monitoring eredményei a 2000/2001-es idényben. [Results of Hungarian Waterfowl Monitoring in the season 2000/2001.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 9: 47-249. (in Hungarian)

FARAGÓ, S. (2002d): Vadászati állattan. [Hunting Zoology.] Mezőgazda Kiadó, Budapest. (in Hungarian)

FARAGÓ, S. (2005a): A Vadlúd Monitoring eredményei a 2002/2003-as idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 2002/2003.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 12: 3-42. (in Hungarian)

FARAGÓ, S. (2005b): A Magyar Vízivad Monitoring eredményei a 2002/2003-as idényben. [Results of Hungarian Waterfowl Monitoring in the season 2002/2003.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 12: 43-224. (in Hungarian)

FARAGÓ, S. (2005c): A klímaváltozás valószínűsíthető hatásai a hazai vadgazdálkodásra. [The probable effects of climate change on Hungarian game management.] „AGRO-21” Füzetek, Klímaváltozás – Hatások – Válaszok. 43: 87-104 (147-148). (in Hungarian)

FARAGÓ, S. (2006a): A Vadlúd Monitoring eredményei a 2003/2004-es idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 2003/2004.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 13: 3-39. (in Hungarian)

FARAGÓ, S. (2006b): A Magyar Vízivad Monitoring eredményei a 2003/2004-es idényben. [Results of Hungarian Waterfowl Monitoring in the season 2003/2004.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 13: 41-214. (in Hungarian)

FARAGÓ, S. (2007a): A Vadlúd Monitoring eredményei a 2004/2005-ös idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 2004/2005.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 14: 3-40. (in Hungarian)

FARAGÓ, S. (2007b): A Magyar Vízivad Monitoring eredményei a 2004/2005-ös idényben. [Results of Hungarian Waterfowl Monitoring in the season 2004/2005.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 14: 41-209. (in Hungarian)

FARAGÓ, S. (2007c): A Vadlúd Monitoring eredményei a 2005/2006-os idényben Magyarországon. [Results of Geese Monitoring in Hungary in the season 2005/2006.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 15: 3-45. (in Hungarian)

FARAGÓ, S. (2007d): A Magyar Vízivad Monitoring eredményei a 2005/2006-os idényben. [Results of Hungarian Waterfowl Monitoring in the season 2005/2006.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 15: 47-220. (in Hungarian)

FARAGÓ, S. (2008): A vonuló vízivadfajok állományainak tér-idő mintázata Magyarországon. Az 1996-2004 közötti időszak elemzése. [Time-space pattern of migratory waterfowl species. An analysis of the period 1996-2004] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 16: 49-200. (in Hungarian)

FARAGÓ, S. – GOSZTONYI, L. (2002): A Magyar Vízivad Monitoring eredményei az 1999/2000-es idényben. [Results of Hungarian Waterfowl Monitoring in the season 1999/2000] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 8: 45-256. (in Hungarian)

FARAGÓ, S. – GOSZTONYI, L. (2003a): A Vadlúd Monitoring eredményei a 2001/2002-es idényben [Results of Geese Monitoring in Hungary in the season 2001/2002.] Magyarországon. Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 11: 3-50. (in Hungarian)

FARAGÓ, S. – GOSZTONYI, L. (2003b): A Magyar Vízivad Monitoring eredményei a 2001/2002-es idényben. [Results of Hungarian Waterfowl Monitoring in the season 2001/2002.] Magyar Vízivad Közlemények – Hungarian Waterfowl Publications 11: 51-252. (in Hungarian)

FARAGÓ, S. – ZOMERDIJK, P. (1997a): Garganey – *Anas querquedula*. In: Hagemeijer, E J. M. – Blair, M.J. (eds.): The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. Poyser, London: 96-97.

FARAGÓ, S. – ZOMERDIJK, P. (1997b): Shoveler – *Anas clypeata*. In: Hagemeijer, E J. M. – Blair, M. J. (eds.): The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. Poyser, London: 98-99.

HARASZTHY, L. (ed.)(1998): Magyarország madarai. [Birds of Hungary] Mezőgazda Kiadó, Budapest

HEATH, M. – EVANS, M. I. (2002): Important bird areas in Europe. Priority sites for conservation. Volume 2: Southern Europe.

KEVE, A. – BERETZK, P. – SCHMIDT, E. (1959): Az egyidejű (synchron) vízimadártani kutatás feladatai és néhány eredménye. [Tasks and some results of synchronous research of water-birds] Állattani Közlemények 47: 119-124.

LORENTSEN, S.-H. – OIEN, I.J. – AARVAK, T. – MARKKOLA, J. – VON ESSEN, L. – FARAGÓ, S. – MOROZOV, V. – SYROECHKOVSKY jr., E. – TOLVANEN, P. (1999): Lesser White-fronted Goose – *Anser erythropus*: 144-161. In: Madsen, J. – Cracknell, G. – Fox, A.D. (Eds.): Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publ. No. 48., Wetlands International Wageningen, The Netherlands. National Environmental Research Institute, Rönde, Denmark

MICHEV, T. – PROFIROV, L. (2003): Mid-winter numbers of waterbirds in Bulgaria (1977-2001). Results from 25 years of mid-winter counts carried out at the most important Bulgarian wetlands. Pensoft, Sofia-Moscow.

MME NOMENCLATOR BIZOTTSÁG (2008): Magyarország madarainak névjegyzéke. [Name list of birds of Hungary]Nomenclator Avium Hungariae. Magyar Madártani és Természetvédelmi Egyesület, Budapest. (in Hungarian)

FARAGÓ, S. (2007a): A Vadlúd Monitoring eredményei a 2004/2

NANKINOV, D. N. (1993): A new wintering area of the Lesser White-fronted Goose *Anser erythropus* in Bulgaria. Ornis Svecica 3: 165-166.

SCHMIDT, E. (1959): Die Ergebnisse der synkronistischen Beobachtung des Wasservögelzuges vom Jahre 1958. Vertebrata Hungarica 1: 171-186.

SCHMIDT, E. (1961): Az 1960 évi synchron vízimadárvonulási megfigyelések eredményei. [Results of synchronous observation of waterfowl migration in 1960] Vertebrata Hungarica 3: 83-104. (in Hungarian)

SCHMIDT, E. (1975): A novemberi és januári réceszámlálások néhány eredménye Magyarországon. I. *Anas platyrhynchos*. [Some results of duck counts in Hungary in November and January. I. *Anas platyrhynchos*.] Aquila 80-81: 149-168. (in Hungarian)

SCHMIDT, E. (1977): A novemberi és januári réceszámlálások néhány eredménye Magyarországon. II. *Anas crecca*. [Some results of duck counts in Hungary in November and January. II. *Anas crecca*.] Aquila 83: 137-141. (in Hungarian)

SCHMIDT, E. (1982): Márciusi réceszámlálások néhány eredménye Magyarországon. [Some results of March Ducks Census] Nimród Fórum 1982. okt.: 22-26. (in Hungarian)

STERBETZ, I. (1967): A Magyarországon telelő lilikek ökológiai problémái. A lilik előfordulása a jelen században. [Oecological problems of white-fronted geese passing the winter in Hungary. Presence of white-fronted geese in this century.] Aquila 73-74: 33-49.

STERBETZ, I. (1976): A vadlúdvonulás alakulása a magyarországi gyülekezőhelyeken. [Development of wild-geese migration on the Hungarian gathering-places.] Aquila 82: 181-194.

STERBETZ, I. (1982): Migration of *Anser erythropus* and *Branta ruficollis* in Hungary 1971-1980. Aquila 89: 107-114.

STERBETZ, I. (1983): A magyarországi vadlúdvonulás alakulása az 1972 és 1982 közötti időszakban. [The trend of the migration of wild-geese in Hungary in the period 1972-1982.] Állattani Közlemények 70: 69-72. (in Hungarian)

TAR, J. (2001): The occurrence and protection of Lesser White-fronted Goose in Hortobágy, Hungary in the period 1996-2000. In: Tolvanen, P. – Øien, I. J. – Ruokolainen, K. (eds.): Fennoscandian Lesser White-fronted Goose conservation project. Annual report 2000. WWF Finland – Norwegian Ornithological Society, Helsinki – Klæbu: 34-36.

TARDY, J. (ed.) (2007): A magyarországi vadvizek világa. Hazánk Ramsari területei. [The world of Hungarian wetlans. Our Ramsar sites] Alexandra Kiadó, Pécs.

TUCKER, G. M. – HEATH, M. F. (1994): Birds in Europe: their conservation status. Cambridge, U.K. BirdLife Conservation Series 3.

WETLANDS INTERNATIONAL (2006): Waterbird Population Estimates – Fourth Edition. Wetlands International, Wageningen.

Acta Silv. Lign. Hung., Vol. 5 (2009) 109-118

Space Use and Activity Patterns of Red Deer in a Highly Forested and in a Patchy Forest-Agricultural Habitat

András NÁHLIK[a*] – Gyula SÁNDOR[a] – Tamás TARI[a] – Géza KIRÁLY[b]

[a] Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry,
University of West-Hungary, Sopron, Hungary
[b] Institute of Geomatics and Civil Engineering, Faculty of Forestry,
University of West Hungary, Sopron, Hungary

Abstract – Red deer (*Cervus elaphus*) were fitted with GPS collars to estimate their habitat use and feeding ethology. The purpose of the study was to find methods to reduce crop damage caused by deer. The collars were programmed to produce an hourly recording of position. Two different types of habitat were studied: a) An undisturbed and variable habitat (Zala County), b) A less variable area much disturbed by human activities (Sopron mountains). Comparisons were made between 1) the expansion of home range, 2) the intensity of open habitats use, and 3) the activity patterns of marked individuals in the two areas.

The seasonal change of size of the home ranges showed similar dynamics in the two regions. The summer home range was always smaller than the autumn-winter ranges. In Zala County, the winter range often overlapped the summer range. In the Sopron mountain area, there was a definite home range shift. The summer home ranges in the Sopron area were examined using the 60 % Kernel method where differences were usually found between the day and night-time home areas. In the Zala region the phenomenon was not observed. The autumn-winter home range of stags is larger than that of hinds particularly in the summer. Examined with the minimum convex polygon method the difference is even larger than the results obtained from the Kernel method, which focuses on density distribution. This shows that the autumn-winter movements mostly represent rambling and only in a lesser, but still significant extent derive from the real extension of home ranges.

Large differences existed at regional and individual levels regarding the use of the open habitats. The red deer in Zala used the open habitats in a more intensive way than those in Sopron.

The daytime activity of the Sopron stags was less than that of the Zala stags.

red deer/ home range / habitat use / activity patterns

Kivonat – A gímszarvas területhasználata és mozgásaktivitása egy magas erdősültségű és egy mozaikos erdei élőhelyen. Gímszarvasokat jelöltünk GPS nyakörvekkel mozgáskörzetük és élőhely-használatuk becslése, táplálkozás-etológiájuk megismerése céljából annak érdekében, hogy vadkárcsökkentő módszereket fejlesszünk ki. A nyakörveket úgy programoztuk be, hogy óránként mérjenek pozíciókat.

A vizsgálatot két, élőhelyi adottságukat tekintve eltérő területen végeztük: (a) Zala megyében, egy viszonylag zavartalanabb és változatosabb élőhelyi adottságú területen és (b) a Soproni-hegyvidéken egy emberi tevékenység által erősen zavart, kevésbé mozaikos területen. A két területen

---

[*] Corresponding author: nahlik@emk.nyme.hu; H-9401 Sopron, POB 132, Hungary

összehasonlítottuk (1) a mozgáskörzetük kiterjedését, (2) a nyílt élőhelyek használati intenzitását, illetve (3) a jelölt példányok mozgásaktivitását.

A mozgáskörzetek nagyságának évszakos változása hasonló dinamikát mutatott a két területen. A nyári mozgáskörzet mindig kisebb volt az őszi-télinél, azonban, míg Zalában a téli leggyakrabban tartalmazta a nyárit, addig a Soproni-hegyvidéken határozott mozgáskörzet-eltolódás volt kimutatható. A soproni területen a nyári mozgáskörzetek 60%-os Kernel módszerrel vizsgálva általában szétszakadtak a nappali és éjszakai mozgáskörzetek különbsége miatt, míg a zalai területen ilyen különbséget nem tapasztaltunk. A bikák őszi-téli mozgáskörzete lényegesen jobban kitágul a nyárihoz képest, mint a teheneké. Ez a változás még nagyobb, ha minimum konvex poligon módszerrel vizsgáljuk, mint, ha a sűrűségi eloszlást is figyelembe vevő Kernel módszert, ami azt mutatja, hogy az őszi-téli elmozdulások nagyobb részt elcsatangolásokból állnak, és csak kisebb, bár szignifikáns mértékben beszélhetünk valós mozgáskörzet kiterjesztésről.

A nyílt élőhelyek használatát tekintve nagy eltérések vannak nem csak a két terület között, de a területeken belül az egyes példányok között is. A zalai szarvasok átlagosan sokkal intenzívebben használták a nyílt élőhelyeket, mint a soproniak.

A soproni szarvasok nappali aktivitása lényegesen elmaradt a zalai szarvasokétól.

gímszarvas / mozgáskörzet / élőhely-használat / mozgásaktivitás

1 INTRODUCTION

Research with telemetry equipment on the habitat use and movement of red deer goes back 40 years (Heezen – Tester 1967). In the earlier times use was made of radio telemetry based on triangulation which was also used in Hungary (e.g. Szemethy et al, 1996). The drawback of this method is that it is very expensive and time consuming in studies measuring the position of large herbivores that have a large home range (Kenward 1987). This is why the method is not suitable to examine home ranges over short periods (e.g. monthly or day/night time periods). Another drawback is that it is hard to observe home range shifts, although Georgii (1981) and Kamler et al. (2008) reported successful trials. The definition of habitat use is even more problematic because of the small number and infrequency of observation points. The breakthrough came with the application of GPS telemetry in game biology. This allows observers to get observation data every thirty minutes if required. The aim of this research with GPS telemetry was to estimate the home range, habitat use and patterns of daily activity of red deer. By using knowledge of the feeding ethology and strategy of red deer, methods for the reduction of crop damage can be developed.

2 MATERIAL AND METHODS

Two territories with different habitat characteristics were used in the study. The first in Zala was undisturbed and variable. The altitude of this territory is between 140 and 330 metres above sea level. The climate is a transition to sub-Alpine and to sub-Mediterranean. The habitat is patchy, formed of intensively managed forest with an emphasis on natural regeneration. Agriculture is dominated by maize, clover, oilseed rape and grain crops. The most common forest type is the southern Transdanubian beech forest (*Vicio oroboidi Fagetum*). The distribution of stand forming species is as follows: beech 41%, Turkey oak, respectively sessile oak 41%, Scots pine 12%, others 6%, the main silvicultural activity is selective felling of beech. Collars were fitted on 7 red deer (4 stags and 3 hinds).

The second area was in the Sopron mountains, which has much coniferous forest dominated by spruce and managed under a clearcut system, land use is less fragmented, agriculture being dominated by maize, sunflowers, grain and viticulture. The area is also much disturbed by human activity. The land has a mountain range of medium height with an altitude between 340 and 460 metres above sea level. The Sopron mountains belong to the East Alpine flora domain (Noricum) and the Sopron-Kőszeg flora district (Ceticum). The ratio between coniferous and broad-leaved species in the study area changed to 46:54%, because of preference of decidous species in regenerations and damages by bark beetles (*Ips tipographus*) to spruce trees. In this second territory GPS collars were fitted to 6 deer (1 stag and 5 hinds). One of the hinds subsequently got injured by gunshot on one leg shortly after it was collared, consequently its home range was smaller than that of the other animals although it successfully raised a calf. Therefore this individual was excluded from our calculations of the size of the home ranges.

The collars have two main functions: the transmission of radio signals to faciliate a search for the animal, plus the recording, storage and transmission GPS positions. A separate unit installed on the collar makes it possible to remove the collar from the animal’s neck by using a remote controlled signal. This can be done at a predetermined point in time. The collars were programmed to record coordinates every hour. The collars were fitted in February 2005 and 2006 and each of them was dropped of after 1-year work.

Comparisons were made of the extent of the home ranges and the intensity of use of the open habitats in both territories. Activity patterns of the marked individuals were examined by measuring the distances between the hourly coordinates.

The sizes of the home ranges were compared using the minimum convex polygon method and the Kernel method. The former method combines the most distant observation points, producing a plain figure in which “it is impossible to hide.” It encloses the largest territory within an irregular polygon. The Kernel method focuses on the density of the observation points defining an index based on the points, giving the probability of whether or not the animal entered a certain cell. Using the points, the seasonal home ranges were determined. There were great seasonal differences in autumn, winter and spring (later shortened to winter) and the summer season, although the two periods were not set to calendar dates, but instead to the seasonal change of the size of the home range of each animal. The basis of the change of the separation was the beginning of the autumn expansion of the home ranges, and the regular construction of the summer home ranges. For stags, the two periods of change took place in August-September and the end of April. For hinds the range change was at the beginning of October and the end of April. Certain individuals showed differences of a few days or weeks.

The differences of the home ranges of hinds and stags within the territories and between these territories were compared by using a t-test. The changes of habitat types and activity patterns were examined with a paired t-test.

3 RESULTS

In the course of the year the change of the size of home ranges showed similar dynamics in the two territories; the summer home range was always smaller than the winter one. Measuring with an MCP in Zala County, the summer home range for hinds was 1,310 ± 700 hectares and the winter range was 2,570 ± 1,130 ha. In Sopron the hinds used 530 ± 415 hectares in summer. In winter it was 1,140 ± 600 ha (*Figure 1*).

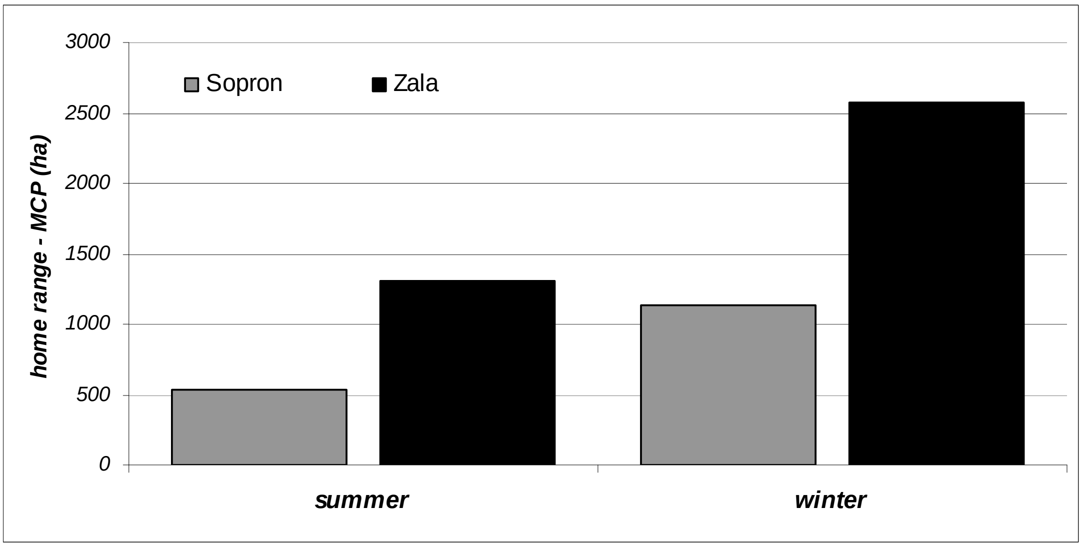


Figure 1. Home ranges of hinds in Sopron and Zala by seasons

The Zala home ranges were obviously bigger. The difference between the summer home ranges was significant ($p = 0.05$). In winter the difference between home ranges was conspicuous, but not significant due to the larger standard deviation. In summer the stags in Zala were moving over 1,500 ± 820 ha. In winter they ranged over 5,310 ± 2,230 ha. In Sopron the home range of the collared stag was 1,180 ha in summer and 4,110 ha in winter (*Figure 2*).

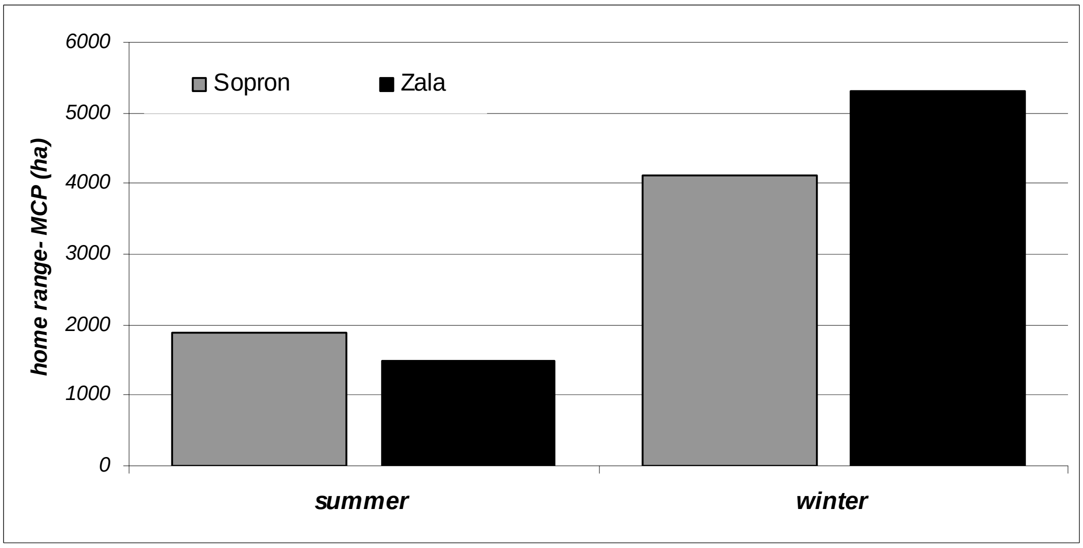


Figure 2. Home ranges of stags in Sopron and Zala by seasons

In Zala the winter home range overlapped the summer range in 5 out of 7 cases. However, in two cases a shift in home range was observed within a certain forested area even if the stags sometimes visited their summer home range during the winter. Red deer moving in higher regions of the Sopron mountains showed a definite home range shift because they were moving toward the foothills at the beginning of winter. There were two exceptions. One hind had a summer home range in the foothills and only expanded its original home range in winter. The other exception was the three legged hind which did not move from its particularly high altitude home range even in winter.

It is striking that in Zala there was no difference between the summer home range of hinds and stags ($p > 0.05$). However, the winter home range of stags was much larger than that of hinds ($p = 0.04$). Examination of the annual home ranges with an MCP method revealed that the average home range of stags (5,307 ha) is larger than that of the hinds (2,576 ha), ($p = 0.02$). When investigated with a 90% Kernel method, the difference was much smaller and was not significant at 1,291 and 705 ha respectively, ($p > 0.05$). In contrast to the MCP method, the Kernel method focuses on the density distribution of points, and consequently the larger home range of stags was mostly due to rambling. The core of their home range did not significantly exceed that of the hinds.

In summer, the daytime home range of the Sopron stags was always smaller than the night-time range ($p = 0.05$). In a number of cases, we observed a shift in the home range, due to the disturbance of the territory (*Figure 3*).

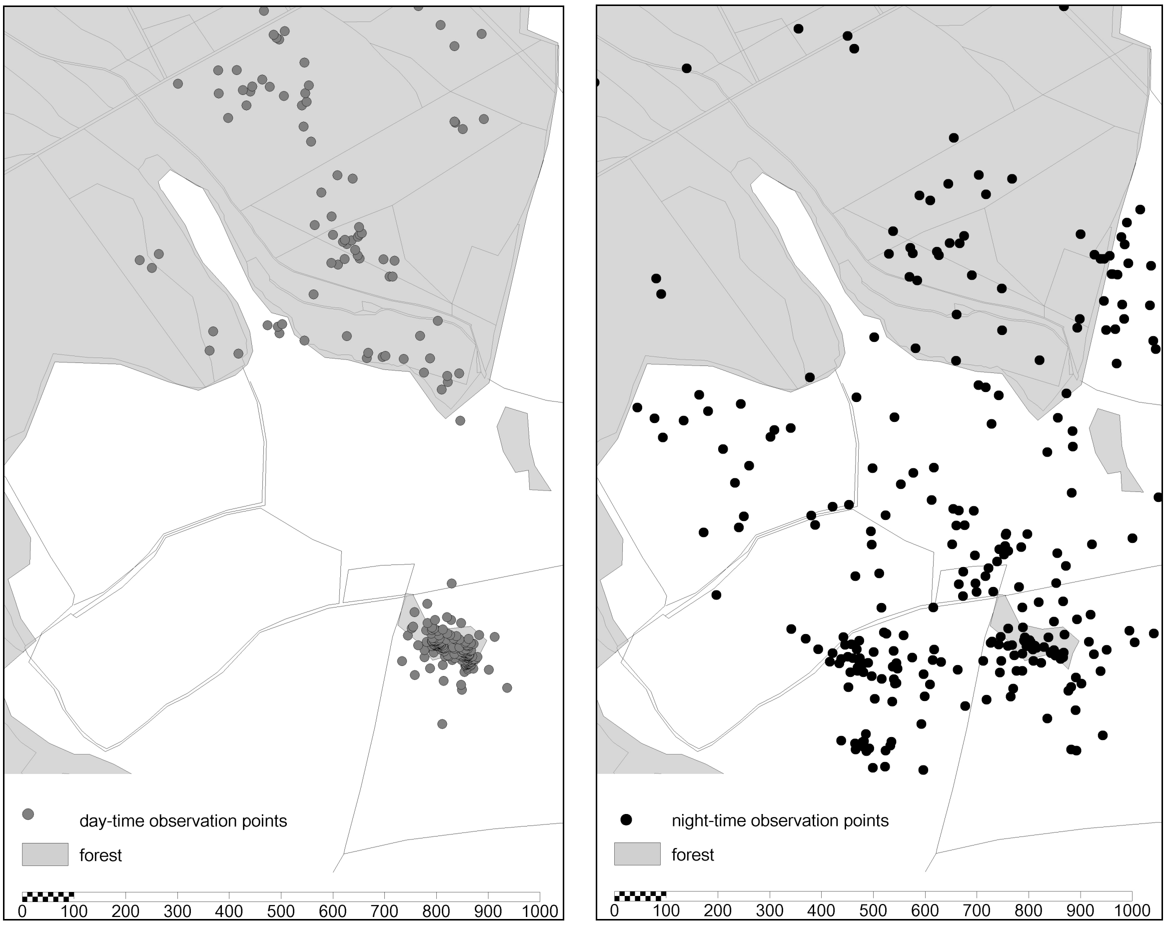


Figure 3. Day and night-time home range of a collared Sopron red deer (daytime observation points, night-time observation points)

In Zala the night-time and daytime home ranges did not differ in most cases.

There were large differences in terms of open habitat use, not only between the two populations, but also between certain individuals within the same population. On average the Zala deer used open habitats in a far more intensive way than the Sopron deer, based on the annual data (42% : 23%). When analysed on a monthly basis, the difference was significant ($p = 0.000$) (*Figure 4*).

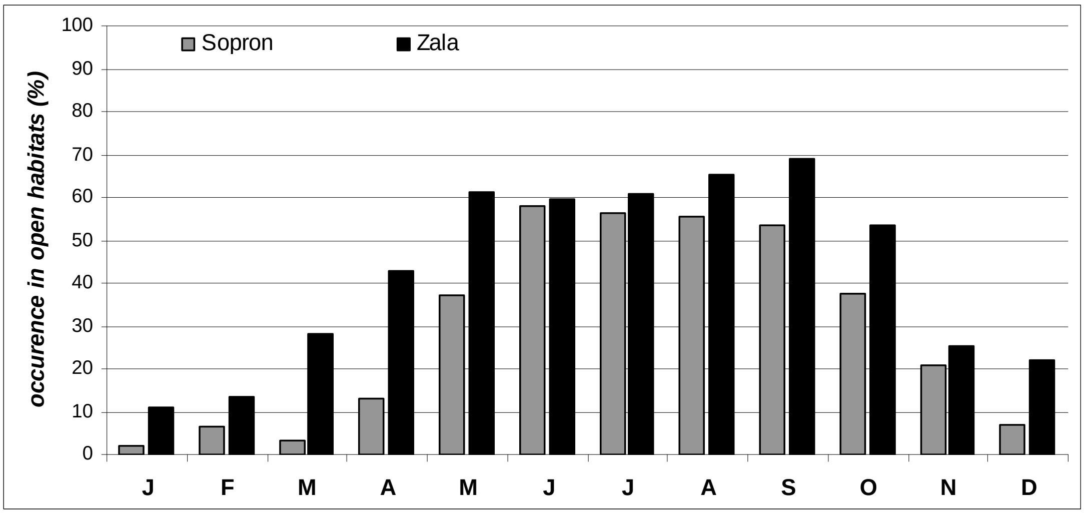


Figure 4. Use of open habitats in the case of Sopron and Zala deer

It was also conspicuous that the hinds used open habitats more often than the stags (p=0.04). The difference was particularly striking in summer during the period of antler growth.

The daily activity of the Sopron deer was less than the Zala deer both in summer and in winter (p= 0.000). The greatest difference in activity was in the winter daylight hours (*Figure 5*).

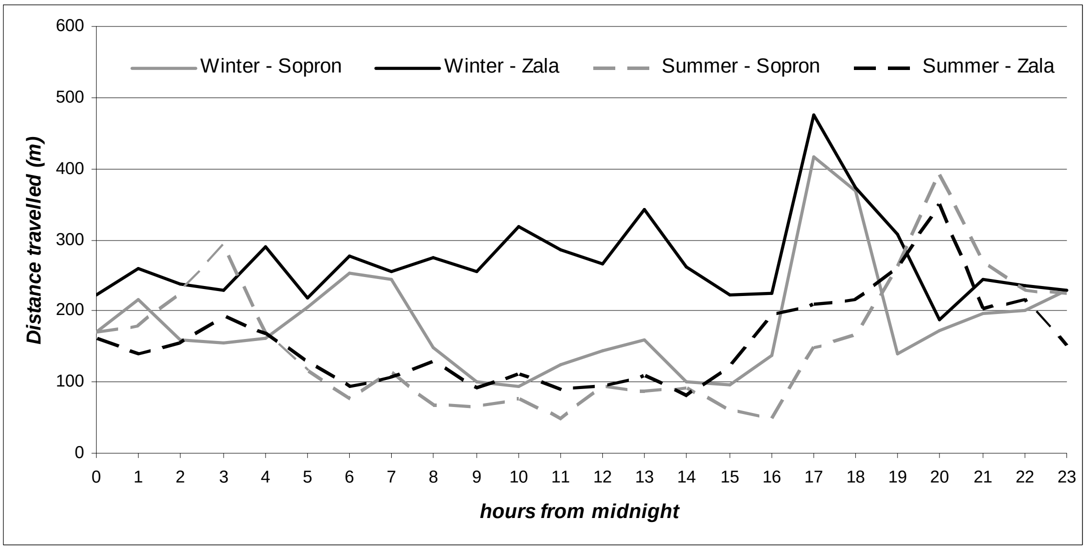


Figure 5. Daily activity patterns of Sopron and Zala deer

This was due to less cover and more disturbances. There were two activity peaks in summer in both territories. The smaller one was in the early dawn hours, the other in the late evening hours. In winter there was no dawn activity peak, but there was an evening peak.

4 DISCUSSION

The size of the home range of deer species may be determined by several factors. These are food supply and the habitat which provides the food, (Said – Servanty 2005), population density (Kjellander et al. 2004), the season, the sex of the deer, feeding style and body mass (Mysterud et al. 2001). In this investigation, the differences between the home ranges of both stags and hinds were significant and the seasonal change in the size of the home range was also proven. In flat territory the presence of large predator species resulted in smaller home ranges as recorded by Kamler et al. (2008). The ratios of the home ranges of the two sexes and the seasonal changes in the size of home ranges as recorded by Kamler were similar to those of this study. The size of the winter home range was significantly larger than the summer range in both territories.

Studies in France by Hamman et al. (1997) and Klein and Hamman (1999) described smaller home ranges of red deer than was observed in this study. Investigating the movement of the stags, Klein and Hamman (1999) found that the core-area of the range of older stags had several centres, an observation confirmed by results from this study. This was also the case for hinds. In the disturbed Sopron territory, one of the causes of the split of core-areas was the difference between night-time and daytime home ranges. In this area the summer daytime home range of deer was always smaller than the night-time range. In Zala there was no such difference between daytime and night-time home ranges. As with the French data, the main reason for the split of core-areas was defined by biological cycles (antler growing, rutting and the late rutting season), as well as the summer/winter home range shift.

In both territories seasonal changes to the home range were observed. This was more characteristic in the mountainous terrain near Sopron. In Zala, the home range shift was less common. In Sopron an exception was the movement of the hind that was close to the foothills in summer. If there is a shallow blanket of snow, the mountain deer which are not provided with supplementary feeding, have a characteristic pattern of behaviour, using the superior food supply found in habitats in non-forested valleys. In contrast the deer provided with supplementary feeding are more closely bound to a particular location, choosing to make their home range adjacent to a feeding site (Schmidt 1993). In case where home range shift was observed, the feeding places were used in a more intensive manner, unlike the deer that have a very localised pattern of ranging behaviour and can more easily use a local food supply (Luccarini et al. 2006). This means the home range shift is not only a characteristic of animals in a complex forest-agricultural habitat as examined by Szemethy et al. (2003) and Bíró et al. (2006). Furthermore the shift of home range is not only a characteristic of red deer in mountainous terrain, but it is also found in areas of low relief and in forested terrain, although to a lesser extent. The difference in the size of the action radius between the home ranges in Sopron (2.1 ± 0.3) and Zala (6.8 ± 3.0) was much smaller than the above mentioned studies, which had the values of 8.9 ± 2.1.

In this study the home range of stags was larger than that of the hinds, but the difference was much smaller when we investigated with an MCP method than with a 90 % Kernel method. The latter method did not show significant difference. This shows that within the home range of stags there was a particular core which was used more frequently. The positions were less common outside of this area. These areas were less frequently used by stags because of their habit of rambling. The conclusion is similar if we look at the research of Kamler et al. (2007), who examined the daily movement of hinds and stags and did not find a significant difference in their daily home ranges, although the stags had a slightly larger range. At the same time 12% of the hinds' annual home range and 3% of the range of stags was used every day. This also proves that the stags' home ranges include areas that are used in a less intensive way. It would appear that the difference of body mass of the two sexes might influence the size of home ranges, but this does not prove the significant difference between their home ranges as shown by the MCP method. The variation may be explained by the behavioural differences of the two sexes because stags moved within large areas between the summer home range, the area used in the rutting season, and from there towards their winter range.

The characteristics of the habitat, namely the forest cover ratio of the home ranges influenced the frequency of use of the open habitats. The disturbance of the area also played a role. Forest cover is important in the protection against predation (Wolff and Van Horn, 2003) and against human disturbance. At the same time the forest also provides thermal protection (Cook et al. 1998; Porter et al. 2002). These factors make it probable that in highly forested but disturbed areas the home range is smaller. These findings correlate very well with the results from this study.

It is also known that the quantity of the feed supply has a negative influence on the size of the home range, while the quality of the feed positively influences the size of the range (Saether and Andersen 1990; Mysterud et al. 2001). When feed is abundant, required dry matter intake is achieved with reduced ranging activity, but when feed quality is lower, the time required for rumination is extended. Taking account of these factors it is striking that the home range and daily activity of the deer in the Sopron study area was smaller than that of the deer in Zala, especially since the body mass and antler size was smaller in the Sopron deer than in the deer in Zala. The habitat of the Zala deer was less uniform, supplying feed in patches where it was found in larger quantities. These results make it probable that the reasons for the smaller Sopron home ranges are due to the following facts: a larger proportion of forested area, less variable habitat, more disturbances, habitat with lower quality and smaller quantity of available feed. Future research could possibly prove the effect and the weighting of these factors.

Hinds frequent the open habitats more than the stags, especially in the summer antler growing period and this supports the empirical experience of the reclusive behaviour of stags at this time.

The fact that the daily activity of the Sopron deer lagged behind the deer in Zala both in summer and in winter and especially in the early dawn hours, can be explained by more cover and more human disturbance in the Sopron region. In the Bavarian Alps Georgii (2004) found a bi-modal daily rhythm (two activity peaks) which was very similar to the results in this study.

Kamler et al. (2007) have drawn attention to the importance of human disturbance influencing the activity patterns of deer. In a primeval forest without human influences, they did not find activity peaks at dawn and dusk. Kamler stated that the activity of deer in undisturbed forests is defined by natural factors of precipitation, temperature, nutrition and rumination.

5 CONCLUSIONS

When home ranges of red deer expand in autumn there is an increased risk of crop damage over a larger area. Consequently from autumn to spring the objective should be to limit deer movements through the use of supplementary feeding, which should be distributed as far as possible from the forest habitats that are susceptible to damage. This is very important because the scattered data from this study also support the statement of McCorquodale (1993) that, when there is a deep blanket of snow, deer change their strategy, become sedentary and less selective about their food, increasing the danger of the browsing of seedlings. Results from previous investigations (Náhlik 2002) have shown that the incidence of browse damage was greatly increased when herbaceous plants of reforestations were covered by snow or in consequence of total removing of undesirable tree and shrub species during weeding.

The small daily home range of the Sopron deer have shown that red deer have a reduced pattern of movement during the day when there is more human disturbance, than at night. Activity patterns were similar in both territories. Increased disturbance and a consequent decrease in daily home ranges result in increased browse damage. This is because the deer are not able to move out of their hiding areas during the daytime. Consequently they have to feed in stands which provide resting place i.e. often in stands formed by saplings or pole-size trees. A similar problem occurs when heavy snow cover limits the movement of deer. In both cases game managers can help by snow ploughing, the provision of supplementary feed of a suitable quality and by seeking to reduce human disturbance.

