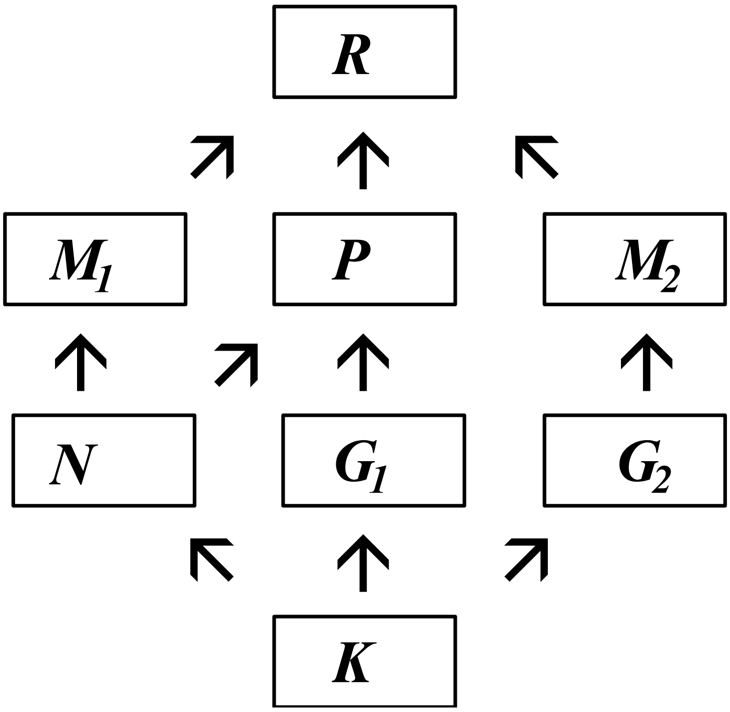
Applied Ecology and Environmental Research

International Scientific Journal



VOLUME 1 * NUMBER 1-2 * 2003

http://www.ecology.kee.hu
ISSN 1589 1623

COMPARABILITY: THE KEY TO THE APPLICABILITY OF FOOD WEB RESEARCH

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(Received 8th April 2003; accepted 9th June 2003)

Abstract. However food webs have always been considered as a central issue of ecology, their value and usefulness are frequently questioned. In this paper, I overview some causes of this skepticism and discuss in which cases two or more food webs can be compared. I suggest that the comparability of different food webs is a key to possible applications. I show how are two important topics of recent community ecology (keystone species and food web aggregation) related to the comparability problem. Finally, I overview some recent applications of food web research, where comparability can help understanding.
Keywords: *food web, indirect interaction, aggregation, keystone species, comparability*

Introduction

In order to understand how an ecological system operates, it is something very fundamental and important what animals feed on. As information on what animals of a certain community feed on has been collected, a matrix or a food web graph can give these trophic relationships. Then, food web graphs are used either only for illustration or as substrates for analyses. Since the acknowledged value of food webs and the appreciation of food web research vary widely between strong enthusiasm and deep skepticism, it is always interesting to review the status of food web studies, in the light of actual problems and results. In this paper, I intend to do this, with emphasis on comparability, and its relationship to the future applicability of food web research.

Food webs, in general

Food web graphs (and the corresponding matrices) represent the trophic relationships between species in a community. In the graph, nodes (points) refer to species (or trophic components) and edges (links) refer to a feeding interaction between them. Trophic interactions are generally asymmetrical, i.e. it is rare that both A eats B and B eats A (but see [7]). Thus, food webs are directed graphs, however, convention permits to sketch undirected graphs, too – in these cases, higher species eat the lower ones (I will frequently use the term „species” instead of „trophic group”, „trophic component”, „trophospecies”, etc; terms to be discussed later). Exceptions are noted (e.g. [94]).