Although in the highly forested Sopron area there are deer that spend their entire lives at higher altitudes within the forest, even in winter moving only to the edge of the forest, red deer usually choose a summer home range that includes an agricultural area with an adequate food supply. The risk of deer damage to agricultural crops is much greater in habitats adjacent to agricultural mosaic territories. If there are areas of land in private ownership or there is land that may be rented, also being suitable for use as ’game fields’, the strategic sowing of attractive fodder crops may help in drawing deer away from cultivated areas.

Acknowledgements: The study was partly financed by the project of the Regional Knowledge Centre of Forest and Wood Utilization (ERFARET) initiated by the National Office for Research and Technology (NKTH).

The authors express their thanks to Mark Malins of the University of Bath for reviewing and commenting on the manuscript prior to publication.

REFERENCES

ANDERSON, D.P. – FORESTER, J.D. – TURNER, M.G. – FRAIR, J.L. – MERILL, E.H. – FORTIN, D. – MAO, J.S. – BOYCE, M.S. (2005): Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landscape Ecology 20: 257-271.

BÍRÓ, ZS. – SZEMETHY, L. – KATONA, K. – HELTAI, M. – PETŐ, Z. (2006): Seasonal distribution of red deer (*Cervus elaphus*) in a forest-agriculture habitat in Hungary. Mammalia p. 70-75.

COOK, J.G. – IRWIN, L.L. – BRYANT, L.D. – RIGGS, R.A. – THOMAS, J.W. (1998): Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildlife Monographs 141: 1-61.

HAMANN, J.L. – KLEIN, F. – SAINT-ANDRIEUX, C. (1997): Daily home ranges of red deer (*Cervus elaphus*) hinds in the area of ‘La Petite Pierre’ (Bas Rhin). Gibier Faune Sauvage 14(1): 1-17.

HEEZEN, K.L. – TESTER, J.R. (1967): Evaluation of radio-tracking by triangulation with special reference to deer movements. Journal of Wildlife Management 31: 124-141.

KAMLER, J.F. – JEDRZEJEWSKA, B. – JEDRZEJEWSKI, W. (2007): Activity patterns of red deer in Bialowieza National Park, Poland. Journal of Mammalogy 88(2): 508-514.

KAMLER, J.F. – JEDRZEJEWSKA, B. – JEDRZEJEWSKI, W. (2007): Factors affecting daily ranges of red deer *Cervus elaphus* in Bialowieza Primeval Forest, Poland. Acta Theriologica 52(2): 113-118.

KAMLER, J.F. – JEDRZEJEWSKI, W. – JEDRZEJEWSKA, B. (2008): Home ranges of red deer in a European old-growth forest. American Midland Naturalist 159(1): 75-82.

KENWARD, R. (1987): Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis. Academic Press, New York

KJELLANDER, P. – HEWISON, A.J.M. – LIBERG, O. – ANGIBAULT, J.-M. – BIDEAU, E. – CARGNELUTTI, B. (2004): Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. Oecologia 139(3): 478-485.

KLEIN, F. – HAMANN, J.L. (1999): Diurnal home ranges and movements of red deer (*Cervus elaphus*) stags in the area of 'La Petite Pierre' (Bas Rhin). Gibier Faune Sauvage 16(3): 251-271.

LUCCARINI, S. – MAURI L. – CIUTI, S. – LAMBERTI, P. – APOLLONIO, M. (2006): Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations and effects of snow and winter feeding. Ethology Ecology & Evolution 18: 127-145.

MCCORQUODALE, S.M. (1993): Winter foraging behaviour of elk in the shrub-steppe of Washington. Journal of Wildlife Management 57(4): 881-890.

MYSTERUD, A. – PÉREZ-BARBERÍA, F.J. – GORDON, I.J. (2001): The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. Oecologia 127: 30-39.

NÁHLIK, A. (2002): Browsing in forest regenerations: impacts of deer density, management and winter conditions. Abstracts of the 5th International Deer Biology Congress. Québec, Canada

PORTER, W.P. – SABO, J.L. – TRACY, T.L. – REICHMAN, O.J. – RAMANKUTTY, N. (2002): Physiology on a landscape scale plant-animal interactions. Integrative and Comparative Biology 42: 431-453.

SAETHER, B-E. – ANDERSEN, R. (1990): Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constrains on behavioural decisions. Canadian Journal of Zoology 68: 993-999.

SAÏD, S. – SERVANTY, S. (2005): The influence of landscape structure on female roe deer home-range size. Landscape ecology 20(8): 1003-1012.

SCHMIDT, K. (1993): Winter ecology of nonmigratory Alpine red deer. Oecologia 95(2): 226-233.

SZEMETHY, L. – MÁTRAI, K. – BÍRÓ, ZS. – KATONA, K. (2003): Seasonal home range shift of red deer in a forest-agriculture area in southern Hungary. Acta Theriologica 48(4): 547-556.

SZEMETHY, L. – RITTER, D. – HELTAI, M. – PETÕ, Z. (1996): A gímszarvas tér-idő használatának összehasonlító vizsgálatai egy dombvidéki és egy alföldi élőhelyen [A Comperative Study of Time-Space Use of Red Deer at a Hilly and a Plain Habitat]. Vadbiológia 5: 43-59. (in Hungarian)

WOLFF, J.O. – VAN HORN, T. (2003): Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology 81: 266-271.

Acta Silv. Lign. Hung., Vol. 5 (2009) 119-130

Algorithms for Stem Mapping by Means of Terrestrial Laser Scanning

Gábor BROLLY[*] – Géza KIRÁLY

Department of Surveying and Remote Sensing, Faculty of Forestry, University of West Hungary, Sopron, Hungary

Abstract – Terrestrial laser scanning is an active remote-sensing technique, which has the potential to provide detailed spatial data for various applications in the fields of forestry and nature conservation. This study introduces algorithms and methods to extract individual tree parameters – such as tree location, stem diameter at breast height (DBH), and tree height – in automatic manner from terrestrial laser scanning data. The efficiency of the algorithms was tested on laser scanning data collected in a permanent sampling plot in the Hidegvíz-völgy forest reserve. The accuracy of the derived individual tree parameters was validated against tree metrics yielded by traditional field methods.

Remote Sensing / TLS / Modelling / Algorithms / Tree parameter estimation

Kivonat – Automatizált eljárások törzstérképek előállítására földi lézeres letapogatás alapján. A földi lézeres letapogatás egy új, aktív távérzékelési technika, mely részletes térbeli adatok szolgáltatásával az erdészeti és természetvédelmi célú térképezések és faállomány-felvételek hatékony eszköze lehet. Jelen tanulmány olyan módszereket és algoritmusokat mutat be, melyekkel egyesfák térképi pozíciója, mellmagassági átmérője, és magassága határozható meg automatizált úton, a földi lézeres letapogatás adataiból. Az algoritmusok hatékonyságát a Hidegvíz-völgy erdőrezervátum egyik állandósított mintapontján készített felmérés adataival teszteltük. A faegyedek helyének és méreteinek pontossági vizsgálatához az algoritmusok eredményeit hagyományos eszközökkel végzett térképezés és törzsenkénti felvétel adataival hasonlítottuk össze.

távérzékelés / TLS / modellezés / algoritmusok / egyesfa paraméterek becslése

1 INTRODUCTION

Forest reserves are strictly protected conservation units. Beyond conservation, study of the diversity and structure of undisturbed forests are prerequisites to understand their dynamics. Data acquisition should be carried out on individual tree level since the traditional metrics are related to single-trees. On this scale the classical inventory methods require manual measurements and a lot of fieldwork. Up-to-date terrestrial remote sensing techniques offer data from which forest-related information could be derived through modelling. *Models have the ability to hold spatially explicit information* such as distances, directions, angles, neighbourhood relations, overlays, and surface roughness, which makes more realistic structure characterization possible. Furthermore, parameters of accuracy are produced by

---

[*] Corresponding author: gbrolly@emk.nyme.hu, H-9401 Sopron, POB 132, Hungary

several modelling methods. Laser scanning is one of the most efficient techniques today, to obtain high-resolution data *on the scale of single trees* that can be utilized to stem mapping, realistic tree modelling and accurate parameter estimation.

Laser scanning, often referred to as LIDAR, is an active remote sensing technique, which can operate on aerial or on terrestrial platform. In both cases, three-dimensional coordinates, acquired by scanning laser range measurements, describe the surfaces of measured objects. Laser scanning is developed for topographical surveying and civil engineering, but can be an efficient tool in forestry-related data capture as well. The primary output, the so-called *raw data*, is a three-dimensional point cloud with high accuracy, however, *without any thematical or structural characteristics*. Considering the amount of data it is often necessary to use automated algorithms with minimal user interaction. To obtain information from raw data, *reduction and generalization is necessary which occurs in filtering and modelling procedures*. In the course of filtering measurements from relevant objects are extracted from the raw data set. Various object-types require special filtering methods. In the stage of modelling g*eometric primitives* - such as planes, surfaces, bodies of revolution, etc. – are fitted on the filtered points. Based on these models not only metric, but topological, structural, or even thematical information can be obtained with simple visual or computer aided spatial analysis.

In this study we focused on the branch-free bole of trees. The main goal was the evaluation of a terrestrial laser scanning for individual tree map and classical forestry-related tree metrics (DBH, tree height). The sample data derived from the first terrestrial laser scanning, which was carried out on a Hungarian forest site. The performance of the highly automated algorithms was validated against classical field measurements.

2 MATERIALS

Forest Reserve ER-46 (Hidegvíz-völgy, *Figure 1*) was selected for this study, due to its near-natural stand structure. This reserve is a mixed, approx. 85-year-old stand with sessile oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*), larch (*Larix decidua*) and spruce (*Picea abies*) species. Forest management had been moderate, which resulted in dense forest stand. The spruces are dying of bark beetle damage. The stand has a sparse lower canopy layer consisting of dying birches (*Betula pendula*), hornbeam and beech. There is a 50 × 50 m sampling grid over the reserve to assign permanent sampling plots for monitoring purposes.

The laser scanning survey was carried out on two permanent sample plots (No. 05-11 and 08-10), in April 2006 with a Riegl LMS-Z420i instrument (*Figure 2*). We investigated only the data collected around the No. 05-11 sample plot. The deciduous trees and bushes were in leaf-less state that time. The scanning was done on the whole upper hemisphere at three different tilting angles of the rotating axis of the instrument, resulting in a vertical range from 40° below the horizon to zenith with a 0.055° angle resolution. The scanning frequency was 24.1 KHz in each recording. The whole raw dataset contained 11,738,206 measurements on this plot. Simultaneously, colour photos were taken with a calibrated digital camera, so red, green, and blue colour components were assigned to each point after the registration. The surveying company Pi-Line performed the data acquisition, the registration and the colour coding. Scanning in single-scan modus (i.e. scanning from only the central position) is enough for forestry-related and individual tree parameter estimation (Thies – Spiecker, 2004); in addition it is highly economical then scanning from more directions. Our algorithms are optimised to evaluate single scans, although they can handle multiple scans as well.

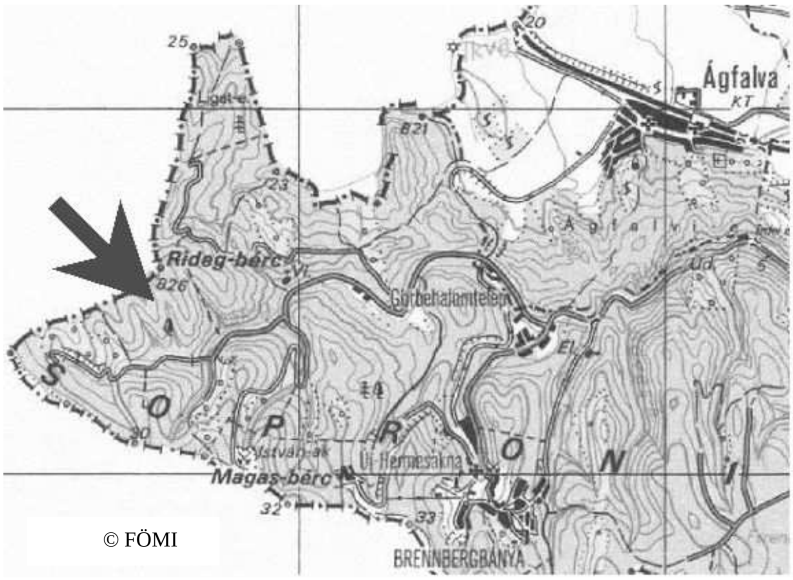


Figure 1. Hidegvíz-völgy forest reserve

Figure 2. LMS–Z420i laser scanner

Reference measurements including tree position, species, diameter at breast height, and tree height were collected with traditional instruments to verify the models. The coordinates of the trees inside the sample plot were acquired with a Leica 1200 Smart Station. Diameters at breast height were measured with measuring tape. The heights of the tree were measured by a digital photogrammetric workstation, utilising a stereo pair of colour aerial photos with 4 cm ground resolution.

3 METHODS

The introduced algorithms contained all the processing steps to obtain stem models from raw data. Beyond the individual stem models, an accurate digital terrain model (DTM) and a digital crown surface model (DSM) of the sample area were produced. The applied workflow was composed of adopted and self-implemented algorithms. At the beginning of the next sub-sections the basic ideas of the algorithms are described followed by the modification and implementation details. The structure of presented algorithms and their outputs are shown in *Figure 3*.

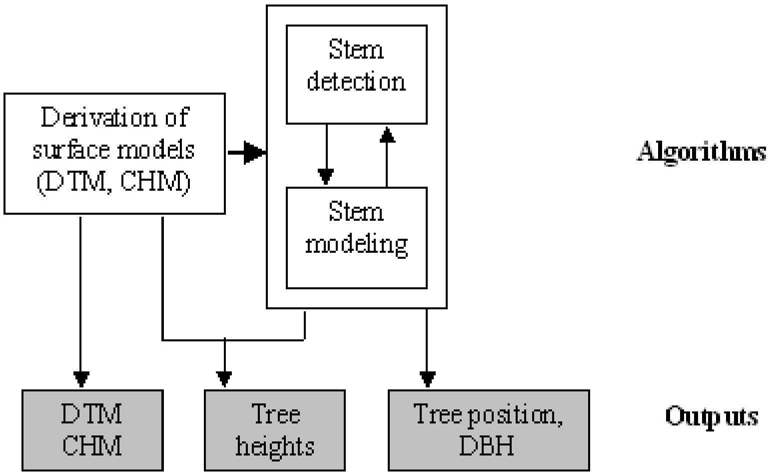


Figure 3. The workflow and outputs of the processing

3.1 DTM generation

The filtering of terrain points from raw data is a prerequisite to extract vegetation points and calculate relative heights above the ground. Simonse et al. (2004), Henning and Radtke (2006) propose regular sampling of locally lowest points followed by further filtering tests, e.g. if a point caused steep slopes on the surface, it could be excluded. Bienert (2006) obtained ground points in rough terrain by height-percentiles based filtering. Király and Brolly (2007) introduced a compound grid and TIN based coarse-to-fine iterative method. The first step was to select the lowest points in each cell of a coarse, regular grid. A TIN model was generated from these points and relative heights from the model were calculated for each point. The points with the lowest relative height were selected within each cell of a grid with double resolution then a new TIN model and relative heights were recalculated. The iteration went from 8 m to 0.5 m cell size. The densification of the point cloud would have permitted a better resolution DTM too, but our purposes did not require a more detailed model at the expense of much more processing time. Unfortunately, in the raw data some points situated below the terrain surface were found to be faulty, so some manual selections were also left, before creating the final DTM.

3.2 Stem detection

Measurements not assigned as terrain points can be tagged as *vegetation points*. Vegetation points contain measurements from stems, branches, foliage, and low vegetation. It is not possible to ascertain which points are measured from the same tree at this stage, so each point has to be assigned to a tree from which it was expectedly reflected. While neither the number nor the coordinates of the trees are known, this *classification procedure requires a pattern recognition algorithm*. This is a crucial issue while the accuracy of the final stem models depends on the reliability of the point-stem association. There were numerous methods developed in recent years aiming at stem detection from a laser scanning point cloud on automatic or semi-automatic manner (e.g. Aschoff – Spiecker 2004, Bienert 2007, Wezyk at al. 2007, Király – Brolly 2007). Most of the algorithms cut thin, horizontal cross-sectional slices in given heights above the ground from the cloud of vegetation points. The points in the same slice were treated as if they were in the same plane. Two-dimensional pattern recognition techniques were used on the points of the slices, e.g. Hough-transformation (Thies – Spiecker 2004). The effectiveness of automatic stem detecting methods varied between 20-100% depending on stand conditions and scanning parameters.

The tree detection method, which we are presenting in this paper, is a ’coarse to fine’ one, and has a well-separated pre-processing, clustering and classifying stage. The pre-processing and clustering stage are introduced in this section, and resulting in separate point clouds which are treated as stem-candidates. The classifying stage includes different shape fitting procedures that are performed on the points of stem candidates. While shape fitting is not only to verify the stem-candidates, but also to represent the geometry of the stems, these are presented in the next section.

In the pre-processing stage those points are selected which heights above the DTM are between 1 and 2 meters. Additionally the absolute heights of these selected points are converted to heights above the ground.

The clustering step has two objectives: (1) Excluding scattered, noisy points of bushes, and small branches, (2) Assigning each of the remaining points to a stem-candidate. These two goals are achieved through the same step, where height coordinates do not have role. The main idea is that the measurements on a stem surface are grouped; they are closer to each other, than those are reflected from thin branches or bushes. With statistical terms the denser stem points form *clusters* in the horizontal plane. Every point fulfilling the same *similarity criterion* is assigned to the same cluster. There are many clustering algorithms; in this study a modificated variant of the *k*-means method was implemented. In classical *k*-means clustering *n* number of data have to be divided to *k* number of clusters, where the similarity criterion is the horizontal Euclidean distance from the cluster's centre, and *k* is a known integer. Unknowns are the centre coordinates of the clusters. The detailed algorithm of *k*-means clustering is found in e.g. Fogaras – Lukács (2005). Since the number of trees was not known beforehand, some modifications of the classical *k*-means method were needed. The utilised clustering method was an iterative process, where the number of clusters, and also their centre coordinates had to be globally optimised considering two constrains: the minimal point number and the maximal cluster radius. The former ensures that small objects cannot become stem candidates, the latter guarantees that neighbouring stems are not merged in one cluster. These constraints make the optimisation process unambiguous, and are given as user-defined parameters. The approximate radius of the expected largest stem can be used for estimation of maximal cluster radius. The minimal point number depends on the data capture and can be given through an exploratory visual analysis. In our study the minimal point number was 100, the maximal cluster radius was 0.50 meter.

3.3 Stem modelling

After classifying stem measurements, the cross-section of the bole can be modelled by different geometric shapes, such as circles (Henning et al. 2004, Bienert et al. 2006), free-form curves (Pfeifer 2004), polygons (Wezyk et al. 2007), or cylinders (Pfeifer et al 2004, Hopkinson et al. 2004, Thies 2004). If the filtering has taken place in several heights, vertical approximation of the overlapping shapes is possible. From this model the position coordinates and diameter are available at any given height, out of which the one at breast height has particular importance. The reported accuracies of DBH estimation in the above mentioned studies are comparable to classical forest inventory methods (e.g. caliper, measuring tape). With the evaluation of overlapping shapes the reliability of stem-classification can be enhanced (Aschoff – Spiecker, 2004) and further spatially explicit data, such as tilting angle, stem profile and tapering of the stems become available (Bienert et al. 2007).

In our work the clusters were handled as stem candidates. In the filtering procedure geometric shapes were fitted onto the points of each cluster. In 2D the circle, in 3D the cylinder was chosen as geometric form to describe a stem. In case of circle the shape fitting was performed only at a thin horizontal section of a given height, while cylinders included all points of the clusters. The circle requires 3, the cylinder 5 parameters to be calculated. The parameterisation of circle (Eq. 1) and cylinder (Eq. 2) were the follows:

$$\| \boldsymbol{c} - \boldsymbol{p} \| - r = 0 \tag{1}$$

where $\boldsymbol{c}$ is a vector (X_c, Y_c) pointing to the center of circle,
$\boldsymbol{p}$ (X_p, Y_p) is a point on the circle,
r is the radius.

$$\| (\boldsymbol{a} - \boldsymbol{q}) \times \boldsymbol{n} \| - r = 0 \tag{2}$$

Where $\boldsymbol{a}$ is a point (X_a, Y_a, Z_a) on the axis,
$\boldsymbol{q}$ is a point (X_q, Y_q, Z_q) on the cylinder,
$\boldsymbol{n}$ (X_n, Y_n, Z_n) is the direction of the axis.

The 7 unknowns ($\boldsymbol{a}$, $\boldsymbol{n}$, r) can be reduced to 5 if $\mathbf{a}$ is defined on the zero level plane (Z_a=0), and $\boldsymbol{n}$ has a length of unit (Thies et al, 2004).

The shape fitting took place with the *least squares adjustment* minimizing the discrepancies in the sense of Euclidean distance between the measurements and the boundary of the fitted form. This procedure suppressed the effects of scattered points on the shape parameters and resulted in a more precise model. The final step was a classification, where the fitted shapes were verified with classification rules to decide if they were similar enough to be a stem. The classification variables were root mean square error (RMSE) of the shape fitting, and the relationship to the vertical neighbours in the case of multiple height sections (existence, difference of diameters). The right sets of classification parameters depend on the user's demands. The stricter rules provide fewer results with higher reliability and more precise models.

The comparison of the three variants of the above-described algorithms is performed in the following. The variants differ in how much the elevation data are involved in the filtering and classification steps. In the first method the filtering shape was a single circle (SC); the filtering took place only at breast height (1.30 m), in 10 cm thickness. The classification rules were minimal number of measurements: 15 and RMSE < 2.0 cm. In the second method the filtering was implemented in three different heights (1.00 m; 1.50 m; 2.00 m, with 10 cm thickness) independently from each other. This method was called multiple circles (MC). The classification rule was extended with a 5.0 cm threshold of radii's standard deviation in case of minimal two overlaying circles. The third method, which was called cylinder (CY), read data from 0.95 to 2.05 meters above the ground, and filtered them based on cylinder fitting. The classification rules were minimally 100 measurements, RMSE < 2.0 cm and maximum 45°-axis inclination. *In the case of CY, the exact elevation coordinates of the measurements were utilised in a 3D adjustment*. The working scheme of the variants can be seen in *Figure 4.*

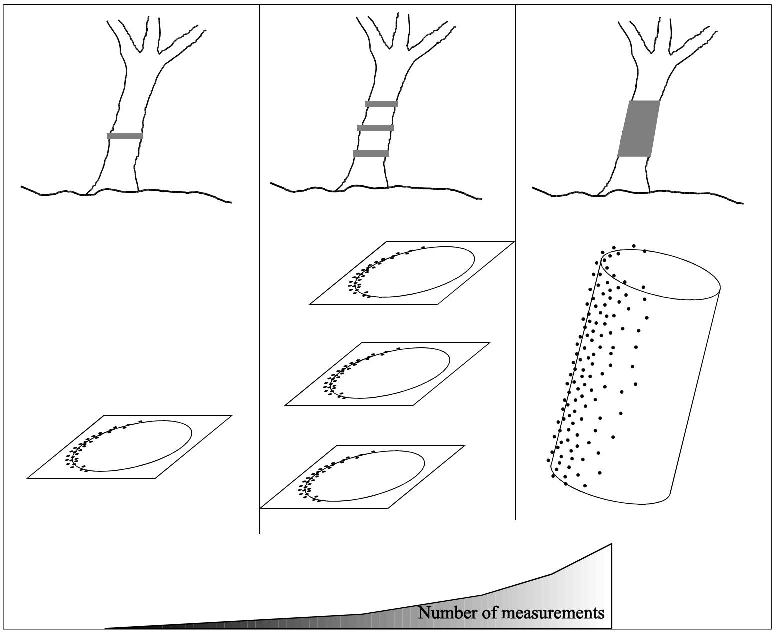


Figure 4. Principles of single circle (SC), multiply circles (MC), and cylinder (CY) tree recognition algorithms

3.4 Tree height estimation

There has not been any automatic method developed yet that would be capable to delineate individual tree-crowns in a middle dense canopy layer, because the point number decreases in this height so much that delineation of fine branches or leaves become impossible. Different *indirect methods* have been developed to locate treetops therefore (Hopkinson et al. 2004, Henning – Radtke 2006) or assess tree height based on stem tapering (Thies – Spiecker 2004, Király – Brolly 2008). The former are more reliable, the latter work even in stands with multiple canopy layers. Indirect tree top location means taking the highest point in the surrounding of the tree ground position then calculating their elevation difference. Actually it does not take into account the tree tilt angle and curvature, in spite of this Bienert (2006) achieved ± 80 cm accuracy, Wezyk (2007) ± 1.1 m absolute mean error against tacheometrically measured tree heights.

In our work, the surface of the upper crown (DSM) was modelled similarly to the DTM, but without iteration and the absolute highest points were selected within each 0.2 m cell. Unfortunately, the point density in the crown layer did not make it possible to make higher resolution digital surface model. It was very important, however, to smooth the DSM for the automatic tree-tip determination, so a minimum-curvature Spline interpolation was applied. The regularised Spline interpolation creates 1) a surface, which passes exactly through the data points, and 2) a minimum curvature smooth surface with a smooth first-derivative surface (Franke 1982). An inverse watershed modelling was applied to delineate individual tree crowns (Gougeon 1995, Király 1998). In these works, very high resolution aerial images with adequate lighting conditions created the basis. Assuming that the pinnacles of the trees are the brightest points in these images, and are separated by shadow area from each other, the task is to delineate them. Treating the image as an inverse digital terrain model, where the brightest pixels are the lowest points, the individual tree crowns are the watersheds, which can easily be separated by well-known algorithms (Jenson and Domingue 1988). These image-based methods were adopted succesfully on airborne laser scanning data, where the top of the trees were determined on the Digital Surface Modell (Hyyppä et al. (1999)).

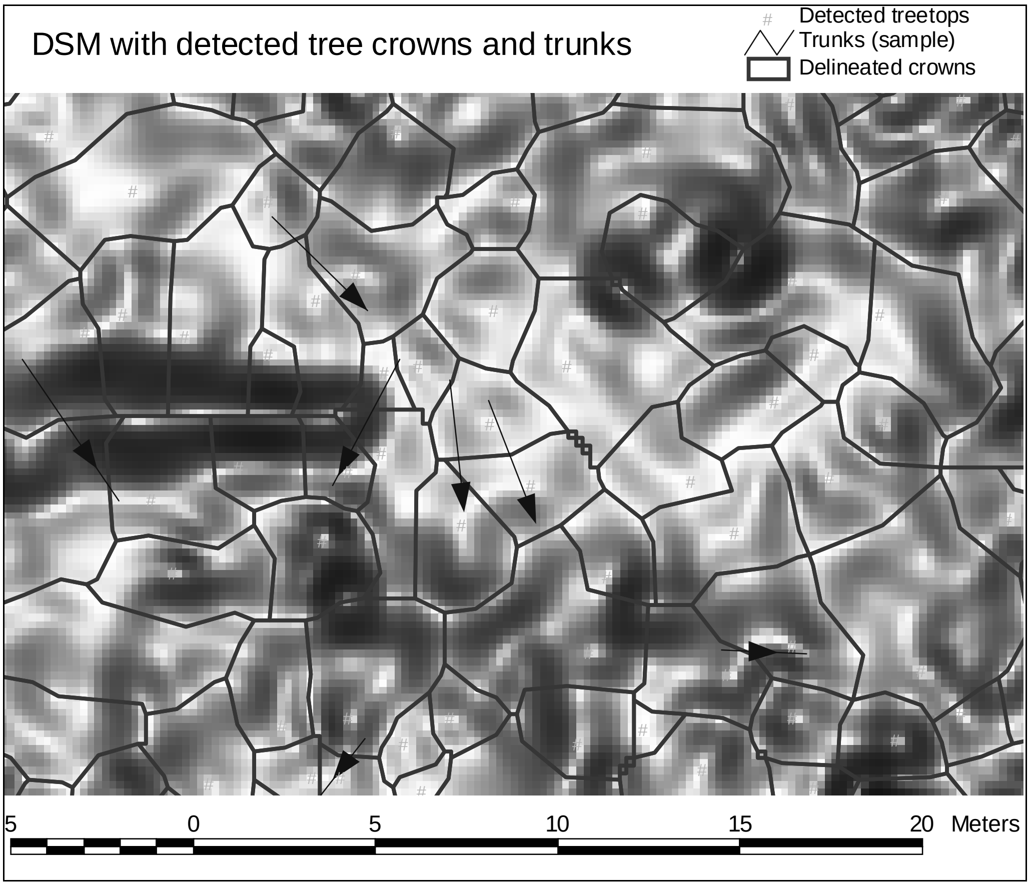


Figure 5. Delineated tree crowns and treetops on the shaded DSM (illumination from zenith). Arrows show the leaning directions of the modelled stems

For tree mapping not only the delineation is necessary but the delineated crowns have to be assigned to the detected stems to calculate individual tree heights. Tree height is estimated as the vertical distance of the stem’s ground position and the highest point of the crown. The first method implies that trees have minimal leaning, so the nearest local maximum to the root of the tree in XY direction has to be found. For two-dimensional stem models (SC and MC methods) this simple method was used in this study. In case of three-dimensional models, the leaning angles are calculated in the course of shape fitting. It was supposed that considering the leaning directions the tree positions and tree tops could be linked with better reliability. As second method that local maximum was accepted as the related tree top, which was horizontally closest to the intersection point of the cylinder's axis and the DSM.

4 RESULTS AND DISCUSSION

4.1 Tree mapping

The tree mapping covered stem detection and determination of central coordinates of the fitted geometrical forms (*Figure 6*). The automatic classification of species was not included in the presented algorithms, although would be possible in the future, based on the colour information. A reference height had to be defined on which the planar coordinates were concerned because of the leaning of the stems. When a tree consists of two or more stems forking below breast height, each stem has to be measured separately (Husch et al. 2003). The reference plane of 1.30 meter above the ground seems to be practical because the number of trees and the number of derived DBHs are equal in this case. *Table 1* shows the efficiency of the presented three variants. Classification errors were either rejection or misclassification. There were 213 trees, but only 173 (81%) were visible in breast height within 30-meter distance from the instrument. In this way the percentage of rejections involves the omissions due to the data capture and the failures of stem detection algorithms. All the three variants detected the stems with similar reliability, the mean proportion of misclassified stems were below 2.0%. On the other hand, the number of rejected trees depended significantly on the chosen variant. The reason of the different performance between circle-based (SC, MC) and cylinder-based stem detection presumably lies in the *degree of freedom* of the fitted primitives. All three algorithms worked iteratively, and required as many approximate starting values as the number of freedom of the primitives, which were 3 and 5 in case of circles and cylinders respectively. The starting values were approximated from the clusters statistics. About 10% of the cylinder fitting routines failed at the first iteration that suggested imprecise starting values. These adjustment routines turned to be successful actually when starting-values were more precisely given manually after visual inspection.

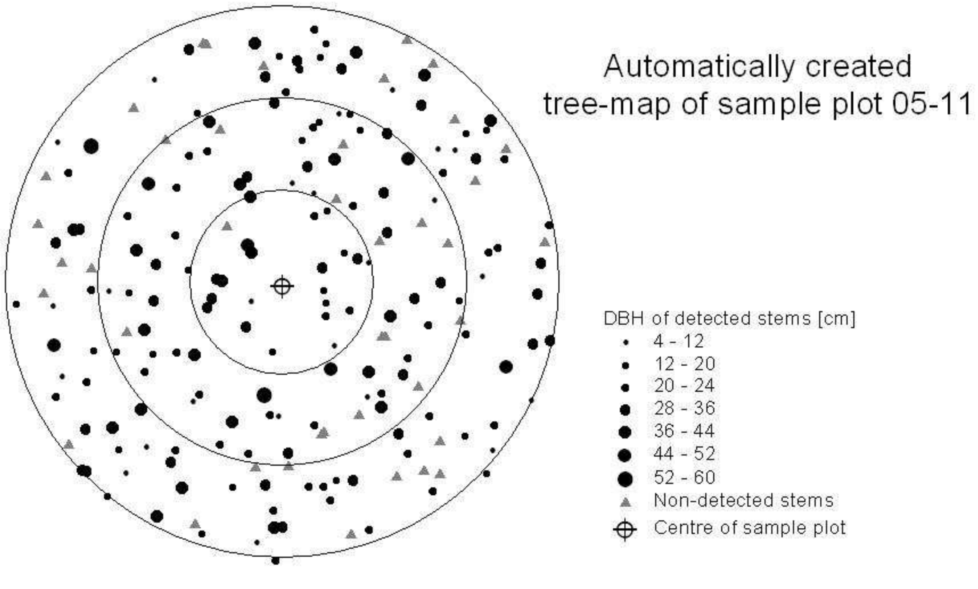


Figure 6. Stem map resulting from automatic tree detection.
Circles depict 10, 20 and 30 meters from the plot centre

Table 1. Reliability of stem detecting algorithms. (SC: single circle in breast height, MC: multiple circles in 3 different heights, CY: cylinder)

	SC	MC	CY
Correct	154	154	134
Rejection	59	59	79
Misclassification	3	0	1
Proportions (%)			
Correct	72.3	72.3	62.9
Rejection	27.7	27.7	37.1
Misclassification	1.4	0.0	0.5

4.2 DBH estimation

The comparative evaluation of different stem modelling on DBH estimation can be seen in *table 2*. The wide error intervals show that gross-errors (absolute errors exceed 3 times standard deviation of errors) were not removed from the statistics, because they can occur in the practical use as well. While these strongly alter the all-over statistics, the distribution of errors is presented in error-classes. The DBH estimations are underestimated significantly ($p<0.10$) in case of SC and MC models. On the contrary, Simonse et al. (2003), and Bienert et al. (2007) observed overestimations. We assumed the observed underestimations are resulted from the bark-roughness, because both the calliper and the tape measured on the outer surface of the bark, but the laser sampled the rifts, too. To make sure of this hypothesis, the typical smooth-barked beech and the typical rough barked larch were tested (one-tailed *t*-tests, $p<0.10$) on SC and MC methods. The mean error of estimations was unbiased for beech ($n=30$), but negatively biased for larch ($n=38$) in both methods. Although this supports our assumption, but it have to be noted that larch has often non-circular cross section, due to the varying bark thickness around its perimeter. This may cause errors when circles are fitted. Moreover, the points were projected to the horizontal plane, therefore a leaning stem even with circular cross-section provides elliptical projection, which leads to overestimation. For exact clarification beyond measuring the perimeter, at least the ellipticity has to be recorded, and a more flexible modelling curves – e.g. splines – are required.

Table 2. Accuracy of DBH estimation. Percentages show the presence within the error classes

	SC	MC	CY
Range (cm)	33.3	22.4	59.8
Bias (cm)	-0.8	-1.6	0.5
RMSE (cm)	4.2	3.4	7.0
Error classes (%)			
+/- 1 cm	23	27	26
+/- 3 cm	60	72	69
+/- 5 cm	84	86	84
+/- 10 cm	97	98	93

Note that the DBH estimation via cylinder-fitting shows twice lower global accuracy as in the case of the other two methods, although *the percentage of error classes are almost the same even up to 10 cm.* Consequently, there are more outliers with the CY method, as it was confirmed by the wider error-interval. The cylinder assumption is a stronger assumption than the circle assumption, mainly on curved stems. The results indicate a cylinder can model the stems more accurately even in one-meter length by series of circles, than. This reflects the problem of higher degrees of freedom also, while algorithms with more variables were more capable to solve the adjustment with noisy, scattered points without decreasing the a-posterior error of adjustment (RMSE of fitting) which had the indicator role in goodness-of-fitting.

4.3 Tree height estimation

The results of the different height calculations can be seen in *Table 3*.

Table 3. Accuracy of height estimations

	SC/MC	CY
min (m)	-9.90	-5.24
max (m)	0.75	2.28
mean (m)	-2.37	-0.27
stdv (m)	2.23	1.8

The height estimation without the consideration of leaning (SC/MC) significantly underestimated the height, and there were several deviations bigger than 5 m below zero. The other height estimation (CY) gave better accuracy, but it also gave some outliers as well. When we look at the visualisation of the cylinder method (*Figure 7*), it apparently gives the impression of over leaning of some trees. Considering that only a one-meter long cylinder defined the leanings, it seems to be promising to estimate the mean direction of the treetop.