Three basic types of food webs were defined by Cohen in his seminal book [12]. Community webs are more or less complete descriptions of trophic relationships of whole communities. A sink web is a subnetwork of a community web showing only a chosen species and all of the pathways (containing nodes and links), which may transport materials from producers to the chosen species (e.g. [65]). A source web depicts which species feed directly or indirectly on a selected species: it contains all nodes and links constituting pathways of energy originating from the source species (e.g. [89]).

Another important property of a food web is whether it is a binary web giving information simply about the existence of a link between two selected species (a link exists between them or does not; in the matrix, „1” stands for yes and „0” stands for no), or it is a weighted web giving any information about differences between links: feeding can be characterised qualitatively (e.g. species A „eats a lot” of species „B” but species „C” eats only a little of species „D”) or quantitatively (species „A” consumes 15 mg of species „B” per year per square meter). Quantitatively weighted webs are much closer to reality. Some authors think that energy flow magnitudes are even more important than standing stocks themselves [83, 95].

It is evident that a food web graph cannot take any shape (imagine a community with a single plant, a single herbivore and 869 carnivore species!). Following the publication of the first food web database [12] early theoretical studies tried to find general patterns in food webs, based on comparative approaches. For example, food webs seemed to have only a few omnivore species [79], and extremely few „non-adjacent omnivores” and short food chains [73, 78, 79]. The most important conclusions of early food web research were given by Pimm and colleagues [75, 77, 81]

At the first glance, it may seem to be very easy (both methodically and conceptually) how to construct a food web. One has to choose a community, list the species living there, determine who eats whom, and draw the graph. Before we go on, we need to discuss the problems of performing this recipe.

Fundamental problems

Food webs represent absolutely important properties of species and the basic architecture of ecosystems. They inform on pathways of energy, routes of nutrient cycling, the topology of trophic interactions, and the feeding habits of individual species. These are crucial for understanding how communities are organised and how do ecosystems work. Moreover, a food web also tells us implicitly where can we hope to find the kinds of indirect interactions which are mediated by only trophic direct links (exploitative competition, apparent competition and trophic cascade). Other kinds of indirect effects that need also non-trophic interactions (i.e. indirect defense, indirect mutualism) cannot be read out from food webs, of course (for excellent overviews of the basic types of indirect effects, see [58] and [1]). But in order to gain all these information we have to construct food webs on solid methodical basis.

The representation of various kinds of organisms is highly heterogeneous in traditional food webs. Trivially, mammals and birds are, first, much easier to identify at the species level, second, typically of higher interest than lower organisms. For example, the food web database of Cohen and colleagues [13] presents 113 webs, only 8 containing fungi, 9 containing Protozoa, and 20 containing bacteria. Nevertheless, microorganisms dominate energy and material fluxes in both marine and terrestrial ecosystems [86] Some basic food web properties seemed not to apply to webs where parasites were included [26, 47].

It is not an isolated phenomenon in recent natural sciences that individual scientists can solve only tiny parts of big puzzles. Accordingly, it is typical in food web research that somebody, working hard in the field, collects dietary data of species, another scientist, possibly sitting in the library, tries to draw a food web graph, and the third part of the machine, mostly sitting in front of a computer, wants to analyse the network. The basic problem is that if we have an aggregated food web (or, in general, a developed field database), it is not easy to regain the original information (see *Figs. 1* and *2* for illustration). This organisation of research is, at one hand, unavoidable, but on the other, it results in many mistakes, misunderstandings, and artefacts. For example, Waloff [106] analysed in the field and published which species consume broom in an English meadow and Dempster [18] described the insect predators of Heteroptera living on broom. Based mainly on these works, among others, Memmott and colleagues constructed the source web of broom (i.e. species feeding directly on or receiving energy indirectly from broom, [57]). Recently, Solé and Montoya [91] analysed this source food web and found an interesting distribution of trophic link number per species. Their conclusions were very interesting from the viewpoint of community organisation and robustness. However, it has been shown that the interest of the original authors, as ecologists, in the sixties, and the questions recently posed by physicists were absolutely different, so, the new results are artefacts [38]. Thus, it is of key importance to emphasize that food webs can be helpful only if we have „intelligent” data produced for answering our actual problem. The problem-dependence of wise data collection, clever network-construction and sensible network analysis is something often forgotten. Many debates have been published on, for example, how to aggregate species into larger trophic groups. This question is absolutely unintelligent until we have a particular problem. If we have a problem, we are able to define reasonable trophic groups, aggregate species, and determine the trophic linkages.