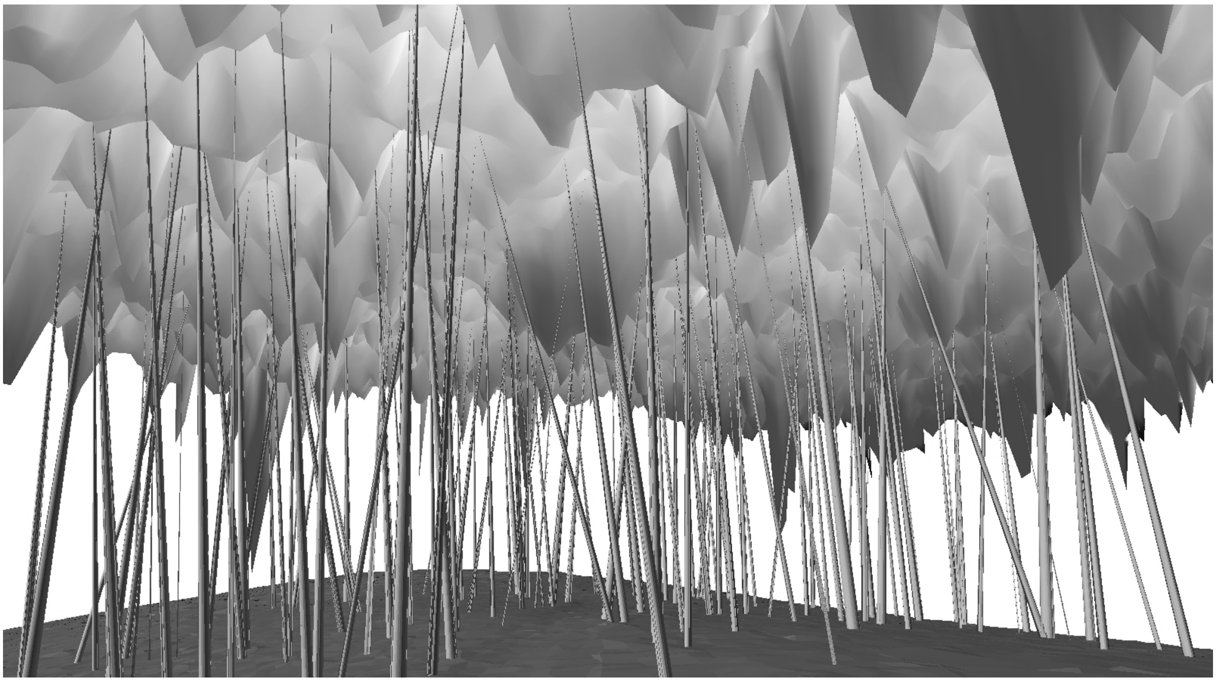


Figure 7. Extrapolation of cylindrical models up to the DSM

5 CONCLUSION AND OUTLOOK

The presented algorithms were tested on over two hundred sample trees per plot, which exceeded the number of sample trees in previous studies. It has to be noted that the conditions were optimal for automatic evaluation. The leaf-off state, the lack of shrubs, the high crown bases, and the moderate terrain variability facilitated the high productivity of automatic stem detection, although in this stage of the algorithms, visual verification of automatic stem detection is necessary. Stem detecting algorithms had a central role in single tree parameter estimation in considering the reliability of the subsequent model. We attempted to extend the filtering domain with height-related data in automatic stem detecting algorithms, and make a step from 2D through the more complex 3D filtering. Misclassifications were slightly decreased with independent repetition of 2D filtering in more height sections, and the reliability of this method exceeded, surprisingly, even the general 3D filtering. The *independence of shape recognition* ensures that initial errors are not spread to other height sections, and the sequence of shape parameters can serve as input for further classification criteria. The accuracy of the selected DBH estimation algorithms was in accordance with traditional field methods in most cases. Special strength of the cylinder-based modelling solution is that it can be efficient at non-vertical stems as well, and capable to filter also tilted branches in the crown. The presence of gross errors denotes that high inner accuracy does not guarantee sufficient shape fitting, especially in case of higher degree of freedom. Consequently a more robust technique is necessary in the future for 3D shape fitting to eliminate outliers. Shape fitting approximates the outer surface of the stem but it may differ physically from what classical instruments detect in case of rough barked trees, which might have caused systematic underestimation of DBH in our study. This could be resolved with the modification of the adjustment, e.g. with use of weights, or by residual distribution analysis. One can assume, that RMSE of fitting would have a potential to discriminate specie-groups according to their bark-roughness. The RMSE of fitting depends not only on bark-roughness however, but on the circularity of stem cross-section and on the random error of laser measurements, which are in the same magnitude. The leaning of the axis was obtained in the modelling procedure with the utilisation of height coordinates, which enhanced the tree top localisation on the DSM. The extrapolation from 1-2 m above the ground to the crown, can lead into mismatching of treetops however. Utilisation of a more complex 3D body can improve the results of height calculations, but also can introduce more gross errors by raising the degree of freedom. Another solution would be the reconstruction of the upper parts of the stems, from which not only the leaning, but the curvature could be estimated too.

Acknowledgements: We thank OTKA (Hungarian Scientific Research Fund, ref. No. T048999) for supporting this work. We also thank PiLine Ltd. for operating the Riegl instrument, processing and providing the laser-scanner data.

REFERENCES

ASCHOFF, T. – SPIECKER, H. (2004): Algorithms for the automatic detection of trees in laser scanner data. In: Proceedings of the ISPRS working group VIII/2, ”Laser-Scanners for forest and Landscape assessment”. Freiburg, Germany. 3-6 October 2004. 71-75.

ASCHOFF, T. – THIES, M. – SPIECKER H. (2004): Describing forest stands using terrestrial laser-scanning. In: Proceedings of the ISPRS working group VIII/2, ”Laser-Scanners for forest and Landscape assessment”. Freiburg, Germany. 3-6 October 2004. 237-241.

BIENERT, A. – MAAS, H. – SCHALLER, S. (2006): Analysis of information content of terrestrial laserscanner point cloud for the automatic determination of forest inventory parameters. In: ”Proceedings of Workshop on 3D Remote Sensing in Forestry”. Wienna, Austria. 14-15 February, 2006. 44-49.

BIENERT, A. – SCHELLER, S. – KEANE, E. – MOHAN, F. – NUGENT, C. (2007): Tree detection and diameter estimations by analysis of forest terrestrial laserscanner point clouds. In: ”Proceedings of ISPRS Workshop on laser scanning 2007 and SilviLaser.” Espoo, Finland. 12-14 September, 2007. 50-55.

FOGARAS, A. – LUKÁCS, A. (2005): Klaszterezés [Clustering]. In: IVÁNYI, A. (ed): Informatikai algoritmusok 2. ELTE Eötvös Kiadó, Budapest, 1397-1423. (in Hungarian)

FRANKE, R. (1982): Smooth Interpolation of Scattered Data by Local Thin Plate Splines. In: Comp. & Maths. with Applls. 8. (4): 237 – 281

HENNING, J. – RADTKE, P. (2006a): Detailed stem measurements of standing trees from Ground-based Scanning Lidar. Forest Science. 52 (1): 67-80.

HENNING, J. – RADTKE, P. (2006b): Ground-based Laser Imaging for Assessing Three-dimensional Forest Canopy Structure. Photogrammetrical Engineering and Remote Sensing. 72 (12): 1349-1358.

HOPKINSON, C. – CHASMER, L. – YOUNG-POW, C. – TREITZ, P. (2004): Assessing forest metrics with a ground-based scanning LIDAR. Canadian Journal of Forest Research. 34. 573-583.

HUSCH, B. – BEERS, T. – KERSHAW, J. A. (2003): Forest mensuration. John Wiley & Sons, INC. New Jersey. pp. 86

HYYPPÄ, J. – INKINEN, M. (1999): Detecting and estimating attributes for single trees using laser scanner. The Photogrammetric Journal of Finland. 16 (2): 27-43.

JENSON, S. K., DOMINGUE, J. O. (1988): Extracting Topographic Structure from Digital Elevation Data for Geographic Information System Analysis. In: Photogrammetric Engineering and Remote Sensing. 54 (11): 1593-1600

KIRÁLY, G. (1998): Multiscale images in forestry. In: ISPRS International Archieves of Photogrammetry and remote sensing. XXXII, 7. ISPRS Comission VII Symposium on „Resource and Environmental monitoring." Budapest, Hungary. 1-4 September, 1998. 365-369

KIRÁLY, G. – BROLLY, G. (2007): Tree height estimation methods for terrestrial laser scanning in a forest reserve. In: "Proceedings of ISPRS Workshop on laser scanning 2007 and SilviLaser." Espoo, Finland. 12-14 September, 2007. 211-215.

KIRÁLY, G. – BROLLY, G. (2008): Modelling single trees from terrestrial laser scanning data in a forest reserve. The Photogrammetric Journal of Finland. 21 (1): 37-50.

PFEIFER, N. – WINTERHALDER, D. (2004): Modelling of tree cross sections from terrestrial laser scanning data with free-form curves. In: Proceedings of the ISPRS working group VIII/2, "Laser-Scanners for forest and Landscape assessment". Freiburg, Germany. 3-6 October 2004. 76-82.

PFEIFER, N. – GORTE, B. – WINTERHALDER, D. (2004): Automatic reconstruction of single trees from terrestrial laser scanner data. ISPRS- International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences. Vol XXXV, Part B. 114-119.

RIEGL (2007): Data sheet, LMS-Z420i. Online: http://www.riegl.com/terrestrial_scanners/lms-z420i_/420i_all.htm

SIMONSE, M. – ASCHOFF, T. – SPIECKER, H. – THIES, M. (2003): Automatic determination of forest inventory parameters using terrestrial laser scanning. In: "Proceedings of the ScandLaser Scientific Workshop on Airborne Laser Scanning of Forests". Umea, Sweden. 2-4 September, 2003. 271-257.

THIES, M. – SPIECKER, H. (2004): Evaluation and future prospects of terrestrial laser scanning for standardized forest inventories. In: Proceedings of the ISPRS working group VIII/2, "Laser-Scanners for forest and Landscape assessment". Freiburg, Germany. 3-6 October 2004. 192-198.

THIES, M. – PFEIFER N. – WINTERHALDER D. – BEN G. (2004): Three-dimensional reconstruction of stems for assessment of taper, sweep and lean based on laser scanning of standing trees. Scandinavian journal of forest researche. 19: 571-581.

WEZYK, P. – KOZIOL, K. – GLISTA, M. – PIERZCHALSKI, M. (2007): Terrestrial laser scanning versus traditional forest inventory first results from the polish forests. In: "Proceedings of ISPRS Workshop on laser scanning 2007 and SilviLaser." Espoo, Finland. 12-14 September, 2007. 424-430.

Acta Silv. Lign. Hung., Vol. 5 (2009) 131-143

Economic Impact of Forest Damage in an Alpine Environment

Sandra NOTARO[a*] – Alessandro PALETTO[b] – Roberta RAFFAELLI[a]

[a] Department of Economics, University of Trento, Via Inama 5/I, 38100 Trento, Italy
[b] Agricultural Research Council, Forest Monitoring and Planning Research Unit (CRA-MPF), Trento, Italy

Abstract – The aim of this paper is to evaluate the situation regarding the main types of damage to forests and their respective economic consequences, with reference to a case study in the Italian Alps (Trentino province). Each kind of damage (wind and snow, defoliation, fire and tillage) has been analysed in terms of its impact on four forest functions (production, protection, tourism-recreation and carbon sequestration) and evaluated in monetary terms. Market value was used to estimate the production and carbon sequestration functions, replacement cost method for protection, and contingent valuation for tourism-recreation. Applying desk research on damage caused by the main biotic and abiotic factors to this particular case study led us to estimate a annual damage of about € 1,624,921 equal to 4.71 € per hectare. This can be considered a lower bound estimate of possibly greater damage. Another interesting result that emerged from the evaluation exercise is that the wealth of information produced through monitoring and scientific research in the last twenty years does not readily lend itself to economic analysis.

forest damage / forest functions / interaction between damage and functions / economic valuation / Alpine forests

Kivonat – Az erdőkárok gazdasági hatása alpesi környezetben. A dolgozat célja, hogy összefoglalja az erdőt érő káros hatások főbb típusait és ezek gazdasági hatásait egy hegyvidéki esettanulmányon keresztül (Trentino tartomán y, Olaszország). A tanulmányban minden fontosabb kártípus (szél, hó, levélvesztés, tűz és mezőgazdasági művelés) elemzése és monetáris értékelése megvalósult az erdő különböző funkciói tekintetében (gazdasági, védelmi, rekreációs és széndioxid megkötés). A gazdasági és széndioxid megkötési funkció értékelése a piaci érték segítségével történt, a védelmi funkció tekintetében a helyettesítési érték módszere került alkalmazásra, a rekreációs funkció pénzügyi értékelése a feltételes értékelés módszerével valósult meg. A tényleges esettanulmány tekintetében a biotikus és abiotikus tényezők által okozott kár évente legalább 1,6 millió €, ami hektáronkénti 4,71 €-nak felel meg. A mintaterület értékeléséből levonható tapasztalat az, hogy az elmúlt húsz évben a tudományos kutatás és monitoring során összegyűjtött adatok nem kifejezetten segítik elő a pénzügyi értékelést.

erdőkárok / erdő funkciói / károk és az erdő funkciói közötti kölcsönhatások / gazdasági értékelés / az Alpok erdei

---

[*] Corresponding author: sandra.notaro@economia.unitn.it; I-38100 Trento, Via Inama 5/I, Italy

1 INTRODUCTION

Over the last couple of decades there has been a growing awareness of the necessity to monitor and evaluate the economic and ecological impact of damage to forest ecosystems (Efremov – Sheshukov 2000) in order to implement adequate prevention policies.

Considerable headway has been made in monitoring, both in setting up international cooperation programmes and monitoring networks, and in determining the status, changes and trends in forest condition indicators on an annual basis. The International Co-operative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests, UN/ECE), which was set up in 1985, represents a milestone in this endeavour. The first Ministerial Conference for the Protection of Forests in Europe (MCFPE 1990) stated the necessity to hone the Pan European Monitoring System. A specific criterion on forest ecosystem health and vitality (Criterion 2) was endorsed by the Lisbon MCFPE in 1998. This was followed by the European Union Directive on National Emission Ceilings for Certain Atmospheric Pollutants in 2001, and the Forest Focus Regulation in 2003.

Despite these measures, the recent report on the condition of forests in Europe (BHF 2006) asserts that 23.3% of trees in Europe are classified as damaged or dead.

The economic consequences of these health conditions are not easy to investigate. Studies tend to focus on the economic impact of a single specific biotic or abiotic agent (see, for instance Lyytikäinen-Saarenmaa – Tomppo 2002 for defoliation by sawfly or Peryron – Bokouma 2001 for windfalls), partly because different evaluation methods are applied for different types of damage, which are often strongly based on hypothesis and may also rely on rough estimates (Peyron – Bakouma 2001).

In spite of these difficulties, this study is an attempt to estimate the economic consequences of the main types of damage found in Alpine forests, with the aim of giving the public decision maker an objective criterion for fine tuning prevention policies. Four selected types of damage (defoliation, fires, wind/snow damage and tillage[1]) have been analysed in terms of their impact on four forest functions (production, protection, tourism-recreation and carbon sequestration) and evaluated in monetary terms. The reference is a case study in the Italian Alps, the small Autonomous province of Trentino (6.207 km^2), where forest covers more than half of the total area.

2 MATERIALS AND METHODS

2.1 Site characteristics/features

2.1 Study site

An evaluation of biotic and abiotic damage to forests was undertaken for the Autonomous Province of Trento (North East Italy). This is a mountainous province, with limited flat areas at the bottom of the valleys, wide-spread terracing and steep mountain slopes. Approximately 60% of the surface area is situated over 1000 m above sea level with more than 50% of the population concentrated in urban areas below 400 m. 56% of the area (345,180 hectares) is covered by forest, prevalently spruce (59.6%), secondarily European larch (17.5%) and silver fir (10.8%). More than 70% of forests are managed according to ten-year plans.

---

[1] We chose these four types of damage because they are widely recognised as the most common ones.

2.2 Valuation of forest functions

In order to evaluate the impact of each type of damage on the forests of the province, we started by estimating the annual monetary value of the main forest functions: production, protection, tourism-recreation and carbon sequestration. Biodiversity was not considered because, even in physical terms, “at present it is impossible to evaluate everything” (Efremov – Sheshukov 2000, p. 59).

Methods used to estimate the various functions were market value for production and carbon sequestration, contingent valuation for tourism-recreation, replacement cost for protection.

In more detail, timber products were estimated by distinguishing two components for each species (Merlo – Ruol 1994): the “real monetary value” of annual increment actually harvested (utilisation), and the “potential monetary value” of the remaining annual increment that could have been used but which was in fact left as an investment in timber capital. According to Merlo and Ruol (1994) the latter was estimated at 50% of the average timber price.

The replacement cost method, employed to estimate the protection function, considers the possibility of replacing ecological services with man-made systems (Faber et al. 2002). The evaluation is based on the cost of setting up human-engineered systems to substitute the protective function of the forest. In detail, we estimated the costs of the building, amortization and upkeep of naturalistic engineering works. The kind of engineering works we considered - terracing with simple palisade and grass, avalanche barrier racks with chequer-board arrangement, fascines with cuttings – was tailored to the three main level of hazard identified (high/low risk of landslides, high risk of avalanches). We also factored in to this estimate the cost of maintaining the river beds of the main waterways with the construction of check dams and sills. We have used this method because it takes into account both the reconstitution of protective forests and the investment costs to maintain it. The method that considers only the investment costs would have produced a lower value and wouldn’t have capture the entire protection value.

A rough estimation of the tourism-recreation value of Trentino forests was undertaken through integrating data of tourism-recreation flows in Trentino forests (for details see Scrinzi et al. 1997) and results of a contingent valuation (Alberini – Kahn 2006; Mitchell – Carson 1989) study carried out on a representative forest of Trentino, the forest of Lavazè (Val di Fassa). A random sample of 724 visitors (response rate 93%) was surveyed. Interviews were carried out during the summer of 2002. Respondents were asked about their willingness to pay an entrance ticket to cover the costs of the naturalistic management (willingness to pay pro-capita was 2.58 €). The scenario explained that the lack of public funds would lead to a modification in the current type of forest management, from selective cutting to clear cutting. This would imply the modification of the recreational experience of tourists (for more details see Notaro et al. 2006).

The carbon sequestration value was first estimated for the forest of Lavazè by quantifying carbon flows in monetary terms (Notaro et al. 2008) and then extended, with due correction, to the entire province. The quantity of carbon contained in trunks, branches, twigs, crowns, dead wood and stumps (Fattorini et al. 2005) was first defined in physical terms, by applying specific estimation methods for plant mass and volume. Fattorini et al. (2005) estimated the above-ground phytomass of a population of trees in a monitoring area using a probabilistic sampling scheme (randomised branch sampling) (Gregoire et al. 1995). The forecast model, seeking to estimate plant mass and volume for each stand and the corresponding total value per surface unit, starts with data from the diameter measurements for all trees and corresponding height measurements for a sample of trees. Results show that, on average, the plant biomass of the spruce and swiss pine populations contain a carbon stock of 217.4 t/ha (Fattorini et al., 2005; Notaro et al., 2008).

The results were re-elaborated on the basis of different conversion factors between tonnes of dry substance and cubic metres of timber, for all the forest stands in the province, ascribing them to the prevailing species. The price per tonne of CO_2 eq. absorbed was as calculated by Lecocq et al. (2004) for the Joint Implementation and Clean Development Mechanism projects in the first five months of 2004 to modulate this price to data collected for the other functions. We did not use prices of carbon markets because we wanted to refer to projects related to the forestry sector. This was determined at 5.52 \$/tCO_2 eq. (equal to 6.79 €/tCO_2 eq., and 24.89 €/tC).

Total and per hectare values for individual functions are presented in *Table 1*. Afterwards the economic impact of each type of damage is estimated and detracted.

Table 1. Use values of Trentino forests

Forest function	Total economic use value (million €/year)	Use value per ha (€)
Timber production	25,97	75.22*
Hydro-geological protection	25,49	73.84[2]
Tourism-recreation (summer season)	13,97	40.47
Carbon sequestration	31,71	91.86

* 46.02 € real value and 29.20 € potential value

2.3 Valuation of forest damage

Forest health and vitality is affected by several external disturbance factors that can be divided into two main macro-categories: abiotic and biotic factors. This second category also included human factors. These abiotic and biotic factors may have positive, neutral or negative impacts on forest ecosystems, the negative impact being considered as damage. In the literature different definitions of forest damage exist. Reimoser et al. (1999, p.48) considers it as "a problem caused by an unwanted condition", while for the WPR (1994) forest damage is the "reduction of tree population in forests caused by acidic precipitation, forest fires, air pollution, deforestation, pests and diseases of trees, wildlife, etc.". In this paper the authors used this second definition, considering the tillage as a reduction of tree population.

In some cases the damage can be attributed with precision to one specific agent (i.e. wind), in other cases signs of damage (i.e. defoliation) may be ascribed to diverse factors, each with a synergistic effect on forest condition. Types of damage will also tend to impact differently on each forest function.

For the above reasons we shall make only partial use of the previous classification, focusing largely on the following **four** observable categories of damage and on their consequences for every single forest function.

- Defoliation caused by biotic agents such as phytophagous insects or root rot, or by abiotic agents such as late frost or drought, deposition of air pollutants or acidification;
- Damage caused by fires, mainly due to intentional or accidental human action and to a smaller extent to natural phenomena;

---

[2] Considering only the public investment costs, the average value (years 2004-2005-2006) of the protective function of forests in Trentino was 118,027 € (0.34 €/ha).

- Wind and snow damage: the uprooting of whole trees or breaking off of branches due to early or late snow, or tornados. This category includes both natural hazards and the results of poor forest management;
- Tillage: deforestation due to change in land use for building and agricultural purposes, or to create ski runs and other infrastructure.

After having estimated the value of every single forest function, the economic impact of each type of damage was estimated and deducted.

Data were collected throughout the provincial territory regarding surface area and cubic metres of timber affected by the main biotic, abiotic and anthropogenic factors. From the forestry literature we extrapolated the parameters for reducing the value of each function.

a) Defoliation

Defoliation intensity is one of the main parameters used in evaluating forest health since leaves immediately indicate a plant's physiological condition. Causes of defoliation are root fungi, nutritional imbalance, defoliating insects (Kurkela 2002) and other abiotic factors. Starting from the hypothesis that, regardless of cause, any degree of defoliation results in a reduction in photosynthesis, we can deduce that this damage will affect three main forest functions. As well as reduced wood growth and carbon dioxide exchange with the atmosphere,[3] there is also the fact that a large number of yellowing plants (depigmentation) and plants without leaves (defoliation) negatively effects the tourist-recreational function (Lovett 2002). On the other hand, Meier et al. (2005) found that defoliating insect attacks have a negligible effect on hydro-geological protection as long as they do not compromise many specimens.

According to the literature, defoliation effects wood growth, causing a decrease in the productivity of a forest stand proportional to the percentage of defoliation. The Pan-European Monitoring System distinguishes five degrees of defoliation based on percentage leaf or needle loss in individual subjects in the stand (BHF 2006). An average range of timber loss for different degrees of defoliation (*Table 2*) was estimated according to results obtained by Straw et al. (2002) and Petràš (2002). Moreover, data from permanent plots (Level I of the Pan-European Monitoring System) provides us with the percentage of trees defoliated in Trentino. After converting this into hectares of damaged surface, we can end up with an estimate of the economic loss in timber value for each defoliation class.

Table 2. Defoliation classes and reduction in timber increment

Defoliation class	Degree of defoliation	Needle/leaf loss (%)	Loss in volume (%)
0	None	< 10	0-10
1	Slight	11-25	11-20
2	Moderate	26-60	21-30
3	Severe	61-99	31-40
4	Dead	100	100

Source: our elaboration on UN ECE (2004), Straw et al. (2002) and Petràš (2002).

---

[3] The relationship between defoliation caused by phytophagous insects and carbon dioxide is more complicated. For example, while an intense attack by insects leads to a lower level of carbon dioxide absorption, a high concentration of CO_2 reduces leaf damage caused by defoliating insects (Knepp et al. 2005).

In a similar way to that described for the production function, leaf loss reduces carbon dioxide exchange with the atmosphere due to the diminished photosynthesis (Knepp et al. 2005). Therefore, the procedure adopted is similar to that used to calculate average loss in timber capital, using fixed carbon flow in lieu of increment. The percentages of reduction in carbon sequestration (5% for defoliation class 0; 15% for class 1; 25% for class 2; 35% for class 3) were deduced from the relationship between cubic metre of timber and the percentage of stored carbon per cubic metre (Matthews 1993; Tucker et al. 2004).

Even if it is likely that tourists perceive the increase in defoliation as a disutility, as far as we know no study exists that investigates the functional form of this relationship. Since Gatto et al. (2005) applied a 20% reduction in the presence of a specific defoliation agent, we decide to increase this percentage (30%) in order to take into account the joint effect of more severe defoliation agents and differences in species affected.

b) Fire

Fire impacts most heavily on forest functions because it indiscriminately affects everything in its path and the drastic rise in temperature causes irreversible damage to vegetation, ranging from injury to the destruction of timber (Pettenella 1997). The passage of fire may even destroy the forest floor and fertile topsoil, triggering erosion, jeopardising the stability of mountain slopes (APPA 2004) and leading to a decrease in carbon sequestration.

The effect of fire on tree vegetation varies according to botanical species (passive pyrophyte or active pyrophyte species) and the nature of the fire. Type of fire are: forest floor fire when the organic ground layers burn slowly, low or grazing fire when it burns the layers of grass and shrubs below the tree canopy, high or crown fire when the fire reaches the tree crowns and spreads from crown to crown (Mazzoleni – Aronne 1993). In every case timber extracted is damaged with, at best, depreciation in value or, at worst, total loss of the wood (Pettenella 1997). In our case study, since most are crown fires, we hypothesised a total timber loss, zero tourism-recreation and zero hydro-geological protection value for the area crossed by fire. The effect of fire on carbon function is a short term slowdown in carbon sequestration due to the vegetation's alteration and/or destruction estimated by Fattorini et al. (2005) at 13.6 tCO_2/ha.

c) Wind and snow damage

Freak weather events can cause forest trees to fall. Heavy early or late snow or very high winds are climatic events that facilitate tree fall and therefore upset the hydro-geological balance (Andreatta 2005). Such phenomena lead to a loss of hydro-geological protection, tourism and recreation, and cause timber depreciation (Nieuwenhuis – Fitzpatrick 2002). However, a positive effect on biodiversity has been noted since "windthrow stimulates arthropod biodiversity in forests" (Wermelinger et al. 2003, p. 79).

Wind and snow damage lead to a total loss of potential value because forced utilisation converts timber capital into real value. Consequently, in order to avoid double counting, the loss of potential value was ignored and a reduction in real value of 30% (Nieuwenhuis – Fitzpatrick 2002) was applied to the entire area damaged. This percentage is justified by the fact that, on average in the case studied, timber was extracted quickly and *Ips typographus* attacks were limited. For tourism-recreation we follow Schneider et al. (2006) and assume a 40% decrease in the economic value. Protection and carbon sequestration, and consequently their value, are to be considered temporarily non-existent over the area affected by wind and snow damage. Consequently we detracted the whole value of these functions for damaged hectares.

d) Tillage

Although tillage is largely limited by legislation in the major European countries, it should not be overlooked as the transformation from "forest" to "other land use" completely wipes out all forest functions.

Tillage leads to total loss of the protective, tourism-recreational and carbon sequestration functions over the area in question. The quality and the economic value of timber is not affected, so the real value of the production function remains the same.

Table 3 summarises all these considerations about the intensity of damage produced by biotic and abiotic factors on the economic value of a forest.

Table 3. Effects of damage by biotic and abiotic factors on the economic value of annual flows of forest products and services

Damage/Function	Defoliation	Fires	Wind/snow damage	Tillage
Production	Negative	Negative	Negative	Total loss
Protection	Negligible	Negative	Total loss	Total loss
Tourism-recreation	Negative	Total loss	Negative	Total loss
Carbon sequestration	Negative	Negative	Total loss	Total loss

The calculation methods applied in this case study, to translate a biological complexity into economic terms, use large scale simplifications and assumptions based on *Table 3*. For example assuming total loss for carbon sequestration function is clearly a simplification of a dynamic process. At the time of tillage only the carbon sequestration flow is lost[4]. Carbon remains stored in wood products but will return to the atmosphere according to the durability of the products: in a short period of time for fire wood, in a longer one for furniture (Gower 2003). Moreover the effects of forest fire on timber depend on intensity and types of fires. In some circumstances forest fires destroy the wood completely, in other circumstances the damages are only superficial and limited. Defoliation has a negligible effect on hydrogeological protection of forest - in cases of slight and moderate degree of defoliation - while severe defoliation can compromise the effect of canopy cover as a physical screen which intercepts precipitation and holds onto a certain fraction of it preventing single drops from reaching the bare soil (Piussi 1994).

3 RESULTS AND DISCUSSION

a) Defoliation

The main causes of defoliation in Trentino's forest ecosystems can be traced to attacks by the pine processionary caterpillar (*Thaumetopoea pityocampa*) (about 4,200 ha in 2000-2001), by larch bud moths (*Zeiraphera griseana*) (defoliation of over 3,800 ha in 1999-2000) and by spruce rust (*Chrysomyxa rhododendri* and *abietis*) (no more than 30% defoliation). During the period 1990-2001 a total of 3,442 m^3 of timber was felled for health reasons, equal to 286.83 m^3 of timber per year (Salvadori et al., 2002). Overall, the last 13 years monitoring of the 18 permanent plots (Level I) located in Trentino Alto-Adige showed average levels (class 2, 3 and 4) of defoliation on 6.7% of all trees (Salvadori et al. 2003). If the plots correctly represented the total forested areas, this would equal a damaged area of 23,127 ha.

---

[4] As we were interested in calculating annual values we refer only to flows.

Assuming that the quantity of timber harvested will remain constant along lines laid down in the ten-year management plan, independently of defoliation, the reduction in value almost only concerns the potential value. Considering the loss in timber for classes 2, 3 and 4 *(Table 2)*, we used a total weighted mean of 35% for the three classes. At a potential value of 29.2 €/ha the total loss is equal to € 236,358.

Similarly, for carbon sequestration we employed an average reduction of 25% in the value of the function for all hectares suffering damage. In this way the total loss is € 531,112 *(Table 4)*.

Table 4. Economic evaluation of defoliation damage

Forest function		Hectares class 2-3-4 defoliation	Reduction in value per ha damaged (%)	Economic value of damage (€/year)	Incidence of damage on value of single functions (%)
Production	Real		0	0	-
	Potential		35	236,358	2.34
Protection			0	0	-
Tourism-recreation			30	280,785	2.01
Carbon sequestration			25	531,112	1.67
Total		23,127		1,048,255	

In order to calculate effects of defoliation on tourism-recreation, the value was reduced by 30% (Gatto, 2005), resulting in a monetary loss of 280,785 € per year. Finally, consequences on hydro-geological protection were not measured because they can be considered negligible. The various causes of defoliation have lead to an estimated annual loss in value of around € 1,048,255.

b) Fire

For the decade 1991-2001 there was a progressive reduction in the number of fires, except for variations associated with climate trends and with a peak during the early nineties, levelling off at 359.34 ha of forestland crossed by forest fires yearly, or 0.1% of the forests in the province (APPA 2004).

The economic loss associated to the productive function, € 16,537 in real value and € 10,493 in potential value *(Table 5)*, derives from the product of the value per hectare of timber by the number of hectares burnt. The same procedure was used for tourism-recreation and protection. For estimating the economic effect of fire on carbon dioxide exchange we applied the previously mentioned values. The passage of fire produces an annual loss of carbon sequestration of € 33,183.

Table 5. Economic evaluation of fire damage

Forest function		Hectares effected by fire (ha)	Reduction in value per ha damaged (%)	Economic value of damage (€/year)	Incidence of damage on value of single functions (%)
Production	Real		100	16,537	0.10
	Potential		100	10,493	0.10
Protection			100	26,534	0.10
Tourism-recreation			100	14,542	0.10
Carbon sequestration			–	33,183	0.11
Total		359.34		101,289	

c) Wind and snow damage

Trees felled by strong winds, and to a lesser extent by snow, are the main source of forced utilisation and timber loss in the province of Trento, where 36,842 m^3/year of forced utilization has been registered for the period 1991-2001 (Salvadori et al. 2002). Given the growing stock for forests in the province (202 m^3/ha), we can estimate that the average area affected per year is equal to 182 ha. The value of the damage was calculated by detracting the full value of all the functions except production and tourism recreation. A 30% reduction was applied to the real value of production and, as previously mentioned, no reduction was considered for the potential value. A 40% reduction was assumed for the tourism-recreational function following Schneider et al. (2006).

The most part of the economic loss due to wind and snow is in the production function (€ 426,409) *(Table 6)*.

Table 6. Economic evaluation of damage from wind and snow

Forest function		Hectares of fallen trees (ha)	Mc of accident timber	Reduction in value per ha damaged (%)	Economic value of damage (€/year)	Incidence of damage on value of single functions (%)
Production	Real			30	426,409	2.68
	Potential			0	0	-
Protection				100	13,467	0.05
Tourism-recreation				40	2,952	0.02
Carbon sequestration				100	16,753	0.05
Total		182.38	36,842		459,581	

d) Tillage

An average of about 67 hectares of forest in the province of Trento was tilled per year over the decade 1991-2001 (APPA 2004). These figures enable us to calculate an annual loss of € 15,796 linked to tillage related factors *(Table 7)*.

Table 7. Economic value of damage from tillage

Forest function		Hectares tilled (ha)	Reduction in value per ha damaged (%)	Economic value of damage (€/year)	Incidence of damage on value of single functions (%)
Production	Real		0	0	0.00
	Potential		100	1,959	0.02
Protection			100	4,956	0.02
Tourism-recreation			100	2,716	0.02
Carbon sequestration			100	6,165	0.02
Total		67.12		15,796	

Adding up the four different types of economic damage we end up with an estimated annual damage of about € 1,624,921 equal to 4.71 €/ha. Considering the lack of data on wildlife damage, this result can be considered a lower bound estimate. If biodiversity had been considered, the final result may have been different because its value is likely to increase noticeably with respect to other flows of environmental benefits (Leslie 2005), but we cannot predict the magnitude of this change.

If we look in detail at the breakdown of this damage, we find that defoliation counts for 65% of lost forest value, and wind and snow damage for 28%. Damage from fire and tillage cause only 6% of the loss.

The order of importance is different if we consider only production *(Table 8)*. Here the main cause of economic damage is wind and snow, whereas defoliation counts for about half of it. This is what is normally reported by forest experts who tend to think mainly in terms of production when judging the seriousness of damage.

Table 8. Economic value of damage on timber and non-timber functions (€/year)

Forest function	Economic value	Defoliation damage	Damage from wind and snow	Fire damage	Damage from tillage
Production	25,967,144	236,358	426,409	27,030	1,959
Protection	25,489,005	-	13,467	26,534	4,956
Tourism-recreation	13,969,435	280,785	2,952	14,542	2,716
Carbon sequestration	31,706,530	531,112	16,753	33,183	6,165
Total		1,048,255	459,581	101,289	15,796

It is interesting to note how the relationship between damage to timber and non-timber functions differs according to damage type. While wind and snow damage weighs more heavily on timber production, the other three kinds of damage preponderantly affect non-timber services.

Pondering on the overall effects of forest disturbance means fully recognising the multi-functional role of forests and realizing the increasing societal demand for non-timber services. On the other hand, it also implies that forest managers must take into account that their decisions may affect the production of timber and non-timber services in a very different way. Without going further into this issue, we shall mention just two aspects. The currently dominating monocultural and even-aged forest structure seems to be more vulnerable to windthrow and other damaging agents (Lekes – Dandul 2000) and failure to tend forests provokes stress in plants, identifiable by a rise in defoliation level (Nicolotti et al. 2005).

4 CONCLUSIONS

It is clearly perceived at a European level that "disturbances have a considerable impact on forestry" and that this impact is likely to increase for at least two reasons: first of all a rise in both total forest area and total stand volume, implies that a "larger resource may be damaged", secondly changes in climate seem to increase the intensity and frequency of storms and contribute to a deterioration in forest health (Schelhaas et al. 2003; UN Economic and Social Council 2003). Moreover, not all European forests are as well managed as in the case study area presented here.

Nevertheless, trying to quantify the economic impact of different forest disturbances proves to be a real challenge. The wealth of information produced in Europe through twenty years of monitoring and scientific research does not readily lend itself to economic analysis. The format in which damages are published in monitoring reports varies greatly (share of standing stock damaged, volume that has actually been removed from the forest, area crossed by fire). Furthermore, the huge amount of information on the occurrence of disturbance, collected at the national level and available for consultation in the Database on Forest Disturbance in Europe, is not immediately usable for economic analysis (Schelhaas et al. 2003).

An evaluation exercise such as that carried out in this study has to resort to numerous hypotheses, due to the lack of data usable for economic purposes. For small areas, such as the one analysed here, this also happens because the few empirical studies generally deal with a single biotic or abiotic factor, or because we are not certain that the areas studied or the plots monitored are truly representative of a wider area. In addition, when estimating the reduction in price due to fires, wind and snow damage and health factors, we had to approximate data supplied by the limited number of studies available, in order to adapt them to our specific case.

However, as our discussion shows, an overall economic estimate of damage to timber and non-timber functions allows us to build a more precise picture of the effects of the different disturbance factors in play, drawing attention also to the reduction in externality production. This knowledge may also facilitates the fine tuning of adequate prevention policies.

Acknowledgements: This paper was written within the framework of the FORTIS Project "Sustainable Innovation and Entrepreneurship for Forestry Institutions" and the EFOMI Project "Ecological Valuation in Alpine Forest Ecosystems by Integrated Monitoring", funded by the Autonomous Province of Trento (research fund).

REFERENCES

ALBERINI, A. – KAHN, J.R. (2006): Handbook on Contingent Valuation. Edward Elgar Publishing, Cheltenham, UK.

ANDREATTA, G. (2005): Problemi di instabilità meccanica in popolamenti forestali della regione alpina. [Mechanical instability in alpine forest stands: causes and possible remediations.] *Forest@* 2: 166-171. (in Italian)

APPA (2004): Rapporto sullo stato dell'ambiente 2003. Provincia Autonoma di Trento. Assessorato all'Urbanistica e Ambiente, Trento.

BHF (2006): The condition of forests in Europe. 2006 Executive Report. UN/ECE, Geneva and Brussels.

EFREMOV, D.F. – SHESHUKOV, M.A. (2000): Ecological and economic evaluation of the consequences of catastrophic fires in the Russian Far East: the Khabarovsk territory example of 1998. IFFN 22: 53-62.

FABER, S.C. – COSTANZA, R. – WILSON, M.A. (2002): Economic and ecological concepts for valuing ecosystem services. Ecol Econ 41: 375-392.

FATTORINI, L. – GASPARINI, P. – NOCETTI, M. – TABACCHI, G. – TOSI, V. (2005): Observation and forecast models for above-ground tree and shrub phytomass in the forest stands of Trentino. Studi Trent. Sci. Nat. Acta Biol. 81: 75-121.

GATTO, P. – BATTISTI, A. – ZOCCA, A. – BARRENTO, M.J. – BRANCO, M. – PAIVA, M.R. (2005): The economic evaluation of integrated pest management strategies: a case-study in Setùbal Peninsula, Portugal. 6th International Conference of the European Society for Ecological Economics, 14-17 June 2005, Lisbon.

GOWER, S.T. (2003): Patterns and mechanisms of the forest carbon cycle. Annu. Rev. Environ. Resour. 28: 169-204.

GREGOIRE, T.G. – VALENTINE, H.T. – FURNIVAL, G.M. (1995): Sampling methods to estimate foliage and other characteristics of individual trees. Ecology 76: 1181-1194.

KNEPP, R.G. – HAMILTON, J.G. – MOHAN, J.E. – ZANGERL, A.R. – BERENBAUM, M.R. – DE LUCIA, E.H. (2005): Elevated CO_2 reduces leaf damage by insect herbivores in a forest community. New Phytol 167: 207-218.

KURKELA, T. (2002): Crown condition as an indicator of the incidence of root rot caused by Heterobasidion annosum in Scots pine stand. Silva Fenn 36: 451-457.

LECOCQ, F. (2004): State and Trends of the Carbon Market 2004. Development Economics Research Group, World Bank based on data and insights provided by Natsource LLC and PointCarbon, 37.

LEKES, V. – DANDUL, I. (2000): Using airflow modelling and spatial analysis for defining wind damage risk classification (WINDARC). Forest Ecol Manag 135: 331-344.

LESLIE, A. (2005): Qu'attendrons-nous des forets. OIBT Actualités des forets tropicales 13: 14-16.

LOVETT, G.M. – CHRISTENSON, L.M. – GROFFMAN, P.M. – JONES, C.G. – HART, J.E. – MITCHELL, M.J. (2002): Insect defoliation and nitrogen cycling in forests. BioScience 52: 335-341.

LYYTIKÄINEN-SAARENMAA, P. – TOMPPO, E. (2002): Impact of sawfly defoliation on growth of Scots pine *Pinus sylvestris* (Pinaceae) and associated economic losses. B Entomol Res 92: 137-140.

MATTHEWS, G. (1993): The carbon content of trees. Forestry Commission Technical Paper 4, 21.

MAZZOLENI, S. – ARONNE, G. (1993): Introduzione all'ecologia degli incendi. Liguori Editore, Napoli.

MEIER, F. – ENGESSER, R. – FORSTER, B. – ODERMATT, O. (2005): Situazione fitosanitaria dei boschi 2004. Istituto federale di ricerca per la foresta, la neve e il paesaggio WSL, Birmensdorf, 22.

MERLO, M. – RUOL, G. (1994): Ipotesi di remunerazione dei servizi pubblici offerti dai beni silvo-pastorali: un'analisi economico-finanziaria. Genio Rurale 4: 9-16.

MITCHELL, R.C. – CARSON, R.T. (1989): Using Surveys to Value Public Goods: the Contingent Valuation Method. Resources for the Future, Washington D.C.

NICOLOTTI, G. – GONTHIER, P. – RETTORI, A. – CELLERINO, G.P. (2005): Fitopatie quale causa di riduzione della funzione ecologica degli alberi. [Decrease of the ecological function of trees due to fungal diseases.] Forest@ 2: 85-91. (in Italian)

NIEUWENHUIS, M. – FITZPATRICK, P.J. (2002): An assessment of stem breakage and the reduction in timber volume and value recovery resulting from a catastrophic storm: an Irish case study. Forestry 75: 513-523.

NOTARO, S. – GIOS, G. – PALETTO, A. (2006): Using the Contingent Valuation Method for ex ante service innovation evaluation. Schweizerische Zeitschrift für Forstwesen, 157: 507-512.

NOTARO, S. – PALETTO, A. – RAFFAELLI, R. (2008): The economic valuation of non-productive forest functions as an instrument towards Integrated forest management. In: Cesaro L, Gatto P, Pettenella D (eds.): The Multifunctional Role of Forests: Policies, Methods and Case studies, EFI Proceedings 55: 301-312.

PETRÁŠ, R. (2002): Reduction of timber value from damaged spruce stand after their dieback. Journal of Forest Science 48: 80-87.

PETTENELLA, D. (1997): La contabilità ambientale delle risorse forestali: un'applicazione all'analisi degli incendi boschivi. Genio Rurale 2: 41-51.

PEYRON, J.L. – BAKOUMA, J. (2001): First Economic Valuation of 1999 Windfalls in France. International IUFRO Symposium The Economics of Natural Hazards in Forestry, Solsona 7h-10h June 2001.

PIUSSI, P. (1994): Selvicoltura generale. [General Silviculture.] UTET, Torino, Italy. (In Italian)

REIMOSER, F. – ARMSTRONG, H. – SUCHANT, R. (1999): Measuring forest damage of ungulates: what should be considered. Forest Ecology and Management 120: 47-58.

SALVADORI, C. – MARESI, G. – BARBIERO, R. (2002): Stato fitosanitario delle foreste trentine Anno 2001. Provincia Autonoma di Trento, Istituto Agrario di San Michele all'Adige, Trento, 29.

SALVADORI, C. – TAIT, D. – VALENTINOTTI, R. – CONFALONIERI, M. – MINERBI, S. – AMBROSI, P. (2003): Stato delle chiome e deposizioni atmosferiche nei boschi del Trentino Alto Adige. Linea Ecologica 35: 51-57.

SCHELHAAS, M.J. – SCHUCK, A. – VARIS, S. (2003): Database on forest disturbance in Europe (DFDE). Technical description. European Forest Institute, Internal Report 14, 44.

SCHNEIDER, J. – VYSKOT, J. – KUPEC, P. – MELICHAROVÁ, A. – FIALOVÁ, J. – SMÍTKA, D. (2006): Wind calamity damages to functions of forest in High Tatras National Park. Zbornik radova, Jahorina - NP. Sutjeska, 05-08: 397-403.

SCRINZI, G. – FLAMMINJ, T. – CUTRONE, A. – FLORIS, A. (1997): Un modello di valutazione quantitativa della pressione turistico-ricreativa sulle risorse forestali. Esempio di applicazione al territorio della provincia di Trento. ISAFA 96/4.

STRAW, N.A. – ARMOUR, H.L. – DAY, K.R. (2002): The financial costs of defoliation of Scots pine (Pinus sylvestris) by pine looper moth (Bupalus piniaria). Forestry 75: 525-536.

TUCKER, S.A. – NEBEKER, T.E. – WARRINER, M.D. – JONES, W.D. – BEATTY, T.K. (2004): Effects of artificial defoliation on the growth of cottonwood: simulation of cottonwood leaf beetle defoliation. In: Connor KF (ed.), Proceedings of the 12th biennial southern silvicultural research conference, Gen. Tech. Rep. SRS-71, Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 169-171.

UN ECONOMIC AND SOCIAL COUNCIL (2003): Progress in implementation: forest health and productivity. Report to the Secretary-General, Geneva, 13th March 2003, E/CN.18/2003/5, 1-17.

WERMELINGER, B. – DUELLI, P. – OBRIST, M.K. (2003): Windthrow stimulates arthropod biodiversity in forests. In: Mason, F.; Nardi, G.; Tisato, M. (eds.) Dead wood: a key to biodiversity. Proceedings of the International Symposium “Dead wood: a key to biodiversity”, 29th-31st, May 2003, Mantova, Italy, Sherwood 95, Suppl. 2: 79-82.

WPR (1994): Encyclopedia of World Problems and Human Potential, 4th Edition, Vol.1: World Problems K.G. Saur, Union of International Associationi, Munchen.

Introduction to Papers on Wild Boar Biology and Management

In line with the increasing population densities of wild boar in Europe and other countries of the world, also research has been increasing steadily in this field. Researchers have to understand the causes of the overpopulation of the species and to find solutions for problems deriving from high densities such as damaging crops and forest regeneration, spreading of diseases or conflicts with humans.

In the series of similar symposia, the 7th International Symposium on Wild Boar (*Sus scrofa*) and on Sub-order *Suiformes* was organised by the Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry, University of West Hungary in Sopron, in cooperation with the Regional Knowledge Centre of Forest and Wood Utilization of the University of West Hungary. The 135 participants from many countries of Europe, from Australia, India, Japan and Taiwan have spent two days with workshop presentations and a one-day field trip. Papers were presented in the field of population dynamics, ethology, reproduction, modeling, space and habitat use, feeding, diseases, anatomy, physiology, hunting and management. The texts of the presentations were published in a proceedings volume[*].

In cooperation with the editorial board, some authors had been invited to submit their manuscripts to Acta Silvatica & Lignaria Hungarica. The papers were selected and reviewed by the scientific committee of the symposium, based on scientific excellence and actuality of the problem investigated. It is the expectation of the organisers that these papers will contribute to the better knowledge of the biology and management of wild boar.

András Náhlik
guest editor

---

[*] Náhlik A. – Tari T. (eds) (2009): Proceedings of the 7th International Symposium on Wild Boar (*Sus Scrofa*) and on Sub-order *Suiformes*. Sopron, Hungary, August 28-30 2008. Institute of Wildlife Management and Vertebrate Zoology, Faculty of Forestry, University of West Hungary and Regional Knowledge Centre of Forest and Wood Utilization of the University of West Hungary, Sopron

Acta Silv. Lign. Hung., Vol. 5 (2009) 147-152

Seroprevalence of Antibodies to Main Porcine Infectious Pathogens in Wild Boar in Some Regions of Russia

Sergey KUKUSHKIN[a*] – Elena BABORENKO[a] – Taufik BAYBIKOV[a] –
Valery MIKHALISHIN[a] – Igor DOMSKIY[b]

[a] Federal Centre for Animal Health (FGI "ARRIAH"), Vladimir, Russia
[b] Prof. B.M. Zhitkov Russian Research Institute of Game Management and Fur Farming, Kirov, Russia

Abstract – Results of testing 107 serum samples from wild boars (*Sus scrofa* L., 1758) for the presence of antibodies to six economically significant porcine infectious disease agents (porcine reproductive and respiratory syndrome (PRRS) virus, porcine parvovirus (PPV), swine influenza virus (SIV) of H1N1 and H3N2 subtypes, Aujeszky's disease virus (ADV), porcine transmissible gastroenteritis virus (TGEV) and *Mycoplasma hyopneumoniae*) are presented in the paper. Wild boar were sampled in seven regions of Russia for diagnostic purposes. The obtained results showed the presence of antibodies to ADV in 32.5% of samples (83/27), to PPV – in 62% of samples (92/57), to *Mycoplasma hyopneumoniae* – in 52% of samples (98/51). All samples were seronegative to PRRS virus (107/0), TGEV (91/0) and SIV of H1N1 (89/0) and H3N2 (58/0) subtypes. The researches demonstrated the extensive circulation of porcine parvovirus, Aujeszky's disease virus and *Mycoplasma hyopneumoniae* among Wild boar in some regions of Russia.

Wild boar *(Sus scrofa L.*, 1758) / PRRS / Aujeszky's disease / monitoring / Russia

Kivonat – A leggyakoribb sertéspatogén kórokozók antitestjeinek szerológiai gyakorisága vaddisznókban Oroszország néhány régiójában. Antitestek kimutatására 107 vaddisznókból nyert vérsavó-mintát vizsgáltunk, különös tekintettel hat gazdaságilag jelentős sertéspatogén kórokozóra (sertés reprodukciós zavarokkal és légzőszervi tünetekkel járó szindrómáját okozó vírus (PRRS), sertés parvovirus (PPV), sertésinfulenza vírus (SIV) a H1N1 és a H3N2 altípusa, Aujeszky-féle betegség vírusa (ADV), fertőző vírusos bélgyulladás (TGEV) és *Mycoplasma hyopneumoniae*). Elemzés céljából hét orosz területen lőttek ki vaddisznókat. A kapott eredmények alapján a következő antitestek jelenlétét mutattuk ki: az ADV a minták 32,5%-ában (83/27), a PPV a minták 62%-ában (92/57), a *Mycoplasma hyopneumoniae* a minták 52%-ában (98/51) fordult elő. Az összes minta szeronegatív volt PRRS vírusra (107/0), TGEV-re (91/0), és a SIV altípusaira, a H1N1 (89/0) és a H3N2 (58/0) vírusra. A kutatás bizonyította Oroszország néhány régiójában a sertés parvovírus, az Aujeszky-féle betegség és a *Mycoplasma hyopneumoniae* széleskörű elterjedését a vaddisznókban.

vaddisznó *(Sus scrofa L.*, 1758) / PRRS / Aujeszky-féle betegség / monitoring / Oroszország

---

[*] Corresponding author: kukushkin@arriah.ru; 600901 Vladimir, Yur'evets, Russia

1 INTRODUCTION

The problem of wild animal diseases is topical in reference to epizootic, epidemic, social and economical situations. Farm and wild animals are often involved in the circulation of pathogenic agents in nature, thereby maintaining the existence of natural foci of some diseases. A significant role in these processes is played by wild boars. Moreover, the presence of such infectious diseases as classical swine fever (CSF), African swine fever (ASF), Aujeszky's disease among domestic and wild pigs has a significant negative effect on international trade. PRRS virus (PRRSV), SIV, *Mycoplasma hyopneumoniae*, porcine circovirus type 2 (PCV2), PPV and some other agents are the most economically significant porcine pathogens.

PRRSV and PPV are the cause of mass reproductive disorders in sows in the form of abortions, barrenness, birth of mummified fetuses, dead and weak piglets. PCV2, PRRSV, SIV and *Mycoplasma hyopneumoniae* are the main causative agents of respiratory disorders in growing and fattening pigs. TGEV causes mass morbidity and mortality of piglets with a diarrhea syndrome from the first days of life.

Many researches in different countries were devoted to the study of circulation of porcine infectious disease agents among wild boars. But in recent years the situation on many topical porcine infectious diseases among Wild boar in Russia remained uncertain.

Our researches were aimed at testing sera from Wild boar (*Sus scrofa* L., 1758) (shot for diagnostic purposes in some regions of Russia) for the presence of antibodies to six economically significant porcine infectious disease agents: PRRSV, PPV, TGEV, SIV, ADV and *Mycoplasma hyopneumoniae.*

2 MATERIALS AND METHODS

One hundred and seven serum samples from wild boars, collected during autumn-winter hunting seasons of 2002-2007 in 7 regions of Russia: Belgorodskaya, Vladimirskaya, Moskovskaya, Tverskaya, Smolenskaya, Kirovskaya Oblasts and Khabarovsky Krai, were tested *(Figure 1).*

Wild boar sera were tested for the presence of antibodies to PRRSV, ADV, SIV of H1N1 and H3N2 subtypes and *Mycoplasma hyopneumoniae* using IDEXX ELISA commercial kits (IDEXX Laboratories, Westbrook, ME, USA), to porcine parvovirus - using hemagglutination inhibition test and to TGEV – using microneutralization test.

3 RESULTS

Table 1 gives brief characteristics of regions where serum samples from Wild boar were collected. As seen from *Table 1*, the wild boar population density varies in different subjects of the Russian Federation. The wild boar-to-domestic pig ratio in the Khabarovsky Krai was 1:6.45, in the Smolenskaya Oblast – 1:14.83, in the Tverskaya Oblast – 1:16.87, in the Vladimirskaya Oblast – 1:23.88, in the Moskovskaya Oblast – 1:31.22, in the Kirovskaya Oblast – 1:94.52 and in the Belgorodskaya Oblast – 1:107.74.

Figure 1. The regions of Russia where samples from Wild boar were collected (Regions of habitats adapted from Lomanov 2004)

Table 1. Characteristics of regions where blood serum samples from Wild boar were collected for the given study

Index	Vladimirskaya Oblast	Moskovskaya Oblast	Tverskaya Oblast	Smolenskaya Oblast	Belgorodskaya Oblast	Kirovskaya Oblast	Khabarovsky Krai
Federal District	Central	Central	Central	Central	Central	Privolzhsky	Far Eastern
Total area, ths. km^2	29.0	47.0	84.1	49.8	27.1	120.8	788.6
Forest area, ths. ha	1520.9	1914	4500	2100	246.3	7340	62030
Area of cropland, ths. ha	930.9	1851	2434.6	1750	2713.4	3322	695.5
Population of domestic pigs, ths. heads (2006)	100.3	161.4	107.1	93.7	548.4	198.5	56.7
Population of wild boars, ths. heads (2003)	4.20	5.17	6.35	6.32	5.09	2.10	8.79

As a result *(Table 2)*, antibodies to ADV, PPV and *Mycoplasma hyopneumoniae* were detected in 32.5% (83/27), 62% (92/57) and 52% (98/51) of tested samples, correspondingly.

All serum samples were tested negative for PRRSV (107/0), TGEV (91/0) and SIV of H1N1 and H3N2 subtypes (89/0 and 58/0, correspondingly).

Table 2. Seropositive status of Wild boar with respect to main porcine infectious pathogens in some regions of Russia

Antibodies to pathogen	**Samples tested / positive**							**Total**
	Vladimirskaya Oblast	**Moskovskaya Oblast**	**Tverskaya Oblast**	**Smolenskaya Oblast**	**Belgorodskaya Oblast**	**Kirovskaya Oblast**	**Khabarovsky Krai**	
Total samples	26	17	21	23	13	1	6	107
PRRSV	26/0	17/0	21/0	23/0	13/0	1/0	6/0	107/0 (0%)
PPV	25/20	11/5	19/13	22/8	13/10	1/1	1/0	92/57 (62%)
TGEV	25/0	11/0	19/0	22/0	13/0	1/0	n.t.	91/0 (0%)
SIV H1N1	25/0	11/0	19/0	23/0	10/0	1/0	n.t.	89/0 (0%)
SIV H3N2	15/0	n.t.	19/0	23/0	n.t.	1/0	n.t.	58/0 (0%)
ADV	25/9	10/4	19/6	18/1	9/7	1/0	1/0	83/27 (32.5%)
Mycoplasma hyopneumoniae	25/11	17/9	19/11	20/13	10/7	1/0	6/0	98/51 (52%)

n.t. – not tested

4 DISCUSSION

The results of our study correlate to the data obtained by other authors. According to the literature, antibodies to Aujeszky's disease virus were often detected in Wild boar in different countries. Albina et al. (2000) reported that antibodies to ADV were detected in 423 (3.5%) out of 12,025 serum samples from Wild boar collected in France during the period from 1991 to 1998. In Germany the results of the broad examination of wild boar sera in 1991-1992 in the federal lands Sachsen-Anhalt and Brandenburg showed that 13 (2%) out of 640 serum samples were tested positive for ADV (Oslage et al. 1994).

During 1996 one hundred and twenty serum samples from Wild boar were tested in 13 districts of Oklahoma (USA) but antibodies to ADV and TGEV were not detected. In the same study 17% and 11% of samples were tested positive for PPV and SIV, correspondingly (Saliki et al. 1998).

Antibodies to PPV were detected in Wild boar in 10% (Vicente et al. 2002) and 56.6% of samples (Ruiz-Fons et al. 2006) in Spain and in 49% of samples (Vengus et al. 2006) in Slovenia. According to Vengust et al. (2006) antibodies to TGEV were not detected in Wild boar in Slovenia, though 21% of tested samples were positive for *Mycoplasma hyopneumoniae*. These data correlate to the results of our study.

There was only one report on detection of antibodies to TGEV in Wild boar in the Czech Republic in one sample out of 134 tested samples. In the course of the same research antibodies to ADV, bovine viral diarrhea virus and PCV2 were detected in 30% (101 out of 338), 1% (2 out of 352) and 43% (57 out of 134) of wild boars, correspondingly (Sedlak et al. 2008).

We detected antibodies to PPV, ADV and *Mycoplasma hyopneumoniae* in Wild boar in the majority of examined regions. Unfortunately, only single samples were tested in the Khabarovsky Krai and Kirovskaya Oblast and this makes it impossible to assess objectively the level of pathogen spread among Wild boar in these regions.

PRRSV is widespread in domestic swine in the world (Cho – Dee 2006). In Wild boar antibodies to PRRSV were found only in 0.3-3.6% of cases in the USA, France and Germany (Saliki et al. 1998; Albina et al. 2000; Oslage et al. 1994). In the United States, there was no evidence of infection in feral swine serum samples collected between 1976 and 1993, and only two positive animals were found in 1994 (Zimmerman 2002). Lutz and Wurm (1996) found no positives to PRRSV among 768 wild boar samples collected in 1992-1993 and in 1995-1996 in Germany. Only one serum sample from a wild boar was found positive for PRRSV antibodies in Poland (Szczotka et al. 2007). Tests of blood sera from Wild boar in Spain, Croatia and Slovenia were negative (Vicente et al. 2002; Ruiz-Fons et al. 2006; Zupancic et al. 2002; Vengust et al. 2006). The specific nucleus acid of PRRSV was detected using PCR in lung samples from Wild boar in Italy and Germany (Bonilauri et al. 2006; Reiner et al. 2007).

In spite of wide spread of PRRSV among domestic pigs in Russia, including regions of sample collection for the given examination (Kukushkin et al. 2008), all tested sera from Wild boar were negative. Thus, Wild boar do not to play any role in epidemiology of PRRS in Russia.

5 CONCLUSION

Unfortunately, we are not aware of direct or indirect contacts between domestic pigs and Wild boar in examined regions. The transmission of infectious pathogens between them is possible in both directions, i.e. from domestic pigs to Wild boar and vice versa.

Thus, the conducted studies show a wide circulation of porcine parvovirus, Aujeszky's disease virus and *Mycoplasma hyopneumoniae* in Wild boar in some regions of Russia. Wild boar can probably be reservoirs of these pathogens.

Acknowledgments: The authors gratefully acknowledge support by local hunters and veterinarians. Without their cooperation these studies would not have been possible. The experiments were in accordance with the current laws of Russia.

REFERENCES

Albina, E. – Mesplede, A. – Chenut, G. – Le Potier, M.F. – Bourbao, G. – Le Gal, S. – Leforban, Y. (2000): A serological survey on classical swine fever (CSF), Aujeszky's disease (AD) and porcine reproductive and respiratory syndrome (PRRS) virus infections in French Wild boar from 1991 to 1998. Veterinary Microbiology 77:43-57.

Bonilauri, P. – Merialdi, G. – Dottori, M. – Barbieri, I. (2006): Presence of PRRSV in wild boar in Italy. Veterinary Record 158(3):107-108.

Cho, J.G. – Dee, S.A. (2006): Porcine reproductive and respiratory syndrome virus. Theriogenology 66: 655-662.

Kukushkin, S.A. – Kanshina, A.V. – Timina, A.M. – Baibikov, T.Z. – MIKHALISHIN, V.V. (2008): Investigation of wild boar *(Sus scrofa)* for porcine reproductive and respiratory syndrome in some territories of Russia. European Journal Wildlife Research 54(3): 515-518.

LOMANOV, I.K. (2004): [Wild boar. In: Status of resources game animals in Russian Federation 2000-2003. Information & analytical materials. Game animals of Russia (biology, protection, study of resources, rational use]. Issue 6, Moscow, GU Centrokhotkontrol'. 23-32 (in Russian)

LUTZ, W. – WURM, R. (1996) Serologische Untersuchungen zum Nachweis von Antikőrpern gegen Viren des Seuchenhaften Spätaborts, der Aujeszkyschen Porzine Parvoviren beim Wildschwein (*Sus scrofa, L.* 1758) in Nordrhein-Westfalen. Zeitschr Jagdwissensch 42: 123-133.

OSLAGE, U. – DAHLE, J. – MULLER, T. – KRAMER, M. – BEIER, D. – LIESS, B. (1994): Prevalence of antibodies against the viruses of European swine fever, Aujeszky's disease and «porcine reproductive and respiratory syndrome» in Wild boar in the federal states Sachsen-Anhalt and Brandenburg. Deutsche Tierärztliche Wochenschrift 101:33-38.

REINER, G. – WILLEMS, H. – HACK, I. – FRESEN, C. – HERTRAMPF, B. (2007): PRRSV, PCV2, Influenza, and other pathogens of the respiratory tract in feral pigs from Germany – prevalences and peculiarities. In: 5th International Symposium on Emerging and Re-emerging Pig Diseases. Krakow. Poland. 183.

RUIZ-FONS, F. – VICENTE, J. – VIDAL, D. – HOFLE, U. – VILLANUA, D. – GAUSS, C. – SEGALES, J. – ALMERIA, S. – MONTORO, V. – GORTAZAR, C. (2006): Seroprevalence of six reproductive pathogens in European wild boar (*Sus scrofa*) from Spain: The effect on wild boar female reproductive performance. Theriogenology 65:731-743.

SALIKI, J.T. – RODGERS, S.J. – ESKEW, G. (1998): Serosurvey of selected viral and bacterial diseases in wild swine from Oklahoma. Journal of Wildlife Diseases 34:834-838.

SEDLAK, K. – BARTOVA, E. – MACHOVA, J. (2008): Antibodies to selected viral disease agents in Wild boar from the Czech Republic. Journal of Wildlife Diseases 44(3):777-780.

SZCZOTKA, A. – PODGORSKA, K. – FABISIAK, M. – STADEJEK, T. (2007): Analysis of wild boar *(Sus scrofa)* meat juice for porcine circovirus type 2 (PCV2) and porcine reproductive and respiratory syndrome virus (PRRS). In: 5th International Symposium on Emerging and Re-emerging Pig Diseases. Krakow. Poland. 89.

VENGUST, G. – VALENCAK, Z. – BIDOVEC, A. (2006): A serological survey of selected pathogens in wild boar in Slovenia. Journal of Veterinary Medicine. B, Infectious Diseases and Veterinary Public Health 53:24-27.

VICENTE, J. – LEON-VIZCAINO, L. – GORTAZAR, C. - JOSE CUBERO, M. – GONZALEZ, M. – MARTIN-ATANCE, P. (2002): Antibodies to selected viral and bacterial pathogens in European Wild boar from south-central Spain. Journal of Wildlife Diseases 38:649-652.

ZIMMERMAN, J.J. (2002): Porcine reproductive and respiratory syndrome virus: Epidemiology. In: Morilla, A. – Yoon, K-J. – Zimmerman, J.J. (eds.) Trends in emerging infections of swine. Iowa State Press A Blackwell Publishing Company, Iowa, Ames. 331-337.

ZUPANCIC, Z. – JUKIC, B. – LOJKIC, M. – CAC, Z. – JEMERSIC, L. – STARESINA, V. (2002): Prevalence of antibodies to classical swine fever, Aujeszky's disease, porcine reproductive and respiratory syndrome, and bovine viral diarrhoea viruses in Wild boar in Croatia. Journal of Veterinary Medicine. B, Infectious Diseases and Veterinary Public Health 49: 253-256.

Acta Silv. Lign. Hung., Vol. 5 (2009) 153-157

Current distribution and population status of wild boar (*Sus scrofa* L.) in Greece

Efstathios P. TSACHALIDIS[a*] – Eleftherios HADJISTERKOTIS[b]

[a] Laboratory of Ecology – Wildlife Management, Department of Forestry and
Environmental Management and Natural Resources, Democritus University of Thrace, Greece
[b] Ministry of the Interior, Nicosia, Cyprus

Abstract – This is the first attempt to estimate wild boar *(Sus scrofa* L.*)* population density and distribution in Greece. The study took place in 2004, in all 38 Greek counties of the mainland, as well as in the larger forested Greek islands: Crete, Rodos, Samos, Lesvos, Limnos, Thasos, Corfu, Kefalonia and Zakinthos. It was observed that the species was present in every county in continental Greece, with the exception of the two counties Attica and Evia. Attica, which includes the capital city of Athens, is densely inhabited not allowing much space for wildlife. Evian is an island connected to the mainland with a bridge. Wild boar can be found in an area around 19,495 km^2, which is about 14% of the country. The mean distribution altitude reaches 686 ± 266 m. The average population number was estimated at 19,033 (0.98 ± 0, 21 ind/km^2) individuals with maximum population level 23,030 animals, and a minimum of 16,536. The highest mean density was observed in the prefecture of Sterea Hellas (1.26 ind/km^2) and the lowest in the prefecture of Thrace (0.89 ind/km^2). The maximum density was found in Sterea Hellas (3.14 ind/km^2) and the minimum density in Thrace (0.13 ind/km^2). The above results are expected to provide valuable information for the management of wild boar in Greece.

questionnaires / demography / mean density / habitat / management

Kivonat – A vaddisznó (*Sus scrofa* L.) populációinak jelenlegi eloszlása és státusza Görögországban. Ez az első kísérlet a vaddisznó-populációk sűrűségének és elterjedésének becslésére Görögországban. A felmérés 2004-ben a görög szárazföld mind a 38 megyéjére, valamint a legerdősültebb görög szigetekre – Kréta, Ródosz, Számosz, Lészvosz, Límnosz, Thászosz, Korfu, Kefalinía és Zákinthosz – terjedt ki. A faj jelen volt a kontinentális Görögország összes megyéjében, kivéve Attikát és Éviát. Attika, ami magában foglalja Athént, a fővárost, nagyon sűrűn lakott, így nem biztosít élőhelyet a vadnak, Évia-szigete pedig egy híddal kapcsolódik a kontinenshez. A vaddisznó hozzávetőlegesen 19 495 km^2-en fordul elő, amely az országnak kb. 14%-a, elterjedésének átlagos tengerszint feletti magassága 686±266m. Az átlagos becsült populációnagyság 9 033 (0,98 ± 0,21 egyed/km^2) egyed, a becslés maximuma 23 030 egyed, minimuma 16 536 egyed. A legnagyobb átlagos sűrűség Szterea Hellász megyében (1,26 egyed/km^2) volt, a legalacsonyabb pedig Trákia megyében (0,89 egyed/km^2). A maximális sűrűséget Sterea Hellász megyéjében (3,14 egyed/km^2), a minimumot Trákia megyében (0,13 egyed/km^2) mutattuk ki. A fenti eredmények értékes információt nyújtanak a vaddisznó-gazdálkodáshoz Görögországban.

kérdőív / demográfia / átlagos sűrűség / élőhely / gazdálkodás

---

[*] Corresponding author: etsaxal@fmenr.duth.gr; GR-68200, Orestiada, Evros, Greece

1 INTRODUCTION

Wild boar has the largest distribution of any wild ungulate worldwide. Since the 1990s wild boar have gone through a population explosion, which increased their range and their density where they were already common (Sáez-Royuela - Tellería 1986, Marsan et al. 1995, Ueda – Kanzaki 2005, Tsachalidis- Hadjisterkotis 2008). Based on hunting bag estimates, wild boar populations in Greece (contrary to many other parts of the world) are stable (Thomaides et al. 2001), but actual data of the wild boar population in Greece are still missing (Tsachalidis – Hadjisterkotis 2008). Wild boar in Greece is native and a popular big game species, with a wide distribution all over continental Greece. In 1988, it was successfully reintroduced in the region of Peloponnesus, from where it was driven to extinction in 1830 (Tsachalidis – Konstantopoulos 2004, Tsachalidis 2008).

The wild boar hunting is allowed from 15/09/… to 20/01/… about four months and only for 3 times per week (Wednesday, Saturday and Sunday). (Tsachalidis 2008a).

Studies on wild boar in Greece includes ecology and management (Sfougaris et al. 1999) hunting management (Karampatzakis 2006, Tsachalidis 2008) hunter behavior, hunter characteristics and socioeconomic trends (Tsachalidis- Hadjisterkotis 2008, Tsachalidis et al. 2008a), wild boar diet (Tsachalidis et al. 2004, Papageorgiou et al. 2006, Paralikidis et al. 2006) and wild boar population status (Tsachalidis – Konstantopoulos 2004, Tsachalidis – Konstantopoulos 2005, Tsachalidis et al. 2008b). However, there are no studies on distribution, habitat selection and population density, necessary for the proper management and conservation of this species. Herein, we report for the first time the distribution, habitat selection and population density of wild boar in Greece.

2 MATERIALS AND METHODS

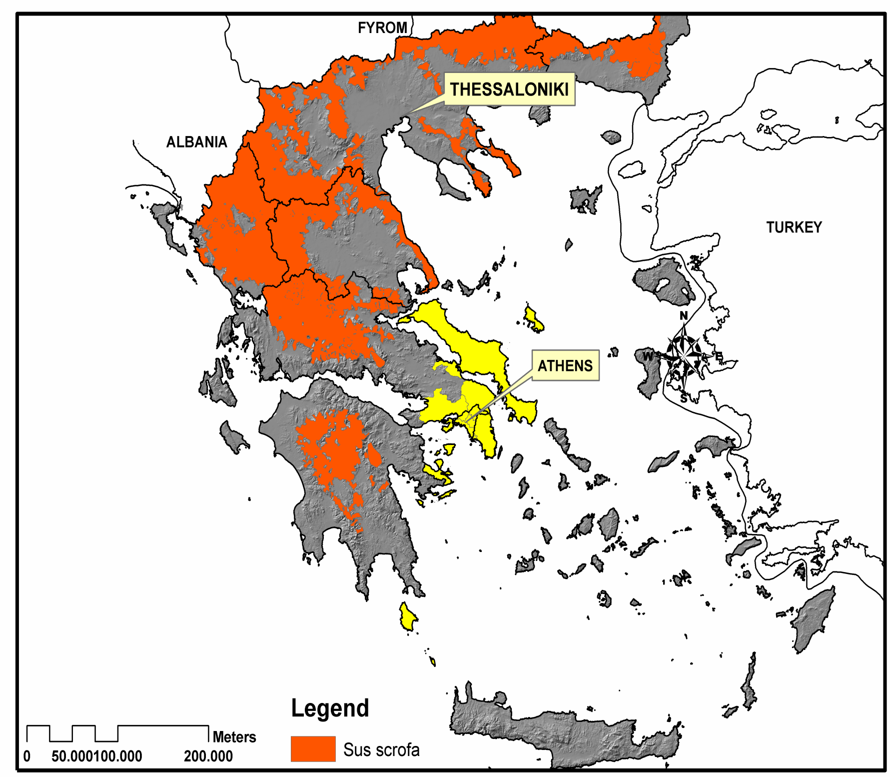
The study took place in the year 2004. Data were gathered from all 38 counties of the Greek mainland, as well as from the larger forested Greek islands: Crete, Rodos, Samos, Lesvos, Limnos, Thasos, Corfu, Kefalonia and Zakinthos. Data were gathered through a questionnaire distributed to 169 Federal Rangers (Tsachalidis et al. 2005) at the local hunting clubs of the Hellenic Hunting Association, after the wild boar breeding season. Each ranger recorded his observations only from his jurisdiction. In their attempt to locate localities of wild boar they requested information from foresters, farmers, hunters, and people working in the forest and in fields. During the survey, they searched for signs of wild boar by searching the gullies on foot and also by travelling the roads using a four-wheel drive car and on foot, searching for signs of digging, scats, footprints, rubbing on trees, and mud wallows, assisted by foresters and hunters (Markov et al. 2004, Monaco et al. 2004). All the questionnaires were returned completed.

3 RESULTS, DISCUSSION

With the exception of Attica, Evian and islands, wild boar was present on all Greek mainland counties. Attica is a densely inhabited area, which includes the largest Greek city of Athens (5,000,000 inhabitants). Also, the species it is not found in Evian, due to the lack of suitable habitat (a lot o *Pinus halepensis*) and it also connected with the rest of Greece with a bridge *(Map 1, yellow area).*

The species can be found in 263 localities, in an area around 19,495 km^2, which is 18,9% of the extent of the study area or the 14% of the country *(Table 1).* The mean distribution altitude reaches 686 ± 266 m. Based on the mean density and deviation (0.98 ± 0, 21 ind/km^2)

the average population number all over Greece was estimated at 19,033 individuals with maximum population level 23,030 animals, and a minimum of 16,536. The highest mean density was observed in the prefecture of Sterea Hellas (1.26 ind/km^2) and the lowest in the prefecture of Thrace (0.89 ind/km^2). The maximum density is observed in Sterea Hellas (3.14 ind/km^2) and the minimum density is observed in Thrace (0.13 ind/km^2) (*Table 1*).



Map 1. Distribution of wild boar in Greece

Table 1. Population distribution and mean density of the species Sus scrofa L. (wild boar) *per geographic district, in the Greece, during 2004*

	Prefecture (geographic district)	Area			Wild boar population (N)	Density (individuals/km^2)		
		prefecture (km^2)	habitat (km^2)	(%)		Mean	Max	Min
1	*Thrace*	8,524	1,025	12.0	915	0.89	1.1	0.13
2	*Macedonia*	35,728	7,192	20.1	6,548	0.91	2.04	0.37
3	*Thessaly*	13,880	2,960	21.3	3,395	1.15	2.43	0.38
4	*Epirus*	9,210	2,860	31.1	1,935	0.68	1.01	0.31
5	*Sterea Hellas*	16,840	3,333	19.8	4,210	1.26	3.14	0.47
6	***Peloponnesus***	19,230	2,072	10.8	2,030	0.98	2.57	0.31
	Total	103,412	19,442	18.9	19,033	0.98±0.21	2.05	0.33

The most important wild boar habitat is oak forests (76,4%), followed by chestnut forests (9,6%) and various coniferous forests (6,2%) (*Table 2*). The species avoids coniferous or broad leaved homogenous forests.