In general, both the nodes and the links of the food web graphs were shown to be hard to define: nodes called for wise aggregation (see below), while links called for the analysis of interaction strength, symmetry and spatiotemporal plasticity. Serious

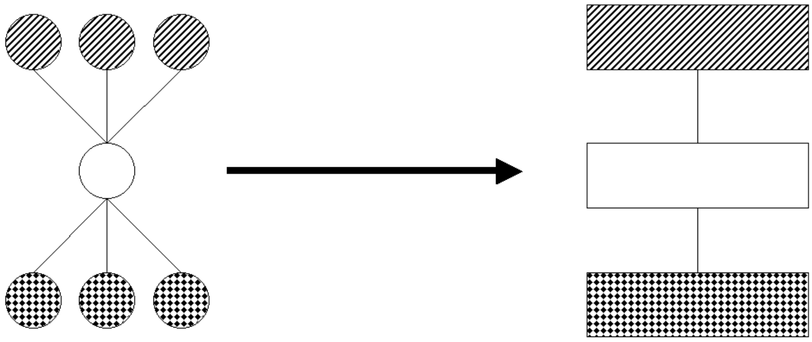

Figure 1*. A hypothetical community consisting of seven species (graph nodes in the food web: three plants, an herbivore and three carnivores) can be aggregated into a system-model of three components (boxes of the trophic network: producers, primary consumers and secondary consumers). In this simple case, the trophic position of aggregated species fulfills the strictest criteria for aggregation (they share exactly the same prey and predators, i.e. these are aggregated into trophospecies, sensu* [105]*). Whether this simplification causes information loss or helps analysis and understanding of the community depends on the actual problem. Indirect interactions between species can be studied on the left food web, while the basic energetics of the system can be investigated better on the right trophic flow network.*

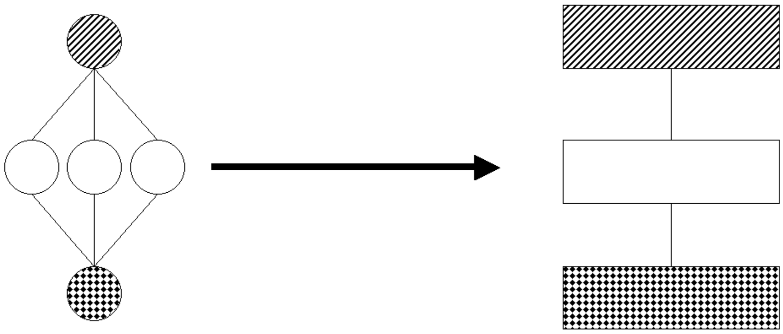

Figure 2. *The aggregated trophic network in Fig. 1 (on the right) may have been constructed from a completely different topological arrangement of species (compared to that on the left in Fig. 1). Low-resolution system models give no information about these details.*

methodological and conceptual criticism [67, 68, 80, 84] led to skepticism at one hand [43], and a novel research programme on the other [14]. Interestingly, one of the first basic problems (how to assess interaction strength on the field, [67]) was tried to be solved first only more than a decade later (and by the same author, [69]).

Linking species to communities: key players

For the majority of ecologists, mostly ones of taxonomist style, constructing a food web is the crown on a project. Collecting individuals in the field, identifying them and their prey items, and determining trophic linkages are the dirty work followed by the elegant step of drawing a web. It is really a reasonably large amount of work but it is less useful if the graph is presented only for *illustration*. For the minority of theoretical ecologists, the work of *analysing* the web just begins. Food webs, if constructed adequately to our problems, may tell a lot information about the community, help a lot in answering our particular question, and reveal emergent or system-level properties of the ecosystem. Moreover, they can generate a number of new hypotheses and questions. Thus, the food web itself is, first, the result of many people's work, and second, the substrate of a good deal of analytical investigation.