Table 2. Types of habitat occupied by wild boar with dominant species

Categories of habitats with dominant species	Area of habitat (km^2)	(%)
Oak	255	1.3
Oak – Broadleaves	1,847	9.6
Oak – Beech	3,530	18.4
Oak – Fir	2,974	15.5
Oak – Holly *(Quercus coccifera)*	4,188	21.8
Oak – Pine	717	3.7
Oak – Chestnut	333	1.7
Broadleaves – Oak	825	4.3
Beech	375	2.0
Beech – Chestnut	480	2.5
Chestnut – Broadleaves	1,365	7.1
Pine	195	1.0
Pine – Fir	498	2.6
Pine – Broadleaves	500	2.6
Holly – Broadleaves	580	3.0
Evergreen broadleaves – Holly	681	3.5
Wetlands	99	0.5
Total	19,442	100.0

The above results are expected to provide valuable information for the management of this important game species.

REFERENCES

KARAMPATZAKIS, TH. (2005): [Research on recording on hunting game and the observation of game population. 6th Hunting Federation of Macedonia - Trace, Thessaloniki.] Panthiras magazine 2005. pp 122-127 (in Greek).

MARKOV, N. – NEIFELD, N. – ESTAFJEV, A. (2004): Ecological aspects of dispersal of the wild boar (*Sus scrofa* L. 1758) in the Northeast European Russia. Russian Journ. of Ecol., Vol. 35(2): 131-134.

MARSAN, A, – SPANO, S. – TOGNONI, C. (1995): Management attempts of wild boar (*Sus scrofa* L.): first results and outstanding researchers in Northern Apennines (Italy). IBEX JME, 3: 219-221

MONACO, A. – CARNEVALI, L. – RIGA, F. – TOSO, S. (2004): Status, distribution and management of wild boar (*Sus scrofa*) on the Italian Alps. Proceedings (abstracts) of Vth International Wild boar and Suidae Symposium. Jagiellovian University, September 1-6, 2004. Krakow, Poland.

PAPAGEORGIOU, N. – TSACHALIDIS, E.P. – PARALIKIDIS, N. – KONSTANTOPOULOS, P. (2006): Food habits of wild boar (*Sus scrofa* L.) in Peloponnesus (South Greece). Proceedings VIth International Symposium on wild boar and sub-order *Suiformes.* Monaster of Kikkos, October 25-29, 2006. Cyprus.

PARALIKIDIS, N. – TSACHALIDIS, E.P. – KONSTANTOPOULOS, P.(2006): Food habits of wild boar (*Sus scrofa* L.) in Macedonia, North-eastern Greece. Proceedings VIth International Symposium on wild boar and sub-order *Suiformes.* Monaster of Kikkos, October 25-29, 2006. Cyprus.

SFOUGARIS, A. – GIANNAKOPOULOS, A. – PARDALIDIS, T. – TSACHALIDIS, E. P. – ANNI, A .(1999): Research on the ecology and management of the Wild Boar (*Sus scrofa*), Roe deer (*Capreolus capreolus*), Red deer (*Cervus elaphus*) and Balkan chamois (*Rupicapra rupicapra balkanika*) in Epirus, Greece. XXIVth International Congress of the Union of Game Biologist (ICGB). Thessaloniki September 20-24, 1999.

Sáez-Royuela, C. – Tellería, J.L. (1986): The increased population of the Wild Boar (*Sus scrofa L.*) in Europe. Mammal Review, 16: 97–101.

THOMAIDES, CHR. – KARAMPATZAKIS, TH. – LOGOTHETIS, G. – CHRISTOPHORIDOU, G. (2001): Program ”Artemis”: The study and record of hunting success and observation of game populations. In: Skordas K., Birtsas P. and Maslarinou O. (eds) PAN-THIRAS, Hunting Federation of Macedonia -Thrace, Thesalloniki, Greece, pp 26-39.

TSACHALIDIS, E.P. – KONSTANTOPOULOS, P. (2004): Reintroduction of the species *Sus scrofa* L. (wild boar) in Peloponnesus, Southern Greece. Proceedings (abstracts) V^th^ International wild Boar and Suidae Symposium. Jagiellovian University, September 1-6, 2004. Krakow, Poland. The Journal of Wildl. Res., 3(1): (in press).

TSACHALIDIS, E. P. – PARALIKIDIS, N. – PAPAGEORGIOU, N. – HADJISTERKOTIS, E. (2004): Food habit of wild boar (*Sus scrofa* L.*)* in Northeastern Greece. Proceedings (abstracts) of V^th^ International wild Boar and Suidae Symposium. Jagiellovian University, September 1-6, 2004. Krakow, Poland. The Journal of Wildl. Res., 3(1): (in press).

TSACHALIDIS, E. P. – KONSTANTOPOULOS, P. (2005): Population demography of the species wild boar (Sus scrofa, L., 1758) in Peloponnesus and Sterea Hellas, South Greece. Proceedings (extend abstract) XXVII^th^ International Union of Game Biologist Hanover, 28 August - 6 September, 2005. Hannover, Germany. pp 502-503.

TSACHALIDIS, E. P. – HADJISTERKOTIS, E. (2008): Wild boar hunting and socioeconomic trends in Northern Greece, 1993- 2002. Eur. Journ. Wildl. Res., 54: 643-649. DOI: 10.1007/s10344-008-0190-y**.**

TSACHALIDIS, E. P. (2008): Reintroduction and hunting harvest of the wild boar (*Sus scrofa* L. 1758) (*Mammalia, Suidae*) in the Peloponnesus, southern Greece. Journal of Biological Research, 10: 215 – 219.

TSACHALIDIS, E. P. (2008a): [The hunting in Hellas. Scient. Annals of the Department of Forestry and Environmental Management and Natural Resources, DUTh.] Vol. I : 207-220 (in Greek).

TSACHALIDIS, E.P. – KONSTANTOPOULOS, P. – GIANNAKOPOULOS, A. (2008a): Personal characteristic and hunting behavior of wild boar hunters in Peloponnesus, South Greece. Proceedings VII^th^ International Symposium on wild boar and sub-order *Suiformes.* Sopron, August 28-30, 2008. Hungary. (*Extended abstract*), pp 112-114.

TSACHALIDIS, E.P. – GIANNAKOPOULOS, A. – BIRTSAS, P. (2008b): Wild boar (*Sus scrofa* L.) distribution and habitat use in Grevena, Western Macedonia, Greece. Proceedings VII^th^ International Symposium on wild boar and sub-order *Suiformes.* Sopron, August 28-30, 2008. Hungary. (*Extended abstract*), pp 115-117.

UEDA, G. – KANZAKI, N. (2005): Wild boar hunters profile in Shimane Prefecture, Western Japan. Wildl. Biol. Pract ., 1(2):146-151.

Acta Silv. Lign. Hung., Vol. 5 (2009) 159-166

Tagging Piglets at the Farrowing Nest in the Wild: Some Preliminary Guidelines

Eric BAUBET[a*] – Sabrina SERVANTY[b] – Serge BRANDT[c]

[a] Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, Birieux, France
[b] Centre d'Ecologie Fonctionnelle et Evolutive/CNRS, Montpellier, France
[c] Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, Châteauvillain, France

Abstract – Neonate ungulate often show high rates of mortality due to predation, starvation, or exposure to bad weather, leading to losses frequently exceeding 50%. Wild boar piglets are known to suffer from thermoregulation insufficiency, which probably explain the nest construction behaviour in sows. We thus tried to develop a method for tagging piglets inside their farrowing (or birth) nest to assess piglet survival from few days after their birth onwards. Sows fitted-out with VHF collars were radio-tracked to determine parturition time, and to get a rough idea of the possible birth nest location. Then, with a handled antenna we approached on foot the birth nest, and piglets were caught, tagged and fitted-out with a backpack transmitter and released inside the nest. Temporal movements of mother and litter association were monitored, as long as possible. Results on sow behaviour and tactic against human approach, piglets body mass, piglet reaction, and survival in their early lifetime were described.

***Sus scrofa* / post-natal survival / farrowing nest / wild boar piglet / transponder / telemetry**

Kivonat – Szabad területen élő vadmalacok jelölése vacokban: néhány előzetes irányelv. Az újszülött patások halálozási rátája gyakran nagyon magas, elérheti az 50%-ot, ami elsősorban a ragadozásnak, a táplálékhiánynak és az időjárási viszonyoknak tudható be. A vadmalacok kezdeti elégtelen hőszabályozása magyarázza a vaddisznó kocák vacoképítő viselkedését. Olyan módszert próbáltunk kifejleszteni, amellyel a malacozó vacokban megjelölt vadmalacok túlélését becsüljük a születésűk utáni néhány napban gyűjtött adatokból. A VHF nyakörvvel ellátott kocákat malacozási időszakban bemértük, és hozzávetőlegesen meghatároztuk a vacok lehetséges helyét. Ezt követően kézi antenna segítségével megközelítettük a vackot, ahol a malacokat befogtuk, majd megjelöltük és háti jeladóval láttuk el. A koca időbeli mozgását és az utódokat a lehető legtovább monitoroztuk. Vizsgálataink eredményeként ismereteket szereztünk a kocák viselkedéséről és az emberi zavarásra alkalmazott taktikájáról, valamint adatokat kaptunk a malacok tömegéről, reakcióiról, és túléléséről életük korai szakaszában.

***Sus scrofa* / születés utáni túlélés / malacozó vacok / vaddisznó malac / jeladó / telemetria**

---

[*] Corresponding author: eric.baubet@oncfs.gouv.fr; Montfort, 01330 Birieux, France

1 INTRODUCTION

Wild boar managers generally cannot rely on reliable estimates of demographic parameters to simulate the efficiency of management scenarios and therefore, they cannot provide useful management rules. To avoid such a problem, modelling attempts have been made by combining information obtained through both a long-term research program and expert opinions for some unknown parameters (Servanty 2007). A population model of wild boar was then elaborated and was based on a pre-breeding matrix model. One of the guess estimate that might lead to fluctuations in population recruitment and then, influence the population dynamics (Coulson et al. 1997) was the post-natal survival (i.e., from birth to weaning). Among ungulate species, juvenile survival appears to be of prime importance (Gaillard et al. 2000) and it can be split into the post-natal and the post-weaning survival (i.e., from weaning to one year of age; Gaillard et al. 1998). In many species juvenile survival could be considered as a critical step of life and neonate ungulates often suffer from high mortality due to predation, starvation, or exposure to bad weather, leading to losses that frequently exceed 50% (Gaillard et al. 2000). Wild boar piglets are known to suffer from thermal deficiency (Mauget 1980), which can explain the nest construction behaviour observed in sows (Gundlach 1968, Diong 1973, Baettig 1980, Dardaillon 1984, Meynhardt 1991, Nakatani 1989, Brandt et al. 1997, Fernandez-Llario 2004). Although little is known about newborn survival in wild boar, juvenile mortality could be as high as 62% (Nakatani, 1989) or even 90% (Fernandez-Llario et al. 1999). Moreover some authors reported that in some cases, the whole litter may die (Kurz – Marchinton 1972). To our knowledge, no study has tried to assess directly post-natal survival of wild boar in natural conditions. Our aim was to carry out a study on the feasibility of tagging piglets inside their birth nest, an initial step to assess the piglet survival from few days after their birth onwards. We aimed to test whether it was realistic to catch and tag piglets inside the farrowing nest and to monitor them until their weaning. By doing so, we looked at getting reliable data on the early survival of piglets as well as information on factors that could induce piglet death. In addition, we aimed to assess the sow's responses to human perturbation through a possible aggressive behaviour against human approach for instance, but also the piglet responses to human approach of the farrowing nest. Finally, the capture events were also an opportunity to get data on body mass and sex of the littermates, for which available information is scarce to our knowledge, especially in wild conditions.

2 METHODS

The study took place in the north eastern part of France (48°02'N; 4°55'E), in the Châteauvillain-Arc-en-Barrois forest. This forest is a homogeneous broadleaved deciduous woodland on a calcareous plateau. It covers 11,000 ha composed of hornbeam (*Carpinus betulus*) coppice with oak (*Quercus petraea*; 41%) and beech (*Fagus sylvatica*; 30%) stands. In winter, during the hunting season, the main peak of the farrowing period was assessed both on adult and yearling sows (Mauget 1982, Fernandez-Llario – Carranza 2000) by genital tract analyses (Henry 1968, Mauget 1980,1982, Servanty et al. 2007). The estimation of the main farrowing peak was used to decide when to perform an intensive radio-telemetry survey on pregnant sows fitted-out with VHF collars *(Figure 1)*. The radio-tracking monitoring began in 2004, after some preliminary field tests of random search of wild boar farrowing nests were performed in 2003 (ONCFS unpublished data). The radio-tracking method was also used in birds (Powell et al. 2005) and with the Eurasian lynx (*Lynx lynx*, Boutros et al. 2007). We used both a car-mounted antenna and a handled antenna for doing telemetry (Kenward 1987).

Tracking from the car enabled us to determine the sow's restricted activity period, which indicates the parturition time (Kurz — Marchinton 1972, Mauget 1980, Janeau – Spitz 1984). As soon as two consecutive locations occurred at the same place, we performed a night survey of the sow's activity. Then, after parturition was expected to have occurred, we used radio-tracking on foot to approach the nest during the supposed period of stability of the piglets inside the nest (from 3-4 days Mauget et al. 1984, to 1-2 weeks, see Kurz - Marchinton, 1972, Janeau –Spitz, 1984, Eguchi et al. 2000). When caught the piglets were fitted-out with both a transponder (FDX - B ISO 11784, Réseaumatique) to identify them for the rest of their life and an adaptable backpack based on the elastic collar process (Brandt et al. 2004; *Figure 2 - a,b,c*) including a VHF transmitter (TW3, 10 gram, Biotrack). All piglets were released inside their birth nest after tagging. Temporal variations of the mother - litter association were then monitored through VHF controls as long as possible.

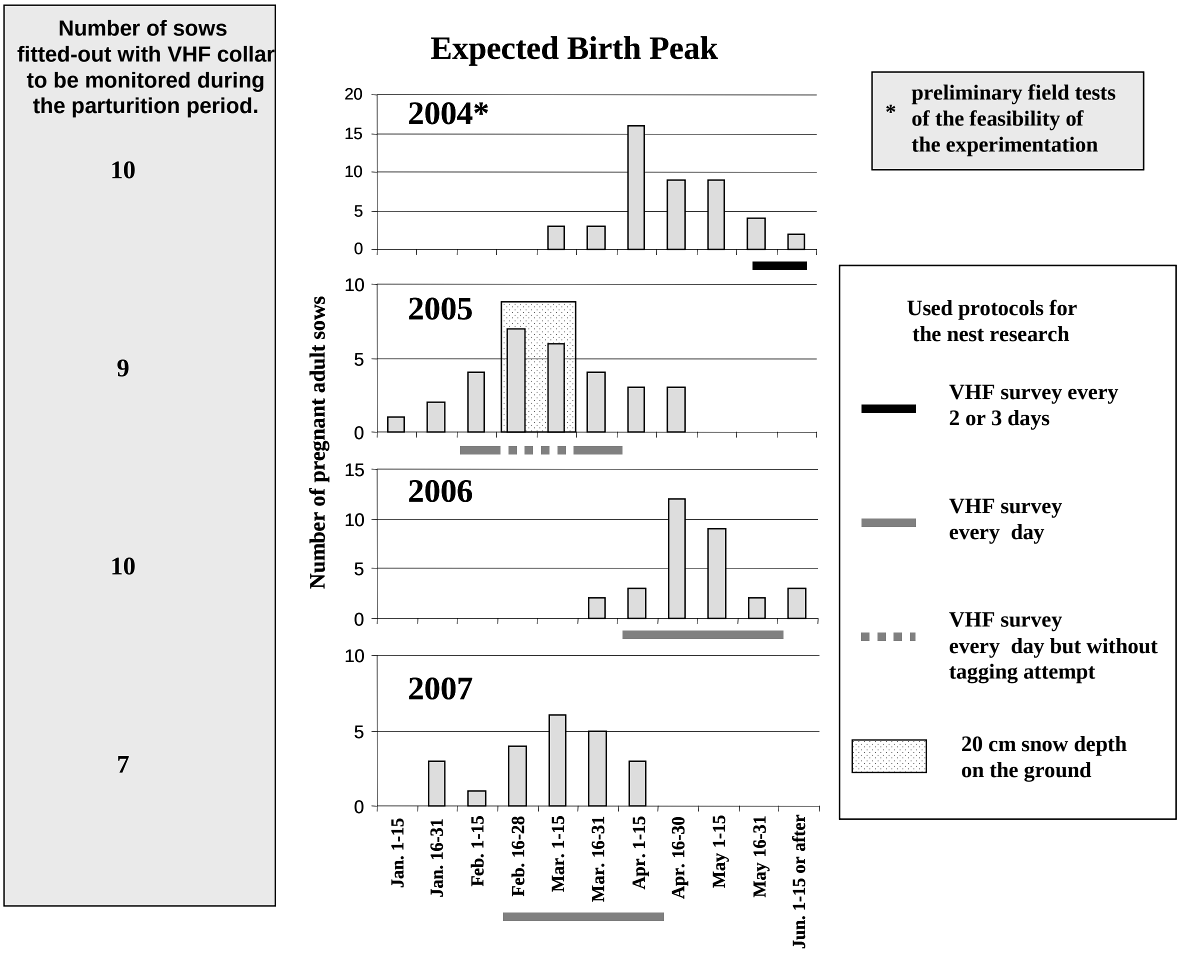


Figure 1. Between years distribution of expected farrowing period of adults sows of the study area. Solid line (black or grey) as well as dotted line under each histogram represent the duration of the VHF survey. Details on the localization rhythm are given in the white box. The total number of sows fitted-out with VHF collar which are monitored each year, are indicated in the grey box, on the left side. During the year 2005, we decided to suspend the tagging attempt during one month due to bad climatic conditions

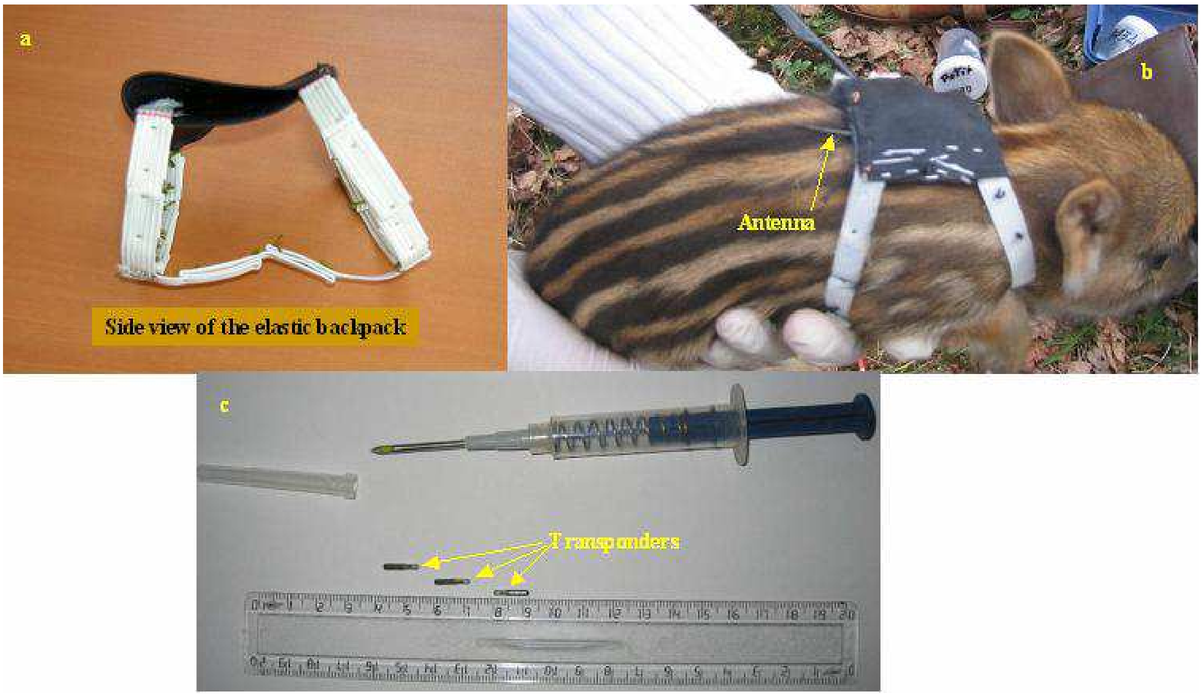


Figure 2. a) Harness system designed to fit out piglets with a backpack. Note that on the white elastic belts of the harness, sewing points are visible. The harness can thus adjust to the piglet during its body growth until the next recapture event. b) Piglet fitted out with a backpack. The pocket of the backpack was clipped once the transmitter was put inside. The antenna was directed toward the back of the piglet. c) Transponders and the applicator used to inject into the subcutaneous tissue. The ruler indicates the size of transponders (cm)

3 RESULTS

In agreement with previous studies (Mauget 1982, Aumaitre et al. 1984, Vassant et al. 1994, Maillard - Fournier 2004) the birth peak varied among years *(Figure 1)*. Although it was possible to catch and tag piglets inside the birth nest, we were successful only in 17% of our attempts *(Figure 3)*. Contrary to what we were expecting, determining the exact day of birth and locating the farrowing nest in the forest plot was far from an easy task. However, we were never in danger because of a sow reaction. Indeed, in any case sows did not even try to defend their litter against us by a direct attack during our approach. However, in some occasions the sow moved from the farrowing nest before we reached the exact position. In half of the cases, the sow abandoned her litter. Quite rapidly after their abandonment (between 24 and 48 hours), the piglets died inside the birth nest or near this place. Once, we only recover transmitters and remains of legs from three piglets, of a litter of four, while the last one was found half-buried in the nest surrounding. In all other cases, the sow picked up back the whole litter and moved piglets away before building a new nest. In 77% of cases (10 out of 13), all the littermates ran away when we were approaching the nest. Generally after a short run, they tried to hide themselves in the vegetation and were not moving anymore except when we tried to pick them up. The location with the vehicle-mounted antenna did not enable us to identify whether the sow reached the exact nest position or whether she was just wandering in its surrounding. We were thus not able to quantify precisely how long it took to the sow to come back to the birth nest after she had run away. However, in all cases, when the sow came back to pick up the piglets, it did that within 24h after the capture event. The backpacks were kept by the piglets for an average of only two and half days. Overall, six litters were caught and 25 piglets were tagged. The overall sex ratio was quite balanced with 14 males and 11 females. Newborns weighed an average of 1096 g ± 203 g (ranging from 650 g to 1390 g) with both the lightest and heaviest piglets being male (*Table 1*).

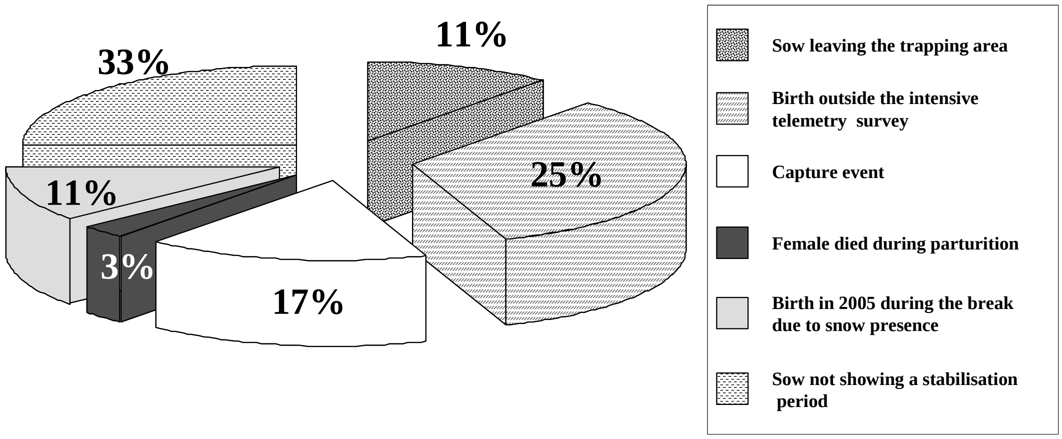


Figure 3. Results of the tagging attempts regarding the 36 sows monitored during the whole study period

Table 1. Description of information recorded both on the sows and on piglets littermate during the course of the study period. The grey cells indicate the females that abandoned their litter after the tagging event

Year	Sow's name	Sow's Age	Number of tagged piglets	Estimated age of the piglet	Sex ratio of the littermate		**Weight in g**	
					male	female	male	female
2004	Flor	Adult at capture	5	Between 36 to 60 hours	5	0	1050; 700; 980; 650; 1030	/
2005	Vrille	Born in 2003	2	Between 6 and 8 days	1	1	1280	1480
2006	Samare	Adult at capture	5	Between 48 to 72 hours	1	4	1380	940; 1340; 1270; 1170
	Ambre	Born in 2002	4	Between 48 to 72 hours	2	2	1390; 1300	1020; 1020
2007	Denise	Adult at capture	4	Between 48 to 60 hours	2	2	1200; 1110	1140; 1040
	Truffe	Adult at capture	5	Between 48 to 60 hours	3	2	1000; 990; 1010	990; 910

The transponder tagging system appeared to be quite efficient. We were able to read it on all the tagged individuals accessible to our check control so far, both through recapture events or during the hunting season. The longest monitoring so far lasted 541 days.

4 DISCUSSION, CONCLUSION

This experiment of piglets tagging was not as successful as we might have expected. Although we showed that newborn wild boar can be safely caught and tagged in wild condition, several constraints need to be overcome. First, to identify the spatial stabilisation corresponding to the nest building implied a very intensive VHF monitoring of the sows fitted-out with collar is required. In one third of our cases, the daily survey of the sow resting places did not allow us to identify precisely the farrowing nest. Our results support that farrowing nest building is a short event, performed within a few hours before parturition as reported by some previous works (Gonyou - Stookey 1987, Meynhardt 1991, Gustafsson et al. 1999). The observed resting period at nest after births have occurred might be shorter than previously reported 3-4 days or even less in the present study *vs* 1-2 weeks, Kurz - Marchinton 1972; Janeau - Spitz 1984, Eguchi et al. 2000, but see Mauget et al., 1984). Moreover piglets are able to go out of the nest within a few hours after birth (Meynhardt 1991, Eguchi et al. 1999). Sows have also been reported to be highly sensitive to any perturbation after the parturition (Eguchi et al. 2000). The odour or the physical presence of a potential predator in the nest surrounding might thus induce the sow to move its piglets in order to protect them from predation. Indeed sows that picked up their litter after tagging event generally moved out their piglets at 300- 400 meters away from their initial position. Overall, our first results highlight that the time-window for tagging of newborns is less than a week. The use of improved technologies, such as GPS/GSM collars (Baubet et al. 2004) might help to identify more accurately the location of the birth nest. Moreover, such equipment might also help to follow more precisely and under a high rate of location, the post-parturition behaviour of sows, in the wild. However, the short time window raised another problem. Although, the aim was to tag piglets as young as possible to get a reliable estimate of the neo-natal mortality, the tagging attempt cannot be run too early after births has occurred. Indeed, the nursing behaviour of the sow could be highly disturbed by the experimentation during the first day of piglet's life which is a crucial period for them (Gonyou - Stookey 1987, Eguchi et al. 1999).

The difficulty we had to locate precisely the farrowing nest might also be due to the post-partum behaviour of the sows. Indeed, their activity rhythm changed after the parturition and sows were becoming more active during daytime to forage nearby the farrowing nest (Mauget et al. 1984, Eguchi et al. 1999). In some cases, changes of the VHF signal (Kenward 1987) informed us that the sow was already active when we were approaching her. In some other cases, they moved away from the nest before we reached its exact position. In these cases we were thus not able to find the nest due to escape movements. Although wild sows seem to be sensitive to human perturbations, they never tried to defend the farrowing nest or their litter by attacking contrary to what has been previously reported (Meynhardt 1991) or observed in captive animals (Eguchi et al. 2000). The mothers abandoned their litters in 50% of the cases although we cannot identify the exact cause with certainty due to our small sample size. Such high rate of failure pases an unexpected problem that might be difficult to overcome to study the early piglet survival.

However, we can conclude that the post-natal survival of piglets is highly variable from year to year due to the human perturbation (and especially hunting activities when birth period occurs in late winter) as well as to the weather conditions.

Acknowledgments: We sincerely thank all who helped capturing and marking wild boar, especially C. Thivet (Fédération Départementale des Chasseurs 52), and M. Marchi (ONCFS) for technical assistance as well as people who helped collecting data on harvested wild boar. We are grateful to the Office National des Forêts and to F. Jehlé, who allowed us to work on the study area. We thank J.-M. Gaillard for his helpful comments on earlier draft of this manuscript.

REFERENCES

AUMAITRE, A. – QUERE, J-P. – PEINIAU, J. (1984): Influence du milieu sur la reproduction hivernale et la prolificité de la laie. Symposium international sur le sanglier, les colloques de l'INRA n° 22.: 69-78. (in French).

BAETTIG, M. (1980): Contribution à la biologie et écologie du sanglier (*Sus scrofa* L.) dans le canton de Vaud. Ph D Thesis. Université de Bâle, Suisse. 196 p. (in French).

BAUBET, E. – BRANDT, S. – VASSANT, J. – GENDNER, J.P. – KLEIN, F. (2004): Can wild boar be surveyed using GPS? Memoirs of the National Institute of Polar Research, Special. Issue 58: 190–197.

BOUTROS, D. – BREITENMOSER-WURSTEN, C. – ZIMMERMANN, F. – RYSER, A. – MOLINARI-JOBIN, A. – CAPT, S. – GÜNTERT, M. – BREITENMOSER, U. (2007): Characterisation of Eurasian lynx *Lynx lynx* den sites and kitten survival. Wildlife Biology 13(4): 417-429.

BRANDT, S. – VOYARD, N. – VASSANT, J. (1997): Le chaudron chez la laie : choix du site et des matériaux. Bulletin Mensuel de l'Office National de la Chasse 223: 4-11. (in French).

BRANDT, S. – VASSANT, J. – BAUBET, E. 2004. Adaptation d'un collier émetteur extensible pour Sanglier. Faune Sauvage 263: 14-19. (in French).

COULSON, T. – ALBON, S. – GUINNESS, F. – PEMBERTON, J. – CLUTTON-BROCK, T. H. (1997): Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology 78: 852-863.

DIONG, C. H. (1973): Studies of the Malayan wild pig in Perak and Johore. Malayan Nature Journal. 26: 120-173.

DARDAILLON, M. (1984): Le sanglier et le milieu camarguais: dynamique co-adaptative. Ph D Thesis, Université Paul Sabatier, Toulouse, France. (in French).

EGUCHI, Y. – TANAKA, T. – YOSHIMOTO, T. (1999) Behaviour of Japanese wild boars, *Sus scrofa leucomystax*, during the first week after parturition in farrowing pens. Animal Science Journal 70(5): 360-366.

EGUCHI, Y. – TANAKA, T. – YOSHIMOTO, T. (2000): Behavioural responses of Japanese wild boars to the person in attendance during the pre- and post-farrowing periods under captive conditions. Animal Science Journal 71(5): 509-514.

FERNANDEZ-LLARIO, P. – CARRANZA, J. – MATEOS-QUESADA, P. (1999): Sex allocation in a polygynous mammal with large litters: the wild boar. Animal Behaviour 58: 1079-1084.

FERNANDEZ-LLARIO, P. – CARRANZA, J. (2000): Reproductive performance of the wild boar in a Mediterranean ecosystem under drought conditions. Ethology, Ecology and Evolution 12: 335-343.

FERNANDEZ-LLARIO, P. (2004): Environmental correlates of nest site selection by wild boar *Sus scrofa*. Acta Theriologica 49(3): 383-392.

GAILLARD, J-M. – FESTA-BIANCHET, M. – YOCCOZ, N.G. (1998): Population dynamics of large herbivores : variable recruitment with constant adult survival. Trends in Ecology and Evolution. 13(2): 58-63.

GAILLARD, J-M. – FESTA-BIANCHET, M. – YOCCOZ, N.G. – LOISON A. – TOÏGO, C. (2000): Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics. 31: 367-393.

GONYOU, H.W. – STOOKEY, J. M. (1987): Maternal and neonatal behavior. Veterinary Clinics of North America : Food Animal Practise. vol. 3(2): 231-249.

GUNDLACH, H. (1968): Brutfürsorge, Brutpflege, erhaltens-Ontogenese und Tagesperiodik beim Europäischen Wildschwein (*Sus scrofa* L.). Zeitschrift für Tierpsychologie. 25: 955-995. (in German).

GUSTAFSSON, M. – JENSEN, P. – DE JONGE, F.H. – ILLMAN, G. – SPINKA, M. (1999): Maternal behaviour of domestic sows and crosses between domestic sows and wild boar. Applied Animal Behaviour Science. 65: 29-42.

HENRY, V.G. (1968): Length of oestrous cycles and gestation in European wild hogs. Journal of Wildlife Management 32:406-408.

JANEAU, G. – SPITZ, F. (1984): Budget espace temps des sangliers (*Sus scrofa* L.) en forêt de Grésigne. Symposium international sur le sanglier, les colloques de l'INRA n° 22.: 123-134. (in French).

KENWARD, R. (1987): Wildlife radio tracking. Equipment, field techniques and data analysis. Academic Press.

KURZ, J.C. – MARCHINTON, R.L. (1972): Radiotelemetry studies of feral hogs in South Carolina. Journal of Wildlife Management 36: 1240-1248.

MAILLARD, D. – FOURNIER, P. (2004): Timing and synchrony of births in the wild boar (Sus scrofa Linnaeus, 1758) in a Mediterranean habitat: the effect of food availability. In: Fonseca, C. – Herrero, J. –Luis, A. – Soares, A.M.V.M. (eds) Wild Boar Research 2002. A selection and edited papers from the "4th International Wild boar Symposium". Galemys, 16 Special Issues: 67-74.

MAUGET, R. (1980): Régulations écologiques comportementales et physiologiques (fonction de reproduction) de l'adaptation du sanglier *Sus scrofa* L au milieu. Université François Rabelais, Tours, France. (in French).

MAUGET, R. (1982): Seasonality of reproduction in the wild boar. In : D.J.A. Cole and G.R. Foxcroft (Eds), Control of pig reproduction. Butterworths - London.: 509-524.

MAUGET, R. – CAMPAN, R. – SPITZ, F. – DARDAILLON, M. – JANEAU, G. – PEPIN, D. (1984): Synthèse des connaissances actuelles sur la biologie du sanglier, perspectives de recherche. Symposium international sur le sanglier, les colloques de l'INRA n° 22.: 15-50. (in French).

MEYNHARDT, H. (1991): Ma vie chez les sangliers. Hatier, Les éditions du Chasseur Français (in French).

NAKATANI, J. (1989): Nest use pattern of the Japanese wild boar *Sus scrofa leucomystax* in Ebino height. Journal of the Mammalogical Society of Japan 14(1): 53-60.

POWELL, L.A. – LANG, J.D. – KREMENTZ, D.G. – CONROY, M.J. (2005): Use of radio-telemetry to reduce bias in nest searching. Journal of Field Ornithology 76(3):274-278.

SERVANTY, S. (2007): Dynamique d'une population chassée de sangliers (*Sus scrofa scrofa*) en milieu forestier. PhD thesis – Université Claude Bernard - Lyon I, France – 266p (in French).

SERVANTY, S. – GAILLARD, J-M. – ALLAINÉ, D. – BRANDT, S. – BAUBET, E. (2007): Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behavioral Ecology 18: 427-432.

VASSANT, J. – BRANDT, S. – COURTHIAL, J-J. (1994): Influence de la production de faînes et de glands sur les dates de mise bas des laies adultes. Bulletin Mensuel de l'Office de la Chasse 187 : 11-16bis (in French).

Acta Silv. Lign. Hung., Vol. 5 (2009) 167-177

Is Non-invasive Genetic Population Estimation via Faeces Sampling Feasible for Abundant Mammals with Low Defecation Rates? A Pilot Study on Free Ranging Wild Boar (*Sus scrofa)* in South-West Germany

Cornelia EBERT[ad*] – Karolina KOLODZIEJ[b] – Tim Frederic SCHIKORA[c] –
Holger K. SCHULZ[b] – Ulf HOHMANN[a]

[a] Research Institute for Forest Ecology and Forestry, Trippstadt, Germany
[b] Institute for Environmental Sciences, University of Koblenz-Landau, Germany
[c] Institute for Ecology, Evolution & Diversity, Goethe-University of Frankfurt, Germany
[d] Department of Wildlife Ecology and Management, University of Freiburg, Germany

Abstract – Wild boar is a widespread and abundant species for which until now reliable and accurate population estimates are still lacking. In this study, a method based on non-invasive genetic sampling applied in a mark-recapture framework is tested. Faeces collected along line transects serve as DNA source. Aim of the study was to evaluate efficiency and practicability of the sampling design and to assess if a sample size sufficient for reliable population estimation can be achieved. In a 12-day sampling trial which was conducted in winter 2006 and covered approx. 25 km², 4 persons collected 141 fresh wild boar faeces originating from 74 different individuals. This sample size was below those recommended for non-invasive mark-recapture studies. Population estimates calculated using program CAPTURE strongly differed between models. Even though the non-invasive approach worked in principle for wild boar, further research will have to focus on increasing sample size while keeping cost and effort acceptable for a large scale application of the method.

mark-recapture / genotyping / transect / sample size/ population density

Kivonat – Alkalmas-e a hullatékgyűjtéses mintavétel a gyakori emlősök non-invazív genetikai populáció becslésére, alacsony ürítési ráta esetén? Esettanulmány szabad területen élő vaddisznókon (*Sus scrofa*) Délnyugat-Németországban. A vaddisznó egy széles körben elterjedt és gyakori faj, amelynek megbízható és pontos genetikai populáció becslése ez idáig nem történt meg. Ebben a vizsgálatban a módszer a non-invazív genetikai mintavételen alapult, amelyet az alkalmazott jelölés-visszafogás módszer keretében valósítottunk meg. A vonaltranszekt mentén gyűjtött hullatékok nyújtották a DNS forrást. Kutatásunk célja volt, hogy megbecsüljük a mintavételi módszer kivitelezésének hatékonyságát és használhatóságát, és megállapítsuk azt a mintaméretet, amely elegendő a megbízható populációbecsléshez, és megvalósítható. A 2006 telén körülbelül 25 km²-en végzett 12 napos mintagyűjtés alatt, 4 fő 141 friss vaddisznó-hullatékot gyűjtött, 74 különböző egyedtől. Ez a mintaszám nem érte el a non-invazív jelölés-visszafogás módszerhez ajánlott elemszámot. A CAPTURE programmal végzett populációbecslés határozottan eltért a modellek között. Annak ellenére, hogy a non-invazív megközelítés alapjaiban működött a

---

[*] Corresponding author: cebert@gmx.de; Hauptstraße 16, D-67705 Trippstadt, Germany

vaddisznó esetében, a további kutatásokban az elemszám növelésére kell fókuszálnunk úgy, hogy a költségeket ne növeljük, és a ráfordított munka elfogadható legyen a módszer alkalmazásánál.

befogás / genotipizálás / transzekt / mintanagyság/ populáció sűrűség

1 INTRODUCTION

Population estimation is an important task for the management of wild boar, in particular with respect to the epidemiological role wild boar play in the transmission of the classical swine fever (Artois et al. 2002) or in order to evaluate efficiency of hunting measures. In research for methods that enable to obtain reliable data and are less biased than most traditional approaches (e.g. hunting bag analysis or traditional mark-recapture), strategies based on non-invasive genetic sampling yield promising results for several species (Piggott – Taylor 2003). The tissue sources most commonly used for population estimation in mammals are hair and faeces. Population estimation via hair sampling has been applied for several different species, e.g. grizzly *Ursus arctos* and black bears *U. americanus* (Mowat et al. 2005) and badgers *Meles meles* (Scheppers et al. 2007). Faeces have served as DNA source e.g. in estimation of coyote *Canis latrans* (Kohn et al. 1999), African elephant *Loxodonta africana* (Eggert et al. 2003) and lesser horseshoe bat *Rhinolophus hipposiderus* (Puechmaille – Petit 2007) populations. After individual identification of samples via genotyping, a modified capture-mark-recapture approach can be applied for population estimation (Woods et al. 1999).

For wild boar, the suitability of both hair and faeces as DNA sources has been tested (Fickel – Hohmann 2006). For wild boar like for other species hair is more favourable compared to faeces in terms of DNA quality and quantity (Franz et al. 2004, Fickel – Hohmann 2006, Regnaut et al. 2006). However, a pilot study conducted in the field revealed that hair sampling at baited stations is not practicable for reliable population estimation (Ebert et al. submitted): behaviour of wild boar at the stations differed strongly dependent on individual age and group status, resulting in heterogeneous individual sampling probabilities. As an alternative, we collected wild boar faeces along transects in a forested area in southwestern Germany. Our aim was to develop a reliable, representative and cost-effective sampling strategy for non-invasive population estimation. In this respect, obtaining a sufficient sample size is an important factor. For non-invasive genetic population estimation, several authors recommend collecting 2 to 3 times as many samples as animals are assumed to be present in the sampled population (Miller et al. 2005, Solberg et al. 2006). This recommendation is based partly on the fact that a certain proportion of the samples will have to be discarded from genetical analysis due to low DNA quality or quantity (Puechmaille – Petit 2007). In general, when intending to apply mark-recapture methods, the best way to obtain estimates with low bias and good precision is to ensure high capture probabilities and a high rate of recaptures (White et al. 1982). This necessitates an intensive sampling. On the other hand, a method has to be kept feasible. Thus, we aimed at evaluating the practicability and efficiency of a faeces sampling design based on line transects. Compared to other ungulates, wild boar have a low defecation rate (Briedermann 1990, Stubbe et al. 1997). Consequently, obtaining a sufficiently large sample is a crucial point in this context. Furthermore, wild boar are a widespread and abundant species, the faeces of which will distribute over wide areas. This exacerbates the difficulty of obtaining a sufficient sample size. Furthermore, it may limit the scope of non-invasive methods in terms of cost and effort for wild boar compared to rare and/ or endangered species.

We conducted our sampling trial in winter in order to keep loss of samples due to degradation and insects as low as possible. Furthermore, sampling during low ambient temperatures has been shown to increase genotyping success e.g. in wolves Canis lupus (Luccini et al. 2002), wolverines Gulo gulo (Hedmark et al. 2004), mouflon (Ovis musimon) and alpine ibex Capra ibex (Maudet et al. 2004). Furthermore, by repeating the same transect routes as accurate as possible for every sampling occasion, we intended to maximize the possibility of collecting fresh faeces (i.e. less than 48 hours old), which has been shown to increase genotyping success (see e.g. Arrendal et al. 2007, Murphy et al. 2007, Santini et al. 2007).

2 METHODS

2.1 Study area

Faeces sampling was carried out in a site of 2500 ha situated in the Palatinate Forest in southwestern Germany (49°12’N, 7°45’ E). Elevation ranges mostly from 250 to 450 m a.s.l. with a minimum of 210 m and a maximum of 609 m. Hills and valleys are orientated mainly from northeast to southwest. The predominant native plant community is beech forest (Luzulo-Fagetum). The area is covered with forest to approximately 90% (44% *Fagus sylvatica*, 26% *Pinus* sp., 10% *Picea abies*, 12% *Quercus petraea* and *Quercus robur*; Reis 2006). Several small settlements with surrounding open areas lie at the periphery of the study area. Annual average temperature is 8-9°C (Weiß 1993), annual precipitation approximates 600 – 1000 mm.

Three ungulate species occur in the Palatinate Forest: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). The annual harvest of wild boar in the state-hunting areas between 1999 and 2006 averages 2.7 individuals per km² (Range: 1.14 to 5.23 individuals per km² and year; Reis 2006). The hunting bag in the study year was comparably low: 1.6 wild boar per km².

2.2 Faeces sampling and genotyping

Sampling was carried out between November 27th and December 12th 2006. Wild boar faeces were collected along 16 transects of approx. 7 to 8 km length each *(Figure 1)*. Transects were installed parallel to each other in direction from north to south (overall length: 104 km). Trails, small roads or streams were crossed, if necessary, but it was avoided to conduct transects along trails or roads, in order to prevent potential bias of sampling results. The parallel N-S transect design was chosen with the aim to cover the study area as representative as possible by including all occurring habitat types and altitudinal levels. Four persons each walked two transects per day. Thus, all 16 transects were searched within 48 hours. The total of 16 sampling days was divided into 2 blocks of 8 days with a break of 4 days in between. Thus, each transect was searched 8 times in total within a period of approx. 3 weeks. In order to ensure that the same transect routes were searched in every repetition, transects were marked using spray paint on trees. The transect width which could be effectively searched for wild boar faeces by a walking person was approximately 3 m.

Whole faeces were stored frozen (-19ºC) in sealed plastic bags until analysis. Genotyping of samples was carried out in the laboratories of the University of Koblenz-Landau, Germany, based on 4 microsatellite loci and one Y-linked sex marker (Kolodziej et al. 2008). In order to obtain reliable consensus genotypes, all homozygous loci were repeated 10 times, whereas for heterozygous loci, 3 successful repeats were carried out.

Based on the genotyping results, population sizes were calculated using program CAPTURE (White et al. 1978). For later comparison, we chose 5 different models from the program:

- the null model (M0) which assumes equal sampling probability for all individuals in the population, no behavioural response to sampling and no variation over time
- Mt assuming a variation in sampling probability over time
- Mh Jackknife (Mh J) and Mh Chao (Mh C) assuming individual heterogeneity of sampling probabilities
- Mth Chao (Mth C) assuming sampling probability to vary over time and due to individual heterogeneity

The two Chao models have been developed especially for use with small sample sizes (Chao 1989).

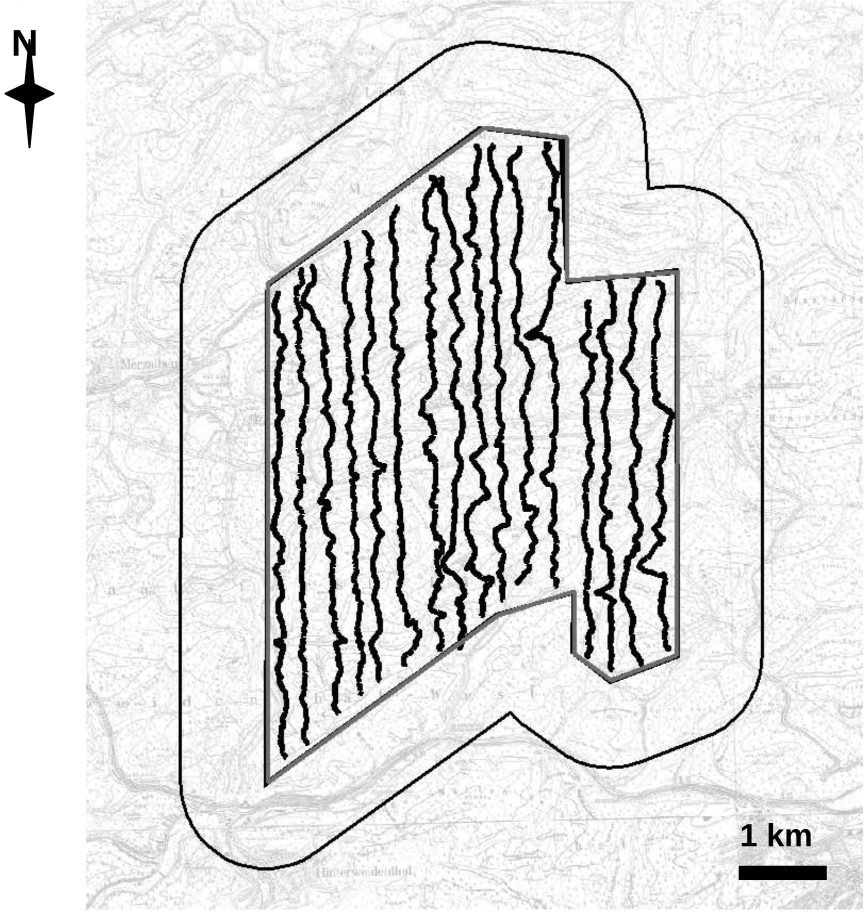


Figure 1. Transect design in the study area (25 km²) and buffer with the width of a mean monthly wild boar home range radius marking the effective sampling area (52 km²)

Additionally, we incorporated the model selection process of program CAPTURE which suggests an ‘appropriate’ model following the results of program-inherent goodness-of-fit tests.

Because in our study area the population can not be assumed to be closed, population densities have been calculated with a buffer of 1000 m around the study area, which corresponds to the radius of an average monthly 95% MCP-home range of wild boar radiotracked in the study area (Ebert et al. 2007). Thus, the area used for density calculation corresponds to 5200 ha.

3 RESULTS

3.1 Faeces sample collection

In 12 sampling days, 141 wild boar faeces were collected (*Figure 2*). To obtain these samples, a total of 622 km of transects were covered. The sampling was carried out by four persons; total time expended was 335 man-hours. This corresponds to 0.23 samples per km of transect and 0.42 samples per man-hour, respectively. The number of wild boar sampled per day varied considerably in both sampling blocks (day 1 to day 6 and day 7 to day 12 respectively). In both cases, it showed a decline from the first day to the last day of each block (*Figure 1*).

Of the 141 samples, 89 (63%) were genotyped successfully, representing 74 individual animals. The frequencies with which wild boar were sampled 1, 2, 3, 4 and 5 times were 66, 4, 3, 0, 1, respectively. This corresponds to 14 resampling events altogether. Of the 74 individuals, 48 were female and 26 were male (sex ratio male : female 1 : 1.84).

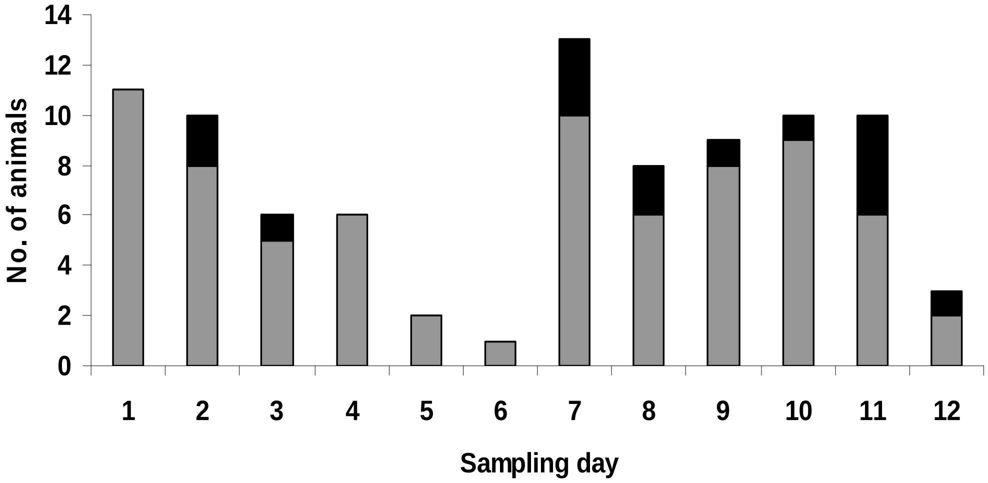


Figure 2. Number of wild boar sampled per day.
The number of animals sampled first time is given in grey, recaptures are given in black.

3.2 Population estimation

Model selection routine in program CAPTURE suggested a time specific variation in the sampling probabilities (Chi² = 39.335, df = 11, $p < 0.001$) as well as the possibility of individual heterogeneity (Chi² = 22.430, df = 11, $p = 0.021$). CAPTURE suggested model Mt as the appropriate estimator. The different models give estimated sampling probabilities of about 0.02 (2%) per sampling day. The point estimates and confidence intervals as well as the population density vary between the different models (*Table 1*). In order to evaluate the degree of coverage, we calculated the ratio sample size/ estimated population size to enable comparison with the recommended sample sizes (see introduction). Averaging over the different models' results, we obtained in mean 0.44 samples per wild boar assumed to be in the sampled population *(Table 1).*

Table 1. Population estimates and population densities derived from wild boar faeces samples using different models in program CAPTURE (see text for descriptions of the models). Population densities (wild boar per km²) were calculated based on an effective sampling area of 52 km². The mean sampling probabilities are estimates generated in program CAPTURE.

Estimation model	M0	Mt	Mh J	Mh C	Mth C
Population size N (95% CI)	225 (153 – 364)	221 (151 – 355)	308 (248 – 391)	619 (270 – 1587)	523 (270 – 1106)
Population density (95% CI)	4.3 (2.9 – 7.0)	4.3 (2.9 – 6.8)	5.9 (4.8 – 7.5)	11.9 (5.2 – 30.5)	10.0 (5.2 – 21.3)
Mean sampling probability	0.032	0.034	0.024	0.011	0.014
Ratio collected faeces/ estimated N	0.63	0.64	0.46	0.23	0.27

4 DISCUSSION

4.1 Sample size considerations

Considering the recommendations and theoretical requirements of traditional mark-recapture methods, the sample size achieved in our faeces sampling trial seems small (see e.g. Otis et al. 1978, White et al. 1982). This also holds true with respect to sample size recommendations based on the experiences of other non-invasive genetic population studies (Puechmaille – Petit 2007, Solberg et al. 2006): In order to achieve the aim of collecting 2 to 3 times as many samples as the assumed number of wild boar in our study area - even if we take the lowest of our estimates (Model Mt) as a measure - the desired sample size in our case would have been 442 to 663 faeces samples. Consequently, the sampling probabilities estimated in program CAPTURE for our data are low. While Otis et al. (1978) state that 'capture' probabilities have to be at least 0.1 for each capture occasion to obtain reliable results, in our study the estimated probabilities ranged model-dependent from 0.011 to 0.034. Thus, even though the faeces sampling procedure worked in principle for wild boar, the number of collected faeces will have to be increased considerably in the future. Consequently, the number of samples collected is only 0.23 to 0.64 times the estimated number of wild boar, dependent on which model is chosen. One reason for the low sample size may be the rather low defecation rate of wild boar compared to other ungulates. While the mean number of defecations per 24 hours in wild boar averages 4.5 (Briedermann 1990), the rate in red deer (*Cervus elaphus*) is 19 and in roe deer (*Capreolus capreolus*) 14, respectively (Tottewitz et al. 1998). A survey of red deer faeces carried out in our study area in spring 2009 yielded a sampling success of 1.6 samples per km of transect (M. Rahlfs, pers. comm.) – this is almost seven times the density of wild boar faeces, even though wild boar are assumed to be more abundant in this area than red deer. However, faeces sampling also has been carried out for some carnivores with defecation rates comparable to those of wild boar, e.g. brown bears *Ursus arctos* and Iberian lynx *Lynx pardinus* (Bellemain et al. 2005, Palomares et al. 2002). But in species like e.g. lynx or under colder or drier climatic conditions, faeces can be suitable for analysis for longer time compared to wild boar in our study area. The condition that even older faeces have to be successfully analyzable can be crucial for the practicability of the method especially when applied to rare and elusive species (Palomares et al. 2002). For wild boar faeces, DNA quality seems to decrease considerably from 48 h after defecation, with some variations depending on weather conditions (S. Eckert, unpublished data). Similar patterns have been shown for several other species (Fernando et al. 2000, Piggot 2004). Thus, frequent searching of transects is important for obtaining samples as fresh as possible. For this reason, we searched all transects every second day in our study, thus ensuring that the age of the majority of samples is less than 48 hours.

The most obvious method to increase sample size is to raise sampling effort. However, this can affect the feasibility of a method dependent on the facilities available. A promising approach for more effective faeces collection, which has already been applied successfully e.g. to grizzly bears (*Ursus arctos*), is the search with trained dogs (Wasser et al. 2004, Long et al. 2007). Dogs have been shown to reach significantly higher faeces detection rates compared to humans (Smith et al. 2005). However in wild boar, depending on area and population, the prevalence of Aujeszky's disease – which is lethal for dogs like for most carnivores (Bastian et al. 1999, Müller et al. 1998) can be more or less strong. This holds the risk of infection for detection dogs, since Aujeszky-Virus has also proven to be present in wild boar faeces (C. Adlhoch, pers. communication). Thus, this sampling method does not seem to be feasible for wild boar. The necessary increase in sample size should therefore be realised by increasing sampling intensity (longer period, more observers, more/ longer transects) or by a change of sampling strategy (e.g. by combination with hunting bag or some other kind of additional sampling).

4.2 Population estimation

The population estimates and confidence intervals derived from the capture histories of the 74 wild boar show considerable variation dependent on the applied models. Models M0 and Mt show very similar results. Resulting from the differences between the trial days in the number of wild boar sampled, CAPTURE model selection suggested model Mt as appropriate. But considering the biology and behaviour of wild boar and also the results of the majority of non-invasive studies, we would expect a certain heterogeneity in the sampling probabilities (Knapp et al. 2002). The Jackknife Mh model, which is known to perform well with large samples (Burnham – Overton 1978, Chao 1987), yielded a higher estimate compared to the models not incorporating heterogeneity. The two Chao models (Mh Chao and Mth Chao), which both incorporate heterogeneity and which are said to be especially suited for small samples like ours, show very high estimates and much larger confidence intervals compared to the others. The densities obtained from our data with those two models lie in the range of the highest wild boar densities reported by Hebeisen et al. (2007). Compared to Mh Jackknife, Mh Chao gives a population estimate twice as high.

The question which one of the estimates is closest to the real population size is difficult to answer. It has been shown previously, that the model selection procedure in program CAPTURE has low power in many cases, especially at low sample sizes (Menkens et al. 1988, McKelvey – Pearson 2001). Furthermore, part of the model selection tests failed with our data because the expected values were too small. As a consequence, we would not consider the suggested appropriate model Mt as the most suitable. Menkens et al. (1988) state that for very small data sets the Lincoln-Petersen estimator may provide more reasonable results as the more complex CAPTURE models. When applying the Lincoln-Petersen estimator (in its bias-corrected form; Chapman 1951) to our data set by setting day 1 to 6 as the ‘capture’ and day 7 to 12 as the ‘recapture’, we obtain a population estimate of 265 wild boar. This estimate lies in between those of the models M0, Mt and Mh Jackknife. Considering the different results while taking into account our very small sample and the statements of Menkens et al. (1988), the real population size may be best reflected by the less complex models. These seem quite reasonable for our study area and the study year: When comparing with densities estimated during previous studies in other parts of Europe (as reviewed in Hebeisen et al. 2007), the densities in habitats similar to our study area were comparable or even lower. Considerably higher densities were mostly reported from habitats with more favourable conditions e.g. due to agricultural crops as food sources. Besides the fact that our study area is a rather poor habitat without agricultural areas, the hunting bag in the study year was very small compared to the years before (even though hunting effort did not change between the years), indicating that the population in 2006 was low even for this area. However, until now the possibility of a biased estimation due to edge effects or due to genotyping errors can not be ruled out and requires further investigations (see Kolodziej et al. 2008).

The sex ratio of the genotypes derived from the faeces samples could either represent the real ratio in the population or be an artefact due to the small sample size. Considering the sampling design, we do not believe the detection probability to vary strongly between the two sexes. In the year of our study, 83 wild boar have been harvested in the study area. The hunting bag of the drive hunts in winter 2006/2007 showed a similarly female-biased sex ratio (male : female 1 : 1.53 in the hunting bag compared to 1 : 1.84 in the faeces samples [Landesforsten Rhineland-Palatinate, pers. comm.]) in the study year compared to our faeces samples. In general, a hunting bag may not represent an unbiased sample of a population. However, in drive hunts harvesting of wild boar is much less selective compared to single hunt, and thus we assume the drive hunt sex ratio to be nearer to the real ratio in the population. Thus, the drive hunt sex ratio supports the idea that the detection of more females than males in our faeces sampling might reflect reality and not be a consequence of the small sample size.

4.3 Cost effectiveness

The costs for personnel and transport during the field work (4 persons working on 12 sampling days plus processing of the field data) amounted to 8,000 Euros (approx. 11,300 US$). Analysis of faeces samples in the lab (1 person working 2 months and costs for extraction kits, PCRs and sequencing) cost approx. 70 Euros per sample (99 US$). Thus, the costs for the analyses of 141 samples amounted to approx. 9,690 Euros (13,710 US$). Total costs of the sampling trial and genotyping thus were approx. 17,690 Euros (25,000 US$), of which 45% represent field work and 55% are laboratory costs.

Comparing this to other studies, our costs and effort, but also our yield (in form of samples) is low: The costs for a one-year study on brown bears (*Ursus arctos*) carried out by Solberg et al. (2006) amounted to 66,700 to 77,700 Euros (95,130 to 110,800 US$). However, in this study a total of almost 700 samples were collected and analysed in two years. In a second bear study, Wasser et al. (2004) used 8 persons and 4 trained dogs to collect bear faeces. They collected 880 grizzly and black bear (*Ursus arctos, U. americanus*) faeces samples in two sampling trials over two years. For the first sampling trial, a minimum of 250 km of transects were searched, the minimum transect length for the second trial was 600 km. Wasser et al. (2004) report costs of about 500 US$ per sample (of these, 44% attributed to personnel, 9% to field transport, 42% to DNA analyses and 5% to hormone analyses). Total costs for their first trial (400 samples) therefore amounted to approx. 200,000 US$ and for their second trial (480 samples) to approx. 220,000 US$.

Compared to our study, both bear studies worked on a much larger spatial scale (7328 km² and 5200 km²). Needless to mention that the abundance of wild boar is much higher and their movement behaviour is considerably smaller scaled compared to brown bears and black bears. The estimated densities of bears range from 0.021 bears per km² (Solberg et al. 2006) to 0.037 bears per km² (Wasser et al. 2004). Thus, even our lowest estimated densities (4.3 wild boar per km²) are two orders of magnitude higher compared to the estimated bear densities. In terms of effectivity and population coverage, the two bear studies yield considerably higher values: Solberg et al. (2006) collected 2.26 and 1.22 times as many samples in their two study years as the estimated number of bears, and Wasser et al. (2004) even obtained 17.14 times as many samples as they estimated bears in their population under study. In contrast to this, we will have to increase the wild boar sample size at least threefold in order to reach the ratio recommended by Miller et al. (2005) and Solberg et al. (2006).

We found no other studies which give an account of their cost and effort, so that material for comparison is scarce. But in relation to the two studies cited above, it becomes apparent that non-invasive population estimation is carried out in a much larger dimension in terms of cost and effort. However, it may be questionable if the same dimension of cost and effort is acceptable for a widespread and abundant (and not endangered) species like the wild boar, especially when application on a larger scale is desired.

4.4 Conclusions

The basic method of non-invasive population estimation via faeces sampling seems to work for wild boar. However, several problems remain to be solved before it will be possible to obtain unbiased and accurate estimates with the approach presented here. First of all, the population estimates presented in this paper depend on reliable lab analyses. With faecal samples from wild boar, accurate genotyping turned out to be particularly challenging. At the time of printing, reliability of the lab results had yet to be confirmed. Thus, presented estimates must be regarded as preliminary. Furthermore, the sample size will have to be increased considerably. Also, additional studies are needed in order to assess if there are sources of bias which until now remain undetected. For example, the female-biased sex ratio we found in our faeces sample genotypes should be verified in order to evaluate if there exists a sex-related heterogeneity in sampling probability.

For wild boar management and to control the spread of the classical swine fever, reliable population estimates are highly desirable. However, if the method presented here is to be applied on a larger scale, a serious concern which deserves further research will be to obtain a sufficient sample size while keeping the cost and effort acceptable.

Acknowledgments: We wish to thank C. Kiffner, H. Lippe and C. Lödige for their great help in the field during the sampling trial. We are furthermore indebted to an anonymous reviewer for valuable comments on earlier drafts of this manuscript. This study was granted by the foundation "Rheinland-Pfalz fuer Innovation" and the Ministry for Environment, Forestry and Consumer Protection in Rhineland-Palatinate, Germany. C. Ebert gratefully acknowledges financial support from the FAZIT foundation.

REFERENCES

ARTOIS, M. – DEPNER, K.R. – GUBERTI, V. – HARS, J. – ROSSI, S. – RUTILI, D. (2002): Classical swine fever (hog cholera) in wild boar in Europe. Rev. Sci. tech. Off. int. Epiz. 21: 287- 303

ARRENDAL, J. – VILÀ, C. – BJÖRKLUND, M. (2007): Reliability of noninvasive genetic census of otters compared to field censuses. Conserv. Gen. 8: 1097-1107

BASTIAN, S. – BUFFEREAU, J.P. – LE DREAN, E. – BIND, J.L. – MÜLLER, T. – TOMA, B. (1999): La Maladie d'Aujeszky en France.- Epidémiologie et santé animale 38, 109-114 [in french]

BELLEMAIN, E. – SWENSON, J.E. – TALLMON, D. – BRUNBERG, S. – TABERLET, P. (2005): Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. Conserv. Biol. 19, 150-161

BURNHAM, K.P. – OVERTON, W.S. (1979): Robust estimation of population size when capture probabilities vary among animals. Ecology 60, 927-936

CHAO, A. (1987): Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43, 783-791

Ebert, C. – BERGER, K. – HUCKSCHLAG, D. – NIKOLOV, I. – SCHIKORA, T. – SCHULZ, H.K. – HOHMANN, U. (2007): Kann man Wildschweine zählen? Eine Unersuchung über die nicht-invasive Gewinnung von Gewebeproben ur Verwendung bei der Bestandesschätzung von Wildschweinen. In DEGENHARDT, A. – WUNN, U. (editors), Proceedings of the „Sektion forstliche Biometrie und Informatik", DVFFA „Die grüne Reihe" Vol. 18, 2007, pp. 63-72 [in german]

EBERT, C. – HUCKSCHLAG, D. – SCHULZ, H.K. – HOHMANN, U. (submitted): Can hair traps sample wild boar (*Sus scrofa*) randomly fort he purpose of wild boar population estimation?

EGGERT, L.S. – EGGERT, J.A. – WOODRUFF, D.S. (2003): Estimating population size for elusive animals: the forest elephants of Kakum National Park, Ghana. Mol. Ecol. 12: 1389-1402

FERNANDO, P.J. – PFRENDER, M.E. – ENCALADA, S.E. – LANDE, R. (2000): Mitochondrial DNA variation, phylogeography and population structure of the Asian elephant. Heredity 84, 362-372

FICKEL, J. – HOHMANN, U. (2006): A methodological approach for non-invasive sampling for population size estimates in wild boars (Sus scrofa). Eur. J. Wildl. Res. 52: 28-33

FRANTZ, A.C. – POPE, L.C. – CARPENTER, P.J. – ROPER, T.J. – WILSON, G.J. – DELAHAY, R.J. (2003): Reliable microsatellite genotyping of the Eurasian badger (Meles meles) using faecal DNA. Mol. Ecol. 12: 1649-1661

HEBEISEN, C. – FATTEBERT, J. – BAUBET, E. – FISCHER, C. (2008): Estimating wild boar (Sus scrofa) abundance and density using capture-resights in Canton of Geneva, Switzerland.- Eur. J. Wildl. Res. 54: 391-401

HEDMARK, E. – FLAGSTAD, O. – SEGERSTRÖM, P. – PERSSON, J. – LANDA, A. – ELLEGREN, H. (2004): DNA-based individual and sex identification from wolverine (*Gulo gulo*) faeces and urine. Conserv. Gen. 5, 405 – 410

LONG, R.A. – DONOVAN, T.M. – MACKAY, P. – ZIELINSKY, W.J. – BUZAS, J.F. (2007): Comparing scat detection dogs, cameras, and hair snares for surveying carnivores.- J. Wildl. Manage. 71, 2018-2025

KNAPP, S.M. – CRAIG, B.A. – WAITS, L.P. (2009): Incorporating genotyping error into non-invasove DNA-based mark-recapture population estimates. J. Wildl. Manage. 73, 589-604

KOHN, M.H. – YORK, E.C. – KAMRADT, D.A. – HAUGHT, G. – SAUVAJOT, R.M. – WAYNE, R.K. (1999): Estimating population size by genotyping faeces. Proc. R. Soc. (Lond.) 266: 657-663

KOLODZIEJ, K. – SCHULZ, H.K. – EBERT, C. – HOHMANN, U. – HUCKSCHLAG, D. – SCHULZ, R. (2008): DNA-based analysis of scats for use in wild boar (*Sus scrofa*) population size estimation – evaluating a lab method. Abstract of the 7th Int. Symposium on Wild Boar and Sub-order Suiformes, Sopron, Hungary

LUCCHINI, V. – FABBRI, E. – MARUCCO, F. – RICCI, S. – BOITANI, L. – RANDI, E. (2002): Non-invasive molecular tracking of colonizing wolf (Canis lupus) packs in the western Italian Alps. Mol. Ecol. 11: 857-868

MAUDET, C. – LUIKART, G. – DUBRAY, D. – VON HARDENBERG, A. – TABERLET, P. (2004): Low genotyping error rates in ungulate feces sampled in winter. Mol. Ecol. Notes 4: 772-775

MCKELVEY, K.S. – PEARSON, D.E. (2001): Population estimation with sparse data: the role of estimators versus indices revisited. Can. J. Zool 79, 1754-1765

MENKENS, G.E. – ANDERSON, S.H. (1988): Estimation of small-mammal population size. Ecology 69, 1952-1959

MILLER, C.G. – JOYCE, P. – WAITS, L.P. (2005): A new method for estimating the size of small populations from genetic mark-recapture data. Mol. Ecol. 14: 1991 - 2005

MÜLLER, T. – TEUFFERT, J. – ZIEDLER, K. – POSSARDT, C. – KRAMER, M. – STAUBACH, C. – CONRATHS, F.J. (1998): Pseudorabies in the European wild boar from Eastern Germany.- Journal of Wildlife Diseases 34, 251-258

MURPHY, M. – KENDALL, K. – ROBINSON, A. – WAITS, L.P. (2007): The impact of time and field conditions on brown bear (*Ursus arctos*) faecal DNA amplification. Conserv. Gen. 8: 1219-1224

OTIS, D.L. – BURNHAM, K.P. – WHITE, G.C. – ANDERSON, D.R. (1978): Statistical inference forv capture-recapture experiments. Wildl. Monogr. 107, 97 pp.

PALOMARES, F. – GODOY, J.A. – PIRIZ, A. – O'BRIEN, S.J. – JOHNSON, W.E. (2002): Faecal genetic analysis to determine the presence and distribution of elusive carbivores: design and feasibility for the Iberian lynx. Mol. Ecol. 11, 2171-2182

PIGGOTT, M.P. (2004): Effect of sample age and season of collection on the reliability of microsatellite genotyping of faecal DNA. Wildlife Research 31, 485-493

PIGGOTT, M.P. – TAYLOR, A.C. (2003): Remote collection of animal DNA and its applications in conservation management and understanding the population biology of rare and cryptic species. Wildl. Res. 30: 1-13

PUECHMAILLE, S.J. – PETIT, E.J. (2007): Empirical evaluation of non-invasive capture-mark-recapture estimation of population size based on a single sampling session.- J. Appl. Ecol. 44: 843 – 852

REGNAUT, S. – LUCAS, F.S. – FUMAGALLI, L. (2006): DNA degradation in avian faecal samples and feasibility of non-invasive genetic studies of threatened capercaillie populations. Conserv. Genet. 7, 449-453

REIS, M. (2006): Schalenwildbewirtschaftung im Forstamt Hinterweidenthal (Pfälzerwald) in den Jagdjahren 1999/00 bis 2005/06. Diploma Thesis, University for Applied Forest Sciences Rottenburg, Germany

SANTINI, A. – LUCCHINI, V. – FABBRI, E. – RANDI, E. (2007): Ageing and environmental factors affect PCR success in wolf (*Canis lupus*) excremental DNA samples. Mol. Ecol. Notes 7, 955 - 961

SCHEPPERS, T.L.J. – FRANTZ, A.C. – SCHAUL, M. – ENGEL, E. – BREYNE, P. – SCHLEY, L. – ROPER, T.J. (2007): Estimating social group size of Eurasian badgers *Meles meles* by genotyping remotely plucked single hairs. Wildl. Biol. 13: 195-207

SMITH, D.A. – RALLS, K. – CYPHER, B. – MALDONADO, J.E. (2005): Assessment of scat-detection dog surveys to determine kit fox distribution. Wildl. Soc. Bull.33, 897-904

SOLBERG, K.H. – BELLEMAIN, E. – DRAGESET, O.-M. – TABERLET, P. – SWENSON, J.E. (2006): An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biol. Conserv. 128: 158–168

TOTTEWITZ, F. – STUBBE, – AHRENS, M. – DOBIÀS, K. – GORETZKI, J. – PAUSTIAN, K.-H. (1998): Die Losungszählung als Methode der Bestandesschätzung von wiederkäuenden Schalenwildarten. Z. Jagdwiss. 42, 111-122 (in german with english summary)

WHITE, G.C. – BURNHAM, K.P. – OTIS, D.L. – ANDERSON, D.R. (1978): User's Manual for Program CAPTURE, Utah State Univ. Press, Logan, Utah.

WHITE, G.C. – ANDERSON, D.R. – BURNHAM, K.P. – OTIS, D.L. (1982): Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, New Mexico, LA-8787-NERP, 235 pp.

WOODS, J.G. – PAETKAU, D. – LEWIS, D. – MCLELLAN, B.N. – PROCTOR, M. – STROBECK, C. (1999): Genetic tagging of free-ranging black and brown bears. Wildl. Soc. Bull. 27: 616-627

Acta Silv. Lign. Hung., Vol. 5 (2009) 179-188

Sus scrofa: Population Structure, Reproduction and Condition in Tropical North-Eastern Australia

Peter M. HEISE-PAVLOV[a*] – Sigrid R. HEISE-PAVLOV[a] – John E. NELSON[b]

[a] PavEcol Wildlife Management. Queensland, Australia
[b] Department of Evolutionary Biology, Monash University, Melbourne. Australia

Abstract – Three feral pig populations inhabiting contrasting environments along the north eastern coast of Australia have been investigated with respect to population structure, individual condition and reproduction. The population on Prince of Wales Island contains a large proportion of juvenile and sub-adult pigs but lacks pigs in the higher age classes. Individuals also breed at an earlier age than animals of the mainland populations. Pig populations on Cape York Peninsula show a larger proportion of older animals and feral pigs living in rainforest habitats show a low proportion of animals in very young and very old age classes. Pigs from the lowland rainforest population are in better condition than those of the other populations for most of the year, reflecting the availability of food all year round in this environment. Differences in the population structure of the three populations are discussed with respect to fecundity and several mortality factors such as predation and diseases/parasites.

pigs / age structure / breeding / condition index

Kivonat – A vaddisznó-populáció szerkezete, szaporodása és kondíciója a trópusi északkelet Ausztráliában. Három, Ausztrália északkeleti partvidékén vadon élő vaddisznó populációt vizsgáltunk a populáció struktúrája, az egyedek kondíciója és reprodukciója szempontjából. A Wales herceg-szigeti populációban legnagyobb arányban a fiatalok és a szubadult vaddisznók vannak jelen, az idősebb korosztályokból hiányoznak a vaddisznók. Az egyedek itt korábban szaporodnak, mint a kontinens állatai. A Cape York-félsziget populációja, amely az esőerdei élőhelyen él, az idősebb egyedek nagyobb arányát mutatja, kis arányát mutatja azonban a nagyon fiatal és a nagyon öreg korosztályoknak. Az alföldi esőerdők vaddisznó populációi az év nagy részében jobb kondícióban vannak, mint a többi populáció, jól mutatva a táplálék egész évi hozzáférhetőségét közvetlen környezetükben. A tanulmány megvitatja a három populáció szerkezetének különbségét a születési arányszám, valamint a különböző halálozási tényezők, a ragadozás és a betegségek/paraziták figyelembe vételével.

vaddisznó / korszerkezet / szaporodás / kondíció index

---

[*] Corresponding author: alectura@bigpond.com; 211 Turpentine Road, Diwan via Mossman. 4873. Queensland, Australia

1 INTRODUCTION

Amongst the ungulates, the wild boar (*Sus scrofa*) is one of the most adaptable species. (Dexter 1990, Choquenot 1998). They have the highest potential reproductive rate of any ungulate, potentially breeding all year round with two litters per female (Barrett 1978). In combination with a low impact of predators, this may result in high population densities when conditions are optimal (Taylor et al. 1998). Population growth rates of 0.78 have been reported and are amongst the highest for an ungulate species (Mauget et al. 1984, Giles 1980). Detailed studies on population dynamics of feral pigs have been conducted in various areas of Australia, such as in the semi-arid rangelands (Giles 1980, Choquenot 1994), subalpine areas (Saunders 1988, 1993), tropical woodlands and floodplains (Corbett 1995) and tropical rainforest (Pavlov – Edwards 1995, Mitchell 2001).

These studies suggest that food availability is the most obvious factor determining the growth of pig populations in seasonally dry habitats of Australia. Additionally, predation by dingoes and the impact of diseases and parasites have been identified as factors affecting pig populations in the wet-dry tropics of Australia (Corbett 1995, Heise-Pavlov – Heise-Pavlov 2004). However, comparative studies on feral pig populations in north eastern Australia are few in number, but essential for better management of this pest species.

This study focuses on the analysis of population structure, the condition of animals, the average litter size and the age of first reproduction of females in feral pig populations living in three different habitats in NE Australia which differ in respect to seasonality, food availability and predation. Comparing pigs on an island with strong seasonal variation in food, a seasonally dry woodland habitat and a lowland rainforest habitat with low seasonal variability and an abundance of food, we would expect pigs from the rainforest habitat to be in better condition and have larger litters than those from the other contrasting habitats examined.

2 MATERIALS AND METHODS

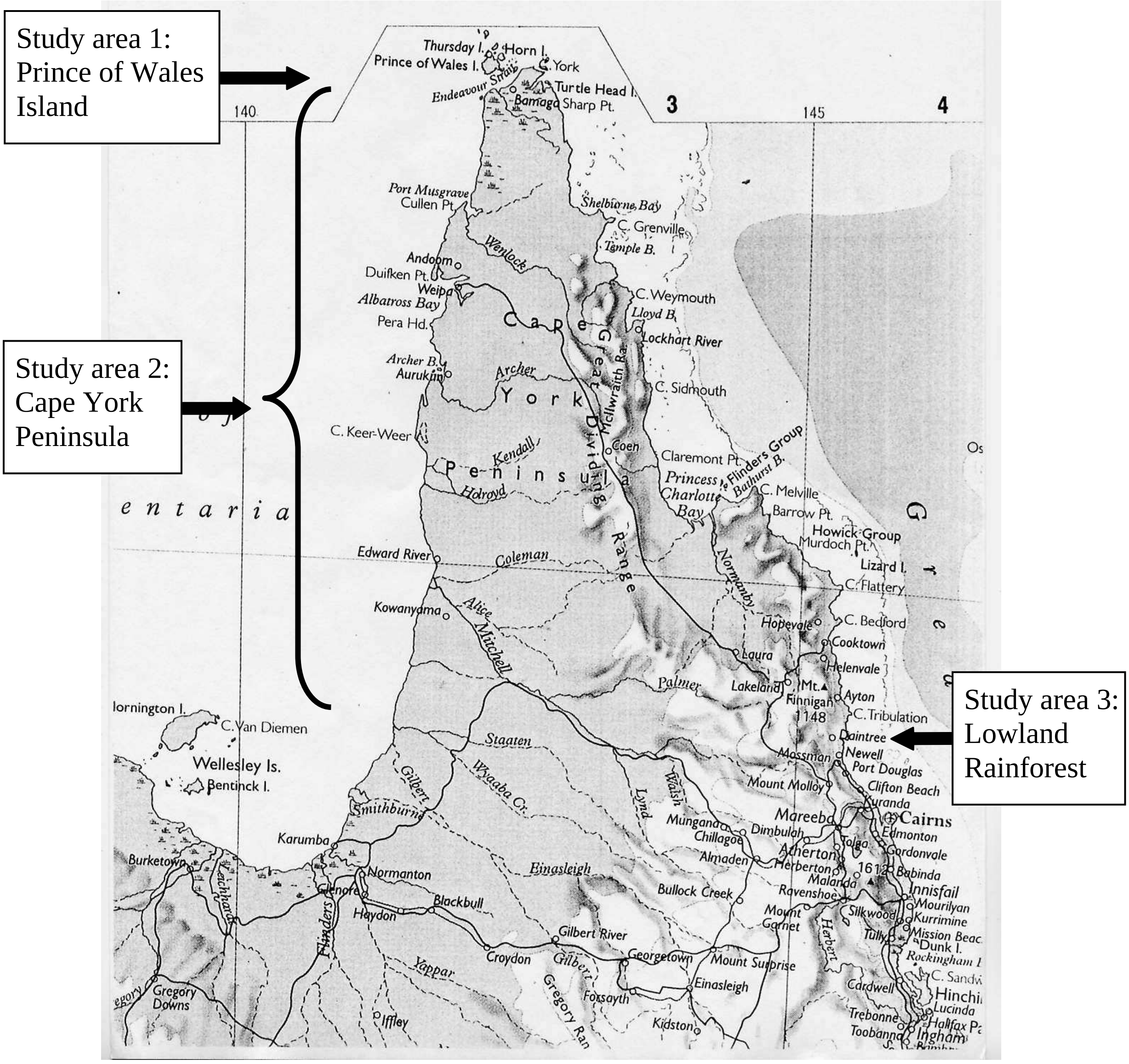
2.1 Study areas

The three studied populations are located in areas of north Queensland above 16 degrees 12 minutes of Latitude South *(Figure 1)*. The areas differ regarding the duration and intensity of dry and wet seasons which can be expressed by a seasonality index (SI), developed by Walsh - Lawler (1981). SI is the sum of absolute deviations of mean monthly rainfall from the overall monthly mean, divided by the long term mean annual rainfall.

The first population of feral pigs was studied on Prince of Wales Island (in text POW) at 142°12’E and 10°40’S. It is a 50km² Island, 30 kilometres north of the mainland of Australia. The island has a tropical monsoon climate with 3-4 months of rain followed by 8-9 months of dry weather. The average annual rainfall is 1,800 mm. The vegetation is dominated by savanna eucalypt woodland (*Eucalyptus tetradonta*) on well drained soils, patches of Blady grass (*Imperta cylindrical var. major*), patches of Paperbark (*Melaleuca viridiflora*) on poorly drained soils and occasional outcrops of mixed vine forest on rocky slopes.

The second population of feral pigs was sampled on Cape York Peninsula (in text CY) (a rough triangle shape, with the tip 142°33’E 10° 42’S, the south western corner 141°25’E, 16°12’S and the south eastern corner 145°24’E, 16° 12’S) approximately 126,000km² in area. CY Peninsula has a tropical monsoon climate similar to POW Island with the amount and timing of the rain being variable. Rainfall varies between 700mm and 1,800 mm per year. There are many permanent streams and lagoons. The watercourses flowing east are less than 120 kilometres long, while the streams flowing west, across eroded floodplains, are up to 300km long. The vegetation is varied with the most widespread communities being Open

Savanna Woodland (dominated by *Eucalyptus tetradonta* and *E. sp. aff. polycarpa* with a range of grasses in the understory), Gallery Forest (strips of forest occurring along all significant drainage lines with dominant *Ficus spp.*, *Parinari nonda*, *Nauclea orientalis* and the introduced mango *Mangifera indica*) and Grassland (dominant grass species are: *Dichanthium sp.*, *Panicum maximum*).


Study area 1: Prince of Wales Island

Study area 2: Cape York Peninsula

Study area 3: Lowland Rainforest

Figure 1. Study sites

The third feral pig population studied was sampled in the wet tropical lowland rainforest (in text LR) at 145°25'E 16°5'S. It has an area of 400 km². Coastal ranges with peaks up to 1,300 metres, at right angles to the prevailing south east wind, produces orographic winter rainfall as well as monsoonal summer rains, totalling an average of 3.5 metres of rain per year. The vegetation is primarily complex vine forest (1A) and mesophyll vine forest (2A, 2B) (Tracey 1982) with up to 150 vascular species per hectare. Permanent streams are common and usually short (less than 10 kilometres long). High humidity persists all year round in this environment.

2.2 Sampling methods

Pigs were mainly shot after hunting on foot with dogs (CY), or from a vehicle (POW). In the LR many pigs were caught in welded mesh traps incorporating a spring-loaded gate with the trigger mechanism consisting of a horizontal bar. The bar would be lifted when the animal fed on the supplied food and the door would snap shut. Pigs were killed by a head-shot according to the guidelines "Model Code of Practice for the Welfare of Animals" (SCA Technical Report Series, No. 34 1996). 351 pigs were sampled from 1982 to 1985 from Prince of Wales Island, 470 pigs were sampled from 1981 to 1986 from Cape York Peninsular and 337 pigs were sampled between 1992 and 2000 from the lowland rainforest site.

2.3 Population structure

The age of caught pigs was assessed by a modified classification of tooth eruption (Matschke 1968) up to an age of 26 months. For ages between 26 and 72 months ages were assessed on tooth wear and loss (modified by Barrett 1978). There is a progressive tooth eruption until 36 months of age and a generalised wear pattern (related to abrasiveness of the food) of the molars until 72 months. This is a simplified ageing method, but in the absence of knowledge of wear patterns on wild animals (from specific areas), no further precision can be attained. The following age classes have been used: 1 (0-5.5 months), 2 (6-12.5 months), 3 (13-24.5 months), 4 (25-36.5 months), 5 (37-48.5 months), 6 (49-60.5 months), 7 (61-72.5 months) and 8 (> 73 months). The number of animals per age class was compared by x^2test between the populations.

2.4 Individual condition

In order to assess the condition of animals, the weight of its mesogastric fat (StoFat) was related to the weight of the carcase (Gutted Weight = GW) by using the following formula describing a condition index [CondInd = (StoFat/GW) x 1000]. Mesogastric fat is associated with the 'net' of blood vessels on the outer circumference of the stomach. This structure can be easily dissected away from the stomach and weighed. Gutted weights were used to standardise carcase measurements of the sows without having pregnant sows and their attendant embryos confounding the measurement. In order to minimise the effects of seasonality, the CondInd was compared between the populations based on available data collected at the same time of the year. Therefore monthly average CondInd were compared between CY and LR using the Mann Whitney U-test for the months January to June and September and December while the Kruskal Wallis test was applied to compare the monthly average CondInd for the months July, August, October and November between all three populations (Fowler – Cohen 1990). This was necessary as sampling on POW occurred only in the months July/August and October/November.

2.5 Reproduction

Females were classified as pregnant/lactating according to the presence of foeti in the uterus and the presence of active teats respectively. Sows classified as early pregnant, had foeti less than 20mm long. The average litter size was calculated based on the number of active teats (expressing milk).

The mean gutted weight and mean age of reproducing females were compared between the three populations by the Kruskal Wallis test with subsequent significant tests for multiple comparisons (see Siegel – Castellan 1988). The age of the youngest reproducing female was determined for each population.

3 RESULTS

The three investigated populations live in habitats which differ in the duration and intensity of dry and wet seasons. While the habitats of populations on CY and POW show a similar seasonality index of 1.137 and 1.127, indicating a high seasonality, the population in the LR lives in a less seasonal climate but is still characterised by distinct wet and dry seasons, with a seasonality index of 0.676.

3.1 Population structure

The distribution of sampled pigs into the above mentioned age classes showed a younger population on POW *(Table 1 and Figure 2)* with significantly more individuals at age class 1 and 2 than the CY and LR populations. An older population was recorded on CY with significantly more individuals belonging to age class 7 and 8 than in the other sampling sites. The pig population on LR were the most evenly distributed per age class.

Table 1. Comparisons of age classes between sampled pig populations of Cape York Peninsular, Prince of Wales Island and Lowland Rainforest – results of X^2 *Tests*

age class	$CY_1 – LR_2$		$CY_1 – POW_3$		$LR_2 – POW_3$	
1	$n_1 = 8$	$n_2 = 44$	$n_1 = 8$	$n_3 = 175$	$n_2 = 44$	$n_3 = 175$
	$X^2 = 24.92$	$p < 0.000$	$X^2 = 152.39$	$p < 0.000$	$X^2 = 78.36$	$p < 0.000$
2	$n_1 = 28$	$n_2 = 79$	$n_1 = 28$	$n_3 = 58$	$n_2 = 79$	$n_3 = 58$
	$X^2 = 24.30$	$p < 0.000$	$X^2 = 10.46$	$p < 0.001$	$X^2 = 3.21$	$p < 0.073$
3	$n_1 = 29$	$n_2 = 45$	$n_1 = 29$	$n_3 = 49$	$n_2 = 45$	$n_3 = 49$
	$X^2 = 3.45$	$p < 0.063$	$X^2 = 5.12$	$p < 0.024$	$X^2 = 0.17$	$p < 0.68$
4	$n_1 = 155$	$n_2 = 50$	$n_1 = 155$	$n_3 = 31$	$n_2 = 50$	$n_3 = 31$
	$X^2 = 53.78$	$p < 0.000$	$X^2 = 82.66$	$p < 0.000$	$X^2 = 4.45$	$p < 0.035$
5	$n_1 = 82$	$n_2 = 46$	$n_1 = 82$	$n_3 = 10$	$n_2 = 46$	$n_3 = 10$
	$X^2 = 10.12$	$p < 0.001$	$X^2 = 56.34$	$p < 0.000$	$X^2 = 23.14$	$p < 0.000$
6	$n_1 = 105$	$n_2 = 35$	$n_1 = 105$	$n_3 = 15$	$n_2 = 35$	$n_3 = 15$
	$X^2 = 35.00$	$p < 0.000$	$X^2 = 67.50$	$p < 0.000$	$X^2 = 8.00$	$p < 0.005$
7	$n_1 = 57$	$n_2 = 35$	$n_1 = 57$	$n_3 = 9$	$n_2 = 35$	$n_3 = 9$
	$X^2 = 5.26$	$p < 0.022$	$X^2 = 34.90$	$p < 0.000$	$X^2 = 15.36$	$p < 0.000$

3.2 Individual condition

In July, animals on POW show significantly higher CondInd than those on CY ($p < 0.01$) and from the LR ($p < 0.01$). For the months January, April and June, animals from the LR show a significant higher CondInd than those from CY *(Figure 3)* ($p < 0.01$ for January and April, $p < 0.05$ for June). In September, the CondInd is significant higher in animals of CY than in the LR ($p < 0.001$). In November, animals of the LR show significantly higher CondInd than those from CY and POW (both $p < 0.05$).

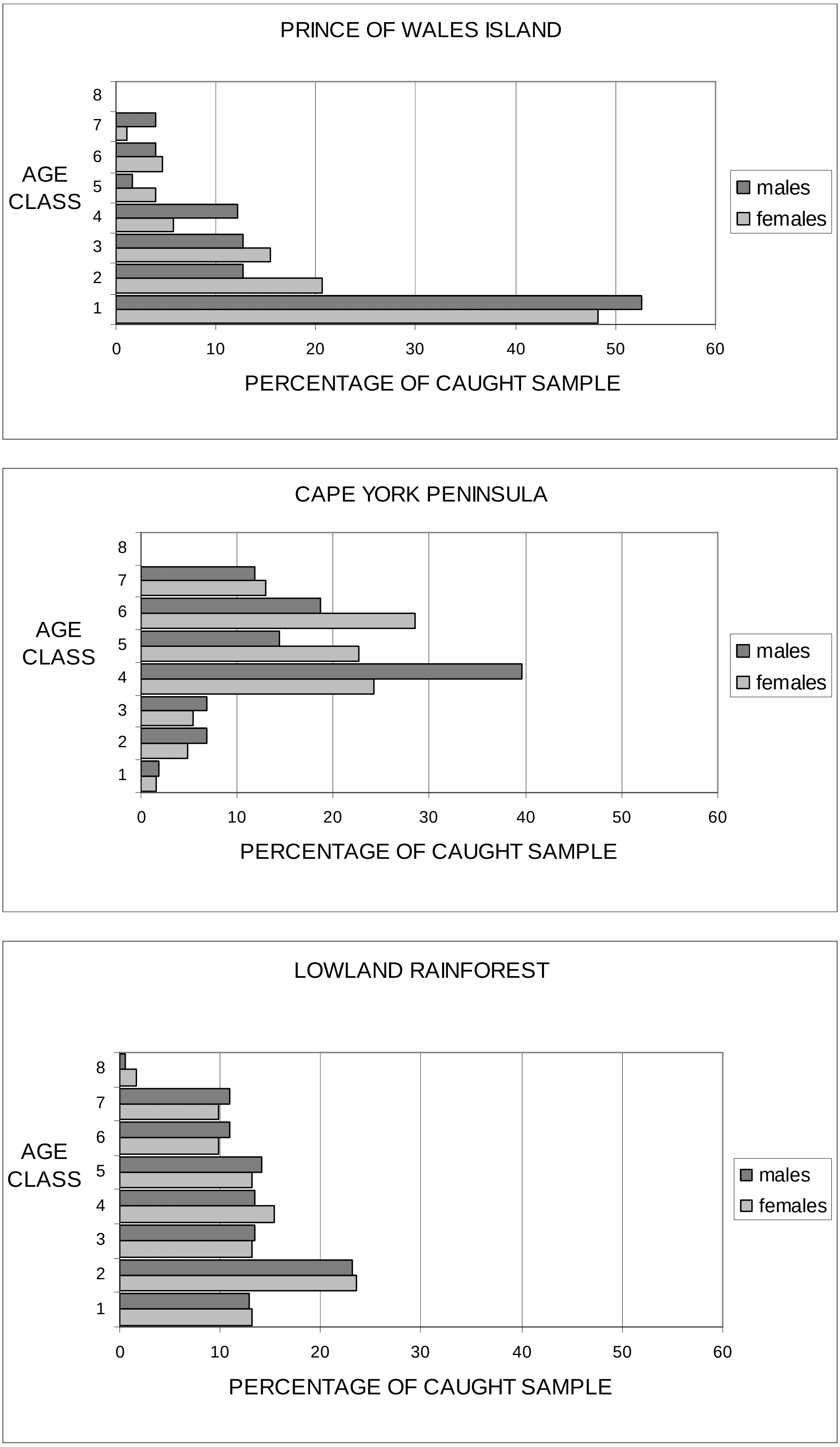


Figure 2. Population structures of three feral pig populations in tropical northern Australia

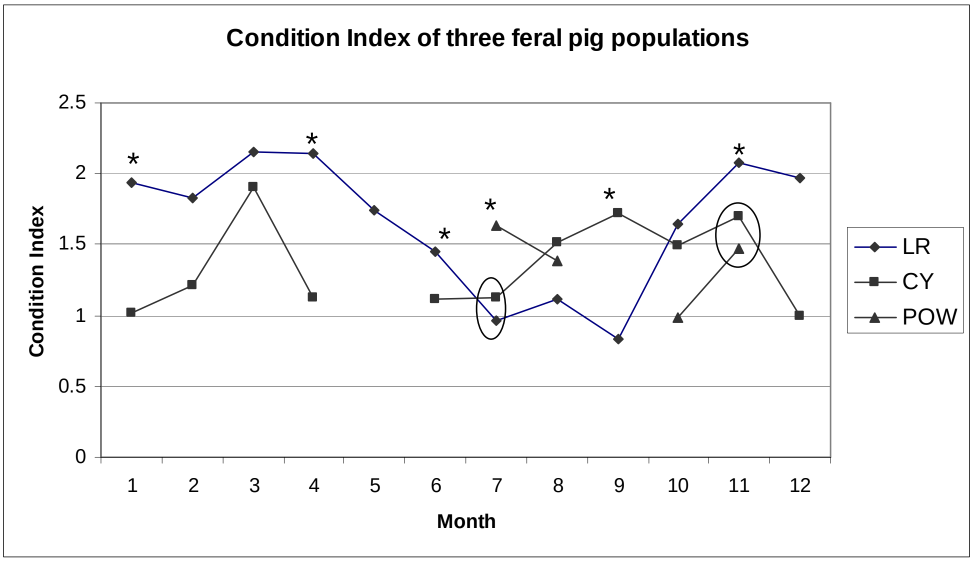


Figure 3. Condition Index of feral pigs from three different populations in tropical northern Australia

3.3 Reproduction

The average gutted weight of reproducing females was significantly lower in the POW population compared to CY and LR populations (mean GW POW: 16.03 kg ±1.18, CY 37.96 kg ± 1.13, LR 37.83 kg ± 2.29; Kruskal Wallis test: $X^2 = 53.11$, $p < 0.000$) *(Figure 4)*. Females in the POW and LR populations reproduce at an earlier age compared to females on CY (mean age of reproducing females: POW: 21.91 months ± 2.52, CY 47.76 months ± 1.76, LR 24.56 months ± 2.98; Kruskal Wallis test: $X^2 = 51.87$, $p < 0.000$). For the population in the LR, an average litter size of 5.11 ± 0.46, for CY of 6.60 ± 0.59 and POW of 4.25 ± 0.272 have been calculated. On POW, the youngest reproducing female was found at an age of 7 months while the youngest reproducing female on CY was at an age of 12 months. In the LR, the youngest reproducing female was found at an age of 6 months.

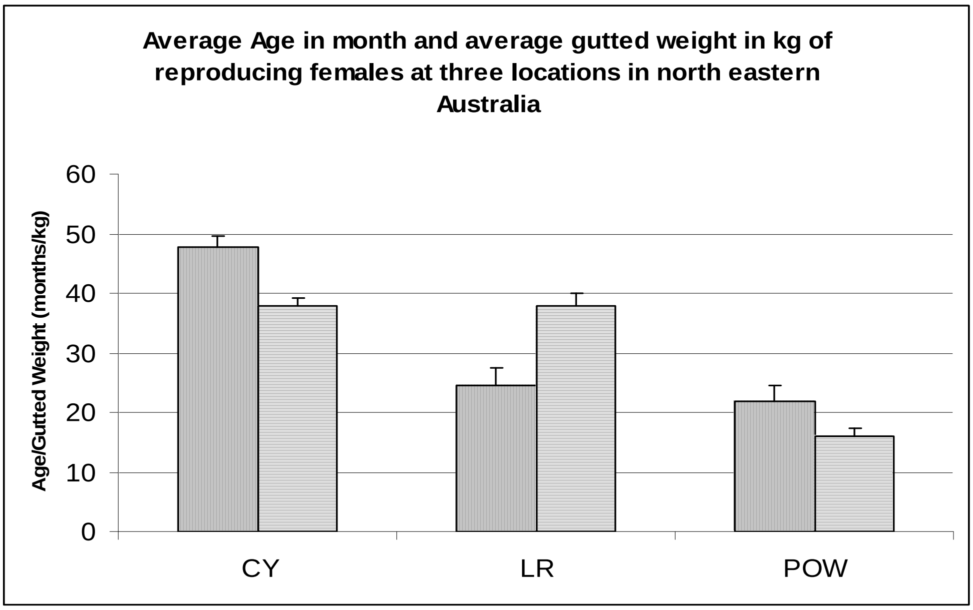


Figure 4. Average age and gutted weight of reproducing females of three feral pig populations in tropical northern Australia

4 DISCUSSION

The three populations of feral pigs occupy habitats that differ climatically and floristically. This high variability indicates that pigs are highly adaptable and are able to use a wide range of food sources (Giles 1980). Populations on Prince of Wales Island (POW) and Cape York Peninsula (CY) live in areas with markedly seasonal rainfall that is reflected by the seasonality index of 1.127 and 1.137 respectively (Walsh – Lawler 1981). Both areas have a humid tropical climate with a distinct wet season between December and March (that is connected with the monsoonal trough over northern Australia creating large flood plains) and a long dry season extending over the other 8 months causing a food shortage for pigs. In contrast, lowland Rainforest (LR) is characterized by a seasonality index of 0.676 indicating a low seasonality (seasonality indices with values less than 0.4 indicate an equal distribution of rainfall, Walsh – Lawler 1981). As on POW and CY, the climate shows a distinct wet season between December and March, but only a short dry season (October) leading to a more sufficient food supply all year round. This was reflected in LR pigs having better condition than those caught on CY or on POW, for most of the year. This indicates that more food is available in the LR habitat than in the other two sites. CY pigs showed a significantly higher condition index in September compared to the LR sample. In September, pigs were caught on CY in the northern part, mainly in riverine habitats that still provide protein rich food in the form of fruit and litter dwelling insects at this time of the year.

The generally higher condition index of animals in the LR habitat enables them to use their high potential reproductive rate in this environment. Although having a higher condition index in the LR population, females of this population do not show a significantly higher litter size compared to the population on CY. However, females on POW have the lowest litter size with 4.25, compared to the populations on either CY or LR. This suggests that the availability of food along the gallery forests in CY allows the sows to fulfil their reproductive potential in the dry season when food is otherwise limited in monsoon woodlands. The high litter size on CY does not reflect the population structure analysis and is likely to be a consequence of dingo predation (Pavlov 1991). In contrast, the high proportion of piglets in the POW population can be attributed to a lower mortality of piglets due to the absence of dingoes on the island. The presence of the dingo on CY may cause a high juvenile mortality in this feral pig population. Piglet survival appeared to be influenced by the activity of dingoes in south-eastern Australia (Newsome et al. 1983). Pavlov (1991) observed dingo predation on CY peninsula. Dingoes are also present in the rainforest, but in low numbers due to the presence of bandicoots in the area carrying the paralysis tick (*Ioxides holocyclus*), which is fatal to dogs limiting their effect on the survival of piglets in this environment. Therefore, factors other than predation must act in the rainforest habitat leading to a lower survival of piglets than on POW and also results in a relatively low proportion of pigs belonging to younger age classes in the LR population. Mitchell (2001) calculated a juvenile mortality of 51% in his study of feral pigs in the wet tropics where he found a high proportion of juvenile and sub-adult pigs. Higher mortality rates of piglets in the LR may be attributable to the presence of external and internal parasites and diseases (Heise-Pavlov - Heise-Pavlov 2003). Although the average litter size was calculated as 5.1 for this environment (Mitchell 2001) gives an average litter size of 6.4), lactating sows are rarely seen with more than 4 piglets in LR. Rates of intrauterine mortality are currently being investigated for this population, but are likely to be high due to the impact of high infection rates of leptospirosis amongst these pigs. Leptospirosis infections in pigs are known to cause abortions, stillbirths and neonatal disease in piglets (Leman et al. 1981). A survey of Leptospirosis infection in each population indicated a 2% infection rate on POW, 7% infection rate on CY (Pavlov 1991) and an infection rate between 52% and 58% in the LR population with 10 different serotypes represented and up to 4 serovars (strains) per pig (Heise-Pavlov - Heise-Pavlov 2004). The higher prevalence of diseases and parasites in the LR population may also affect adult mortality. Fewer pigs over 50 months of age have been caught in the LR than on CY and POW. The adult mortality on CY seems to be lower than on POW. Both sites show a similar climate with a prolonged dry season and a short wet season. However, the variety of habitats and places of permanent water supply on CY may reduce mortality of older pigs. The older population on CY leads to an older mean age of breeding females in this population (47 months), compared to the other two investigated populations (21-24 months of age).

The high proportion of pigs up to 12 months of age in the POW population can also be due to the onset of breeding at an earlier age. Our study shows that females on POW contribute to breeding at a younger age than those of the CY population. Females in the LR and POW populations start breeding at an age of 6 to 8 months. The reduced age of sexual maturity and reproduction of animals on islands is often attributed to an accelerated growth potential (Sondaar 1977) and will be investigated in more detail for the POW population.

The study shows that feral pig populations in northern Australia have adapted to various food sources in contrasting environments and their potentially high reproductive output is affected by predation and diseases/parasites resulting in different age structures of the populations. The management of susceptible feral pig populations along the "top end" of Australia is essential and requires more detailed studies on the dynamics of these populations.

Acknowledgments: We wish to thank Government contributors to the Cape York Peninsula/Prince of Wales Island study: The Queensland Departments of Natural Resources, Primary Industries and Environment. The Wet Tropics Management Authority and the Department of Environment partly financed the Lowland Rainforest Study. Many property owners throughout the study area are thanked collectively.

REFERENCES

BARRETT, R.H. (1978): The feral hog on the Dye Creek Ranch, California.- Hilgardia 46: 283-355.

CHOQUENOT, D. (1994): The dynamics of feral pig populations in Australia's semi-arid rangelands. PhD thesis, University of Sydney.

CHOQUENOT, D. (1998): Testing the relative influence of intrinsic and extrinsic variation in food availability on feral pig populations in Australia's rangelands. Journal of Animal Ecology 67: 887-907.

CORBETT, L.K. (1995): Does dingo predation or buffalo competition regulate feral pig numbers in the Australian wet-dry tropics? Wildlife Research 22: 65-74.

DEXTER, N. (1990): Population density and management at Arakun, North Queensland. Bureau of Rural Resources Report R/11/90. Canberra. 123 p.

FOWLER, J. – COHEN, L. (1990): Practical Statistics for Field Biology. J. Wiley - Sons Chichester, 227 p.

GILES, J.R. (1980): The ecology of feral pigs in western New South Wales. Unpubl. PhD thesis, University of Sydney, Australia, 368 p.

HEISE-PAVLOV, P.M. – HEISE-PAVLOV, S.R. (2003): Feral pigs in tropical lowland rainforest in north eastern Australia: ecology, zoonoses and management. Wildlife Biology 9: 29-36.

HEISE-PAVLOV, P.M. – HEISE-PAVLOV, S.R. (2004): Prevalence of selected parasites and leptospira in feral pigs from tropical north eastern Australia. Galemys 16: 211-220.

LEMAN, A.D. – GLOCK, R.D. – MENGELING, W.L. (1981): Diseases of Swine. University Press, Iowa State, Ames, Iowa, 832 p.

MATSCHKE, G. H. (1968): Aging European wild hogs by dentition. Journal of Wildlife Management 31: 109-113.

MAUGET, R. – CAMPAN, R. – SPITZ, F. – DARDALLION, M. – JANEU, G. – PEPIN, D. (1984): Syntheses des connaissances actuelles sur la biologie du sanglier: perspectives de recherché. – Symposium International sur le Sanglier. Tolouse. Les colloques de I'NRA No. 22.

MITCHELL, J. (2001): Ecology and management of feral pigs in rainforests. – Unpubl. PhD thesis, James Cook University, Townsville, Australia, 167 p.

NEWSOME, A.E. – CORBETT, L.K. – CATLING, P.C. – BURT, R.J. (1983): The feeding ecology of the dingo. I. Stomach contents from trapping in south-eastern Australia, and non-target wildlife also caught in dingo traps. Australian Wildlife Research 10: 477-486.

PAVLOV, P. (1991): Aspects of feral pig (*Sus scrofa*) ecology in semi-arid and tropical regions of eastern Australia. Unpubl. PhD thesis, Monash University, Melbourne, Australia, 325 p.

PAVLOV, P.M. - EDWARDS, E.C. (1995): Feral pig ecology in the Cape Tribulation National Park, North Queensland, Australia. IBEX Journal of Mountain Ecology 3: 148-151.

SAUNDERS, G. (1988): The ecology and management of feral pigs in New South Wales. MSc thesis, Macquarie University, Sydney, 167 p.

SAUNDERS, G. (1993): The demography of feral pigs (*Sus scrofa*) in Kosciusko National Park, New South Wales. Wildlife Research 20: 559-570.

SCA – STANDING COMMITTEE ON AGRICULTURE (1991): Feral Livestock Animals – Destruction or capture, handling and marketing. SCA technical Report Series No. 34.

SIEGEL, S. - CASTELLAN, N. J. (1988): Nonparametric statistics for the behavioural sciences. McGraw-Hill International Edition, 399 p.

SONDAAR, P.Y. (1977): Insularity and its effects on mammal evolution. In: Hecht, M.K. – Goody, P.L. – Hecht, B.M. (Eds); Major patterns in vertebrate evolution. Plenum Publishers, New York, 213 p.

TAYLOR, R.B. – HELLGREN, E.C. – GABOR, T.M. – ILSE, L.M. (1998): Reproduction of feral pigs in south Texas. Journal of Mammalogy 79: 1325-1331.

TRACEY, G. (1982) The vegetation of the humid tropical region of north Queensland. CSIRO Melbourne 124 p.

WALSH, R.P.D. – LAWLER, D.M. (1981): Rainfall seasonality: description, spatial patterns and change through time. Weather 36: 201-208.

Acta Silv. Lign. Hung., Vol. 5 (2009) 189-197

Human–Wild Pig Conflict in Selected States in India and Mitigation Strategies

N.P.S. CHAUHAN[a*] – Kuldeep S. BARWAL[a] – Devender KUMAR[a]

[a] Wildlife Institute of India, Dehradun, India

Abstract – We investigated the human–wild pig conflict in 5 different states in India. In these states, the wild pig populations are fragmented and relatively isolated all over. Agricultural crop depredation and attacks on humans being by wild pigs is a major problem. During 1990-2008, a total 309 human killing and injury cases were caused by wild pigs in these states. There was marked monthly variation in human casualties. Highest number of casualties occurred in November (n = 61). Wild pigs caused maximum human casualties in forests (73.8%) than crop fields (21.7%) and villages (4.5%). Highest number of 92 human casualties occurred in the age group of 41-50 years. Highest number of 97 human casualties occurred between 0801-1200 h (n = 97). Damage to agricultural crops by wild pigs was of varying extent (5-36%). As a result, people have developed antagonistic attitude towards the wild pigs which adversely affect the conservation efforts. Recommendations have been made for reducing the human–wild pig conflict in these states.

Wild pig / conflict / human casualties / crop damage / mitigation

Kivonat – Ember–vaddisznó konfliktus India néhány államában és mérséklésének lehetőségei. India öt különböző államában vizsgáltuk az ember-vaddisznó konfliktust. Ezekben az államokban a vaddisznó-populációk fragmentáltak és szinte teljesen elszigeteltek. A legnagyobb problémát a mezőgazdasági terményekben okozott kár és az emberek elleni támadások okozzák. 1990 és 2008 között ezekben az államokban 309 esetben okozták ember halálát és sérülését. Az emberi áldozatok száma havonta változott, a legtöbb eset november hónapban fordult elő (n = 61). A vaddisznók a legtöbb balesetet az erdőterületeken okozták (73,8%), ezt követték a termőföldek (21,7%), majd a falvak (4,5%). Leggyakrabban (92 eset) az áldozatok 41 és 50 év közöttiek voltak, és a támadások döntő többsége (97 eset) reggel 8 és déli 12 óra között történt. A mezőgazdasági terményekben okozott kár 5 és 36% között változott. Az emberek ellenséges magatartást vettek fel a vaddisznóval szemben, ami hátrányosan hat a természetvédelmi törekvésekre. Javaslatokat tettünk az ember-vaddisznó konfliktusok csökkentésére ezekben az államokban.

vaddisznó / konfliktus / emberi áldozatok / vadkár / mérséklés

---

[*] Corresponding author: npsc@wii.gov.in; P.O. Box 18, Chandrabani, Dehradun 248001, India

1 INTRODUCTION

The wild pig (*Sus scrofa*) is one of the most widely distributed large mammals. It has always been associated itself with man, and successfully utilises the human altered landscape (Fadeev 1975, Erkinaro et al. 1982). Being a resilient and fast breeding animal, it is capable of expanding and establishing its population in new areas (Erkinaro et al. 1982, Ahmed 1991).

Agricultural crop depredation by wild pigs is a major problem in many parts of India. Wild pigs raid crops and utilises the agro-ecosystem for food resource and shelter. The wild pigs notoriety as a crop pest is universal (Tisdell 1982). Presently the wild pig populations are fragmented and relatively isolated all over. Some of these isolated populations became locally overabundant and depend upon agricultural crops especially in and around protected areas (PAs) or managed forests (MFs) - village interface areas for a major part of their food requirement.

There is paucity of information on ecology and conflict aspects of wild pigs from Indian sub-continent; the available information is of general nature and fragmentary (Anonymous 1890, Mason 1893, Brander 1923, Ali 1927, Morris 1929, Rao 1957, Schaller 1967, Santaipillai – Chambers 1982, Prater 1980, Tiwari 1985, Shafi – Khokhar 1986, Ramachandran et. al. 1987, Ramdas 1987, Ahmed – Samant 1989, Ahmed, 1991). In the western ghats of Maharashtra state, man and wild pigs interaction has been briefly studied by Ahmad (1991).

The problem of crop damage by wild pigs has been widely reported from Rajasthan and Madhya Pradesh (Rajpurohit – Chauhan 1993, 1996). According to Maekin (1970), Andrzejwski – Jezierski (1978) and Genov (1981), the damage to crops increases when there is less natural food available in forest and artificial feeding of wild pigs could reduce crop damage. Besides agricultural crops, it causes damage to ground vegetation, orchards, forest plantations and possibly acts as carrier of some infectious diseases. As a result, there has been increasing trend in the human–wild pigs conflict in and around protected areas, managed forests and human settlements throughout the country. Consequently, people have developed antagonistic attitude towards the wild pigs and which is adversely affecting the conservation efforts. For mitigation of crop damage problem, fencing was suggested as an effective technique (Hone – Ackison 1983). Use of techniques to trap wild pigs has the potential to develop as effective applicable management tool. This paper presents the findings of our study on the human–wild pig conflict in the selected states in northern and central India and suggests mitigation strategies.

2 STUDY AREA

The study was conducted in and around different protected areas in the state of Madhya Pradesh, Uttar Pradesh, Himachal Pradesh, Uttarakhand, and Rajasthan *(Figure 1)*. Tropical, subtropical, and temperate forest vegetation, high altitude mixed forests and sub-alpine & as well as alpine pastures. Forests are interspersed with villages & agricultural areas in the low-lying areas. Villages, hamlets and cultivation are revenue lands under private ownership. People are dependent on the forest resources. Economy based on forest, agriculture and livestock.

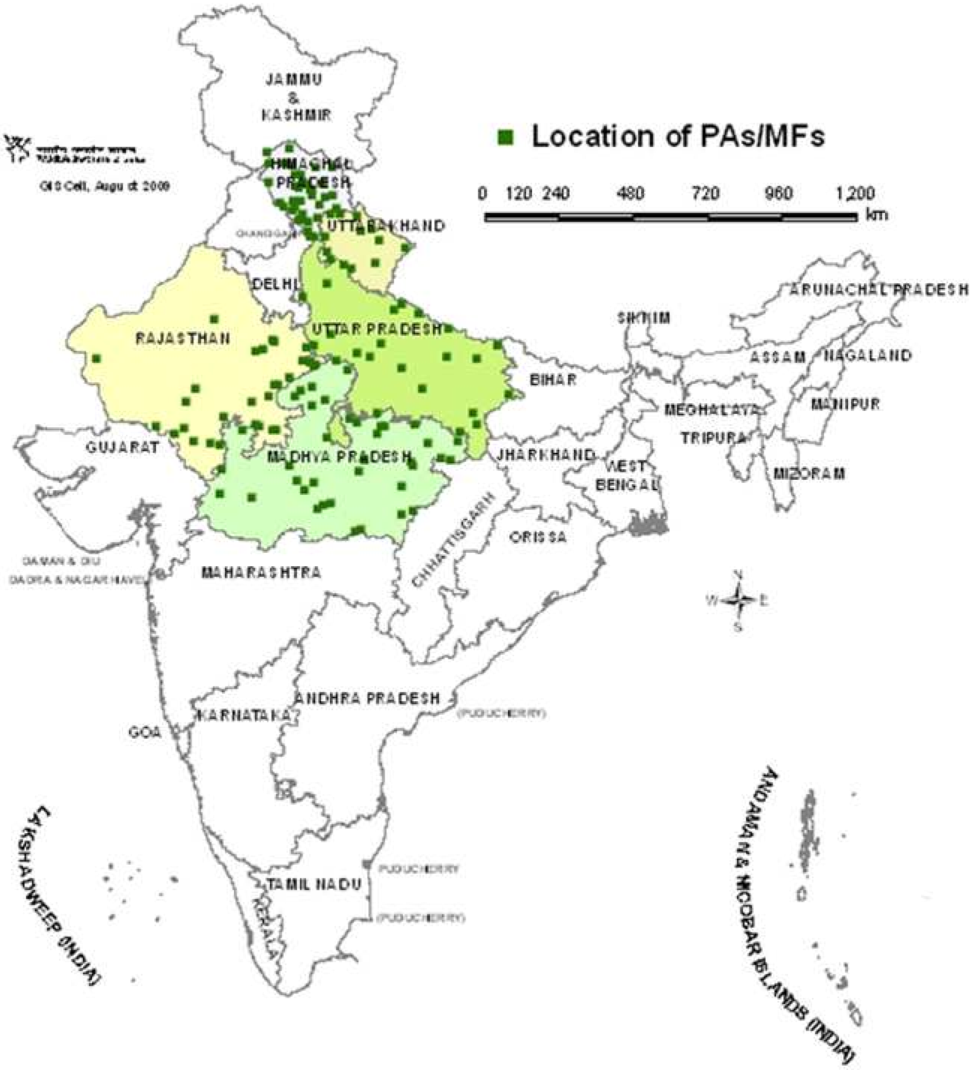


Figure 1. Map of India showing the study areas: five states and location of protected areas and managed forests

3 METHODS

Information on nature and extent of human–wild pig damage problems was collected from the villages located in and around protected areas (PAs) and managed forests (MFs) of Madhya Pradesh, Uttar Pradesh, Himachal Pradesh, Uttarakhand, and Rajasthan states. Wild pigs-human conflict has been evaluated based on the information collected from the office record of forest department, questionnaire survey of the villages and interview of the victims or their families and analysis of human casualty cases. Field managers were also contacted to know about the gravity of the problem in their areas of jurisdiction.

Following this, villages and affected areas were surveyed to collect the information on the area profile, human casualties, and circumstances of attacks, agricultural cropping pattern, and nature and extent of crop damage by wild pigs, collection of non-timber forest produce and fuel wood by the villagers and traditional control methods etc. in well-designed questionnaire formats. After the questionnaire surveys, the villages were categorized as affected and non-affected. Then few agricultural crop fields were randomly selected and the crop damage assessment was done using ocular estimation method. Information on compensation paid for the losses and year-wise payments was also collected.

3 RESULTS AND DISCUSSION

3.1 Human casualties

During 1990-2008, a total 309 human killing and injury cases were caused by wild pigs in 5 states, namely, Madhya Pradesh, Uttar Pradesh, Himachal Pradesh, Uttarakhand, and Rajasthan. Maximum cases occurred in Himachal Pradesh (n = 100, 32.4%), followed by Madhya Pradesh (n = 77, 24.9%), Uttarakhand (n = 61, 19.7%), Rajasthan (n = 48, 15.5%) and Uttar Pradesh (n = 23, 7.4%) *(Figure 2)*. Wild pigs accounted for 12 (3.9%) human deaths as compared to 297 (96.1%) injury cases. Thus the injury cases were significantly high than death cases ($\chi^2 = 24.42$, df = 4, $p << .001$).

Wild pig habitats interspersed with villages and crop fields resulted in frequent encounters with humans. During this period, most of the human casualties by wild pigs occurred in the periphery of the PAs/MFs and few occurred inside. Most of these attacks were accidental and occurred when these victims ventured into the forests for collection of non-timber forest produce in forests, fuelwood, fodder, medicinal plants, or to graze their livestock and while working in their crop fields or providing crop protection or moving in vicinity of villages.

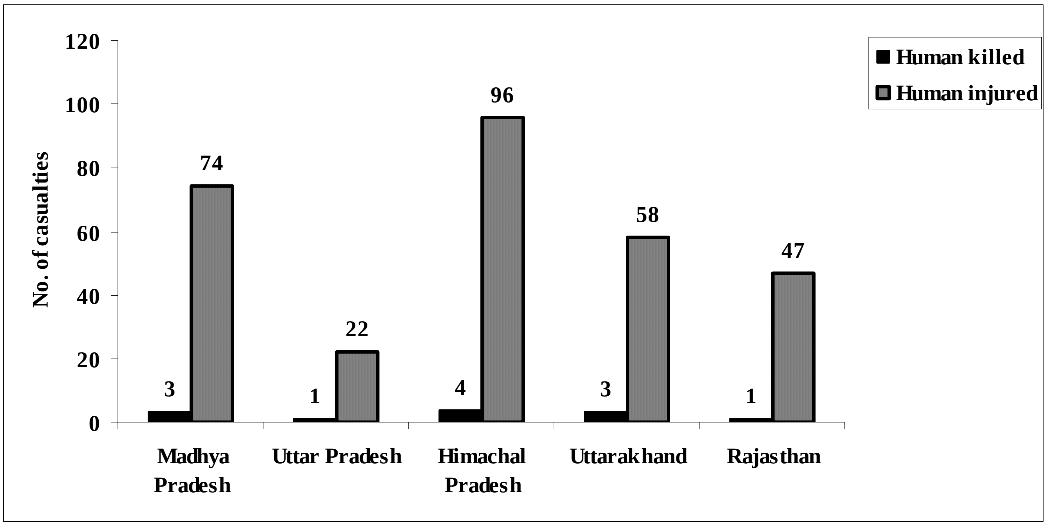


Figure 2. Humans killed and injured by wild pigs in different states during 1990 to 2008

Among males, there were 7 human killings and 204 injury cases, whereas among females, there were 5 human killings and 93 injury cases. All these human casualties showed an increasing trend from 1990 to 2008. Males were found to move extensively inside forest for collection of non timber forest produce and they were engaged more in agricultural fields for farming activity. So they were exposed more and succumbed to wild pig attacks more than the females.

3.2 Monthly variation in casualties

We observed marked monthly variation in human casualties during 1990-2008 **(Figure 3*)***. Human casualties occurred in all the months but they showed variation in different years. Out of 309 cases, highest number of casualties occurred in November (n = 61, 19.8%), followed by December (n = 44, 14.2%), January and August (n = 31, 10% each), October (n = 29, 9.4%), September (n = 23, 7.4%), March (n = 21, 6.8%), July (n = 19, 6.2%) and so on.

Human casualties were comparatively less during April (n = 13, 4.2%), May (n = 9, 2.9%) and June (n = 11, 3.6%). Monthly variation in human casualties is directly correlated with activities of villagers in forests, crop fields and villages.

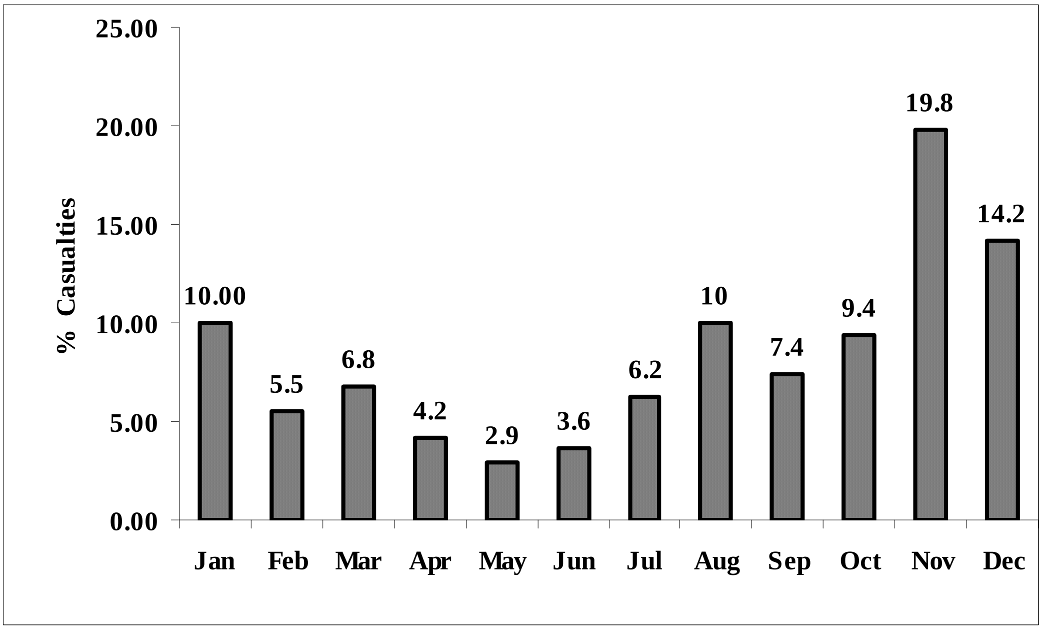


Figure 3. Monthly variation in occurrence of human casualties in different states during 1990 to 2008

3.3 Place of casualties

Wild pigs were responsible for maximum human casualties in forests (73.8%), followed by crop fields (21.7%) and a few incidences occurred in villages (4.5%) *(Figure 4)*. Highest human casualties occurred in the forests of Himachal Pradesh (n = 73), followed by Madhya Pradesh (n = 61), Uttarakhand (n = 44), Rajasthan (n = 37) and Uttar Pradesh (n = 13). Whereas in crop fields, the attacks on human being were highest in Himachal Pradesh (n = 22), followed by Madhya Pradesh (n = 61), Uttarakhand (n = 14), Madhya Pradesh and Rajasthan (n = 12 each) and Uttar Pradesh (n = 7).

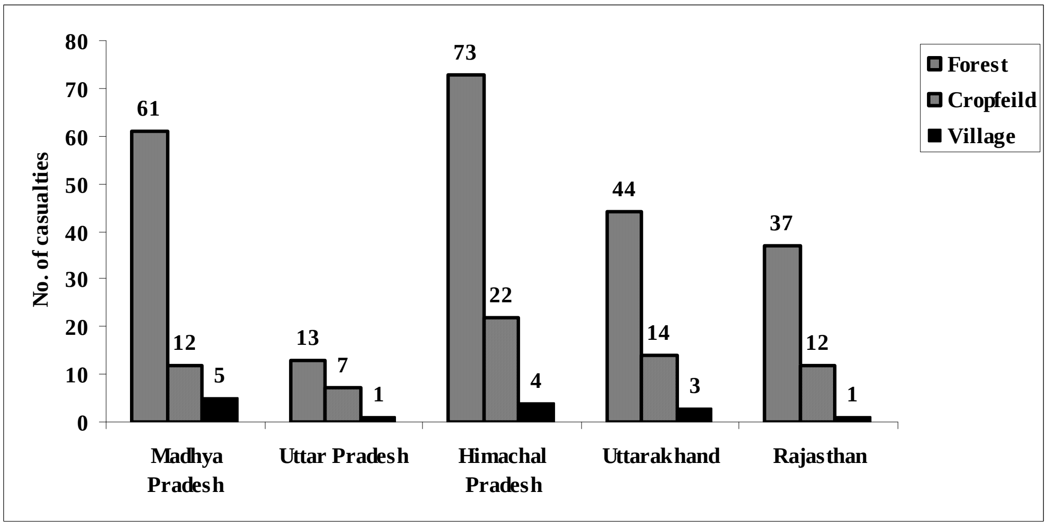


Figure 4. Place of human casualties by wild pigs in different states during 1990 to 2008

Most of these cases occurred when people were engaged in non-timber forest produce collection and livestock grazing; farming activities i.e. crop sowing, crop protection, walking through crop fields, harvesting and defecation activity.

3.4 Age of victims

Out of total 309 human casualties by wild pigs, age group of 289 cases was recorded in five different states during 1990-2008 *(Figure 5)*. Among these cases, highest number of 92 human casualties occurred in the age group of 41-50 years. There were 62, 48 and 44 casualties in the age group of 31-40 years, 21-30 years and 51-60 years respectively. Wild pig attacks on the age group of 61 years and above, 11-20 years and 1-10 years were found to be only few i.e. 23, 17 and 3 casualties respectively.

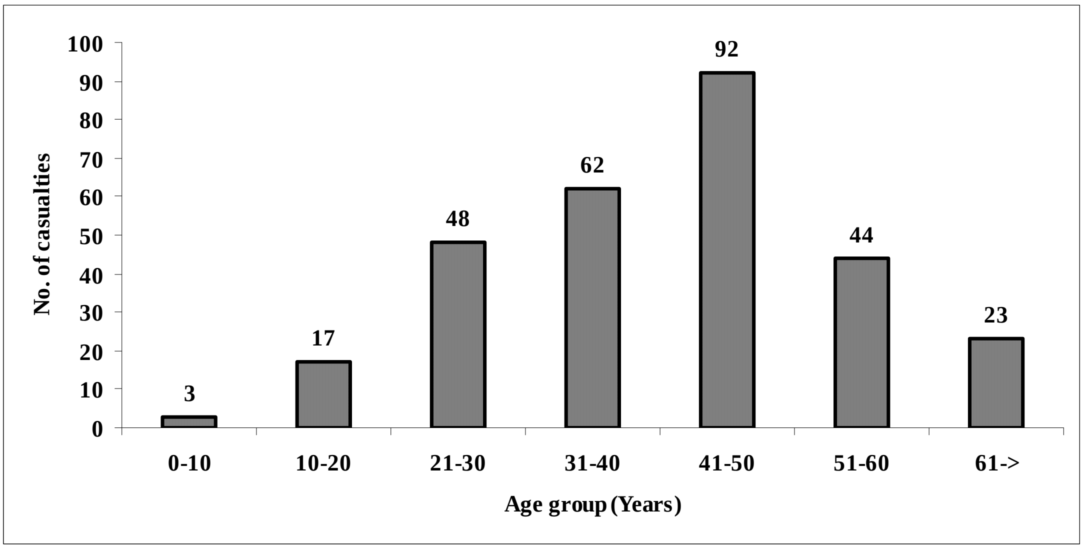


Figure 5. Age group of victims of wild pigs in and around PAs and MFs during 1990-2008.(n = 289)

3.5 Time of attacks

The time of attacks by wild pigs was recorded for 251 cases *(Table 1)*. Highest number of 97 human casualties by wild pigs occurred between 0801-1200 h (n = 97), followed by 1601-2000 h (n = 82), 0401-0800 h (n = 34), 1201-1600 h (n = 26) and so on. Only very few casualties occurred during 2001-2400 h (n = 9) and 0001-0004 h (n = 3).

Table 1. Time of human casualties by wild pigs in and around PAs and MFs during 1990-2008 (n = 251)

Time (hrs)	No. of cases
0401-0800	34
0801-1200	97
1201-1600	26
1601-2000	82
2001-2400	9
0001-0004	3
Total	251

3.6 Crop damage

Crop depredation by wild pigs is enormous. Agricultural crops: sugarcane (*Saccharum officinarum*), maize (*Zea mays*), groundnut (*Arachis hypogaea*), barley (*Hordeum vulgare*), wheat (*Triticum vulgare*), rice (*Oryza sativa*), *gram* (*Cicer aretinum*), bajra (*Pennisetum typhoides*), jowar (*Sorghum vulgare*), *moong* (*Phaseolus mungo*), sweet potato (*Ipomoea batatas*), phaphar (*Phygopyron esculantum*), madua (*Elusine corocana*), cholai (*Amaranthus vulgaris*) and katu (*Sashurea costus*) were found to be damaged to varying extent (5-36%) in different Uttar Pradesh, Himachal Pradesh, Rajasthan and Madhaya Pradesh *(Figure 6)*.

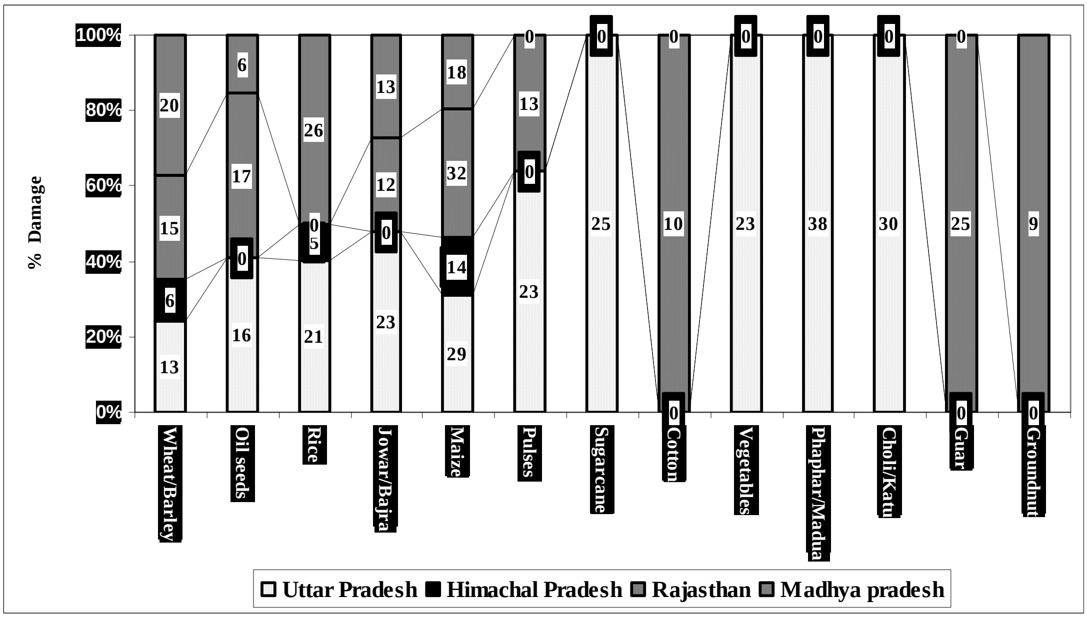


Figure 6. Agricultural crop damage by wild pigs in 5 different states during 1990-2008 (Crop names explained in text)

In Uttar Pradesh, damage to madua crop by wild pigs was highest (38%), followed by damage to cholai and katu (30%), maize (29%), sugarcane (25%) and jowar, bajra and pulses (23%). Wheat and barley crops were least affected by pigs. In Himachal Pradesh, wild pigs caused maximum damage to maize crop (14%), followed by wheat/barley (6%) and rice (5%). In Rajasthan state, damage to maize crop was highest (32%), followed by damage to guar (25%), oil seeds (17%), wheat/barley (15%), pulses (13%) and jowar/bajra (12%). In Madhya Pradesh, wild pigs caused maximum damage to rice crop (26%), followed by wheat/barley (20%), maize (18%), jowar/bajra (13%), groundnut (9%) and oilseeds (6%). Zero level of damage in the chart indicates that the crops were not grown in those areas.

Other oilseed and legume crops damaged are musturd (*Brassica compestris*), til (*Sesamum indicuam*), moth (*Vigna aconitifolius*), guar (*Cyamopsis psoralioides*), matira (*Citrullus vulgaris*), tinda (*Citrullus vulgaris*), jeera (*Cuminus cyminum*), isabgol (*Plantago ispaghula*), methi (*Trigonella corniculata*), raira (*Brassica juncea*), chili (*Capsicum annum*) and pea (*Pisum sativum*). Mature crops were highly susceptible to damage. Today, these problems have aggravated beyond tolerable limits and have resulted into direct conflicts between people and wild pigs.

4 RECOMMENDATIONS

People should remain alert and vigilant while moving in forests and crop fields especially at the time when wild pigs are active.

Use of local protective methods, co-operative guarding of matured crops is necessary. Wire fences with white, flying, flashing ribbons or plastic strips that produce scaring sounds and other frightening devices should be used in and around crop fields. Use of pig-proof barriers for crop protection and elimination or population control strategies in affected areas also needs to be experimented. Villagers should avoid cultivating crops which are highly susceptible to damage near forests and should try changing cropping patterns by growing other cash crops.

Under the given socioeconomic and political framework, one way to mitigate human–wild pig conflicts is to minimize the ill effects of socio-ecological conditions. Education and awareness programs on the ecology and behaviour of wild pigs and on mitigation strategies should be initiated for villagers in affected areas. In the fragmented and degraded forest areas, habitat protection should to be carried out to sustain the existing wild pig population. Discouraging payment of compensation for human casualties in protected areas, and research on ecology and management of wild pigs is necessary.

Acknowledgments: We thank the Director, Wildlife Institute of India and Chief Wildlife Wardens of Madhya Pradesh, Uttar Pradesh, Himachal Pradesh, Uttarakhand, and Rajasthan state forest departments for their help and cooperation in conducting the study. I also thank Prof. Andras Nahlik, University of West Hungary, Sopron for his help and support that enabled my participation in the 7th International Symposium on Wild Boar. We also thank Mr. Panna Lal of WII for his help in the map preparation. Finally we thank all villagers and victims and their families for their cooperation during the fieldwork.

REFERENCES

AHMED, B.H.M. – SAMANT, (1989): Selection of new habitats by wild boar (*Sus cristatus*, Wagner) due to human interaction in the Radhanagari wildlife sanctuary from the Western Ghats. Proc. Nat. Symp. Animal Behavoiur: 184-187.

AHMED, B.H.M (1991): Man and wild pigs (*Sus cristatus*) interaction from the western ghats of south Maharastra. Ph.D. thesis, Shivaji University, Kohlapur.

ALI, S. (1927): Moghul emperors of India as naturalists. J. Bombay Nat. Hist. Soc. 32(1): 42.

ANDREJEWSKI, R. – JEZIERSKI, W. (1978): Management of wild pigs population and its effect on commercial land. Acta Theriologica. 23(19): 309-339.

ANONYMOUS (1890): The preservation of insectivorous birds, birds of plumage and game in the central province. J. Bombay Nat. Hist. Soc. 4(1): 96.

BRANDER, D.A.A (1923): Wild Animals in Central India. Natraj Publication, Dehradun, India.

CHAUHAN, N.P.S. – RAJPUROHIT, K.S. (1993): Survey of Animal Damage Problem in and around protected areas and managed forests: Phase-I Madhaya Pradesh, Bihar and Orissa - A Report, Wildlife Institute of India, Dehradun.

CHAUHAN, N.P.S. – RAJPUROHIT, K.S. (1996): Survey of Animal Damage Problem in and around protected areas and managed forests: Phase-II Uttar Pradesh, Rajasthan and Himachal Pradesh – A Report, Wildlife Institute of India, Dehradun.

ERKINARO, E. – KALEVI, H. – LINDGREN, E. – SULKAVA, S.(1982): Occurrence and spread of wild pigs (*Sus scrofa*) in the eastern Finno Scandia. Memoranda. 58: 39-47.

FADEEV, E.V. (1975): The ecology of the wild pigs in the central Russian SPSR. Biol. Poelroned. 28(5): 20-28.

GENOV, P. (1981): Significance of natural biocenoses and agrocenoses athe source of food for wild pigs (*Sus scrofa*). Ekol. Pol. 29: 117-186.

HONE, J. AND ACKISON, B. (1983): Evaluation of fencing to control feral pig movement. Australian Wildlife Res. 10(3): 499-506.

MAEKIN, R. (1970): Dynamics of damage caused by wild pigs to different agricultural crops. Acta Theriologica. 15(27): 447-458.

MASON, J.M. (1893): Food of wild boar. J. Bombay Nat. Hist. Soc., 8 (3): 447.

MORRIS, R.C. (1929): Partial disappearance of wild boar *Sus cristatus*. J. Bombay Nat. Hist. Soc., 34 (1): 245.

PRATER, S.H. (1980): The book of Indian animals. 3rd ed., Bombay Natural History Society.

RAMACHANDRAN, K.K. – NAIR, P.V.K. – ESA, P.S. (1986): Ecology of larger mammals of Periyar wildlife sanctuary. J.Bombay Nat. Hist. Soc. 83(3): 505-524.

SHAFI, M.M. – KHOKHAR, A.R. (1986): Some observations on wild pigs *(Sus cristatus)* and its control in sugarcane areas of Punjab, Pakistan. J. Bombay Nat. Hist. Soc. 3 (1): 63-67

RAO, H.S. (1957): History of our knowledge of the Indian fauna through the ages. J. Bombay Nat. Hist. Soc., 54: 251-280.

RAMDAS, K. (1987): Some other mammals in Indian wildlife: Eds. H. Hoefer; S. Israel; T. Sindais and B. Grewal: 115-131.

SANTIAPILLAI, C. AND CHAMBERS, M.R. (1982): Aspects of population dynamics of the wild pigs (*Sus scrofa*) in the Ruhana National park, Sri Lanka. Spixiana (Muenchn), 3(3): 239-250.

SCHALLER, G.B. (1967): The Deer and the Tiger. University of Chicago Press, Chicago.

TISDELL, C.A. (1982): Wild pigs: Environmental Pest or Economic Resource? Pergamom Press, Sydney.

TIWARI, S.K. (1985): Zoo Geography of India and South-east Asia. CBS Publishers and Distributors, New Delhi.

Short Communications

Acta Silv. Lign. Hung., Vol. 5 (2009) 201-204

Forests at the limit: evolutionary – genetic consequences of environmental changes at the receding (xeric) edge of distribution.
Report from a researcher workshop

Csaba MÁTYÁS [a*] – Bruno FADY [b] – Giovanni G. VENDRAMIN [c]

[a] University of West Hungary, Sopron, Hungary
[b] INRA Avignon, France
[c] CNR Florence, Italy

In view of expected climatic changes, the adaptive potential of forest ecosystems and the future risks of diversity loss and extinction have received much attention. The behaviour of a species and of a population under changing conditions depends on their adaptive potential (genetic diversity, persistence, plasticity).

In ecology, judging of adaptability is based on the concept that presence of species (distributional patterns) depend – among other factors – on the physiological tolerance limits to climatic effects. This concept has to be extended, however, by the assertion that physiological tolerance is unquestionably determined by genetics. Limits of tolerance are therefore genetically set and will determine the presence or absence of species. Thus, adaptive response to environmental stress is to a large extent a genetic issue, especially at the limits of distribution where shifts are expected.

Publications on climate change-triggered vegetation shifts in the temperate belt are abundant. Studies and analyses deal however mostly with the shift of the thermal ("upper" or "front") limits of distribution. Migration at the front or forward colonisation is the most visible and illustrative response to climate change. On the other hand, retreat at the rear and xeric limits is insufficiently studied in spite of its ecological importance. Xeric species margins may be defined as low altitude and low latitude limits of species distribution along a moisture balance gradient. In the northern hemisphere, xeric distribution limits of forests and forest tree species extend across the woodland ecotones of the Mediterranean, Southeast Europe, South Siberia and North America. The forest cover in these densely populated regions bear high ecological and social values, it is therefore an imperative to evaluate available knowledge with the objective to mitigate effects triggered by rapidly changing conditions. At the xeric limit, selection pressure may narrow genetic variation and the increase in frequency of extreme events may result in growth decline and mortality.

What makes the problem of climatic selection at the xeric margin so special? Processes are there fuzzy, more difficult to follow than at the front limits, and changes cannot be coped by spontaneous processes alone. Human effects are omnipresent and ecological-socioeconomic consequences serious. Therefore additional efforts are necessary to properly

---

[*] Corresponding author: cm@emk.nyme.hu; H-9401 Sopron, POB 132, Hungary

understand the heritable background of ecosystem responses, to involve research communities active in related fields, and to make results understandable for stakeholders.

With the support of the European Network of Excellence „EVOLTREE”, a researcher workshop was organised in Sopron (Hungary) by Prof. Csaba Mátyás (University of West Hungary) to provide a forum for discussions and to support the surfacing of new concepts. The aim of the meeting was to present the state of the knowledge and to identify future research needs with the objective of finding ways to mitigate climate selection pressure effects at the receding edge of distributions of forest tree species. The intention of the organizer was to broaden both the geographic and disciplinal scope of the theme to reveal the global character of the problem and to raise awareness for the issue of the xeric (lower) limits of forests. The location in Sopron was selected because it is situated at the receding (xeric) edge of closed temperate European forests and of main stand-forming species, where predicted effects of climate change are most threatening.

The consultation took place May 11-15, 2009. More than 40 invited scientists from Europe and North America took part in the sessions and discussions which covered three thematic areas:

1. Ecological, demographic and evolutionary perspectives of marginal and receding populations,
2. Genetic implications of extreme selection events: genomics of adaptation, genetic background of tolerance and plasticity,
3. Experiences from field trials, tasks for human intervention and research gaps at the receding edge of ranges.

Two excursions presented symptoms of dieback and pest damages caused by climatic extremes, experiences with human-aided migration (species introductions) and currently applied silvicultural countermeasures in three state forest companies. During the closing discussion, conclusions and recommendations were formulated, the edited version of which is presented here.

MAIN CONCLUSIONS AND RECOMMENDATIONS OF THE RESEARCHER WORKSHOP DISCUSSIONS

Some definitions about range limits

Range limits of species follow the shift of environmental conditions. Receding limits appear at the rear of species ranges moving in one direction. Rear edge margins contain populations that have remained roughly in place for a very long time (usually in favourable topographic situations), at least since the Last Glacial Maximum, and their evolutionary trajectory has been largely independent of population dynamics across the main range. Trailing edge populations are left behind the contiguous range shift.

Xeric species margins may be defined as low altitude and low latitude limits of species distribution areas along a moisture balance gradient. Although determined primarily by climatic factors, xeric receding edges may also be influenced by interspecific interactions, edaphic conditions, anthropogenic effects etc.

Xeric receding species margins are affected by climate change

Receding edges, especially xeric limits are seldom addressed in the literature. This may come from the fact that they are not perceived as endangered because marginal populations often belong to widespread species. Also, no major shifts are noticeable there (although there are documented reports of increased dieback due to climate change and including insect outbreaks triggered by increased drought). Xeric range margins often occur in areas where species do not currently raise economic or conservation concerns. Although all climate models predict an increase in frequency, duration and intensity of drought, there is great uncertainty not only in species distribution models (effects of socio-economical and political decisions, lack of ecological variables, spatial resolution) but also in predicted climate scenarios themselves. This may have a disproportional impact on our ability to predict the fate of marginal populations. Current bioclimatic envelope models, set at species level are not accurate for determining the fate of xeric as well as of other edge populations.

SOME QUESTIONS THAT NEED URGENT ANSWERS

1 Where are xeric range margins?

Current xeric range limits of species (external limits) are often not well defined and difficult to assess for at least four reasons: (1) species range margins are ecologically very heterogeneous and fuzzy, especially where orography is complex (Mediterranean, Balkans) and soil is very heterogeneous; (2) low elevation / low latitude land has mostly been converted to agriculture, often leading to local extinction of marginal occurrences; (3) forest management is often artificially influencing survival and regeneration, thus obscuring natural processes; (4) lack of coordinated research. Without this information, processes affecting local population persistence at range margins will not be properly understood. Delineating xeric range margins will also help improve climate envelope models.

2 Can changes at the receding edge be predicted reliably?

On ecosystem level, climatic change triggers alteration of competitiveness and brings manifold risks. The response of populations to climatic extreme events at the xeric limit will be decided on the one hand by species-specific response set by the genetic system, and on the other hand by difficult-to-forecast interactions and calamities, caused by known and/or newly emerging pests and diseases. There is a need for long term monitoring using for example remote sensing, permanent field plots, multi-species (community level) age class spatial structures and reproductive success measurements, dendroecology, etc, to assess past and future changes at range limits.

3 Are xeric edge populations valuable for conservation and future adaptation?

Populations at range margins are often perceived as not valuable for conservation assuming that they may contain less genetic diversity. However, many ancient lineages may persist in edge populations. Because of selection and drift (among other factors), these may also contain divergent genetic resources and unique adaptations. Under climate change, sites of xeric edge populations will undergo strong ecological changes. Purifying selection may be strong, in spite of potentially significant gene flow.

Extreme events may cause population extirpation and ancient lineages may disappear, along with their original genetic make-up. On the other hand, populations have strong ecological resilience, reasons of which clearly need to be better understood, such as evolutionary history, genetic system of species, epigenetics and phenotypic plasticity, or community dynamics. Basic information on genetic (neutral and adaptive) and phenotypic diversity of populations is still needed at xeric range margins.

4 What are the adaptation processes involved at xeric range margins?

Xeric margins are areas where populations face significant genetic adaptation challenges under any type of environmental change, but particularly under climate change. Several cutting edge tools and approaches are relevant to address adaptation at the xeric edge. Molecular genetic methods allow for the identification of selection signatures, clinal variation of adaptive traits and association between marker loci, genotypes and related adaptive traits (*e.g.* genes related to stress tolerance, to phenology, to hydraulic conductance, etc). Association mapping is particularly promising for trees. Also, epigenetic processes, their duration and the species they are expressed in should be better understood, as they could contribute to explain phenotypic plasticity, and can counteract maladaptive gene flow. Hybridization is another process that need to be more deeply investigated (*e.g.* in species complexes such as *Quercus*, *Pinus*, *Abies*, etc) and may be exploited for genetic rescue. As a tool, provenance tests (and reciprocal transplants) are very valuable although new tests are needed that include marginal populations as well as marginal test sites (and possibly also species mixtures). More generally, a better understanding of the relative importance of gene flow, drift, selection and genetic buffering (plasticity, epigenetics) processes, locally at range margins as well as range-wide, is definitely needed.

5 A combined genetic and ecological (demographic) approach is needed

General models and investigations, including demographic (mating system, seed production, dispersal, recruitment dynamics) and genetic processes, possibly set at the community level (*e. g.* including at least insects) and including population level information, are needed to describe, understand and then simulate receding edge population dynamics under climate change. Functionally meaningful phenotypic traits that are easy to monitor, need to be measured over large sample sizes and over long time.

IMPLICATIONS FOR FOREST MANAGEMENT AND CONSERVATION

Research findings have to gain access to long-term management and conservation strategies. This includes principles of selection and maintenance of conservation areas, rules for reproductive material use (seed zone delineation, seed/plant transfer) and adjustment of silvicultural methods (regeneration techniques, regulation of stand structure) of managing ecosystems at the receding edge of distributions. Compared to spontaneous natural processes, shifts triggered by current and future climatic changes are too fast. Therefore human support for persistence and resilience of ecosystems seems to be inevitable, including human-aided migration (introduction, transfer) of species which bears additional risks.

These alternative approaches, with all the uncertainties they may contain, need to be tested very soon.

Guide for Authors

Acta Silvatica et Lignaria Hungarica publishes original reports and reviews in the field of forest, wood and environmental sciences. Submission of an article implies that the work has not been published previously (except in the form of an abstract or as part of a published lecture or academic thesis), that it is not under consideration for publication elsewhere. Articles should be written either in English or in German. All papers will be reviewed by two independent experts.

Authors of papers accepted for publication should sign the Publishing Agreement that can be downloaded from the homepage (http://aslh.nyme.hu)

All instructions for preparation of manuscripts can be downloaded from the homepage (http://aslh.nyme.hu)

The publisher provides ***1** copy of the Journal* and ***20** reprints* for the author.