For example, if the food web is drawn, our focal species of interest can be put in a network context, meaning that we have impressions to the identification of its exploitative competitors, cascading interactors, or apparent competitors. We can have some information about its trophic height, about its position in the web, or whether one of its interacting partners is a key network element (i.e. positional keystone species, [37]).

A very important problem for both fundamental and applied research (e.g. conservation biology) is how to link species to communities. This means two things, according to an *inter*relationship. First, how disturbing a species will cascade through the whole interaction network, e.g. [65, 66], which species will be affected and to what extent. Second, how will certain species be affected by a given system-level perturbation e.g. [98, 32]. However there are very intensive recent investigations on this area [31], we hardly can say anything nice. Especially, we lack quantitative approaches. To predict, by numbers, which species are of central importance to the community, is the essential problem of keystone studies [9, 59, 87].

Some species in ecological communities have exceedingly large effects on others. This can be possible because of their large effect on the abiotic environment (ecosystem engineers, [30]), or because their cascading interspecific interactions. Either a few or many, as well as either weak or strong direct interactions may lead finally to a community-wide effect, depending on the details of ecosystem function and the dynamics of interactions (e.g. types of functional responses). Interactions themselves can be of either trophic (like predation) or nontrophic (like facilitation) nature. An important species is termed a keystone species [66] if its large effect is disproportionately large to its biomass (after Tilman [87]). Keystones have been identified in all trophic positions (top-predators, plants, intermediate species, parasites, etc. [9, 82]). According to a simple but informative and inspirative definition, keystones are one-species functional groups [9] while as the number of species increases in a certain well-defined functional group, they are less close to be a keystone. Thus, ecological redundancy is roughly the contrary of „keystoneness”. Of course, this approach is mostly of conceptual value, since functional groups are also dependent on the actual problem and do not „exist” *a priori* (many ecologists’ failure is to refer to functional groups as they were „real” ecological objects; *a priori* defined functional groups can be termed „fictional groups” – Malmqvist, pers. comm.).

An issue easier to study for theoreticians than for experimentalists is what will be the effect of deleting a species from a community. Earlier works with dynamical emphasis [72, 74] were recently followed by purely structural analyses [21, 37, 46, 91]. Exciting theoretical constructions, unfortunately, are rarely followed by nice field studies.

A major problem with keystone research is how to identify exactly (quantitatively) keystone species. Quantitative approaches could provide predictive power and the possibility of *a priori* identification instead of recognising the large effect of a species only after it has gone extinct. Following an early attempt (CI, community importance, [59]), recent investigations on outlining a quantitative framework are based on the positions of species in food webs; critical network positions may refer to species whose deletion (extinction) would cause a dramatic effect on the whole community. These studies, thus, refer to keystone species mainly on theoretical grounds [21, 27, 28, 34, 37, 38, 54, 91]. Approaches searching for the topological connection of local to global scales may help in understanding the „linking” problem [34, 38, 102]. The importance of a species, based on these trophic assumptions, can be highly contingent with environmental factors and is expressed only in the context of a single community. However, for the purpose of inter-community analyses, the construction of comparative food webs would be a minimal criterion. The changes in importance of a certain species can now be traced only in a single ecosystem, where comparable food webs characterise different states of the system (four seasons: [33, 35], stress versus no stress: [32]).

Why only species? – problems of aggregation

One of the rare food webs of uniformly species-level resolution, maybe the only one, is the source web based on broom described in an English meadow [57]. The final aim, according to the view of many food web researchers, is to include exclusively species in food webs. I try to show shortly why is this aim impossible, conceptually senseless and absolutely illogical. Finally, I will show how could wise aggregation help in comparability.

Mammals and birds are surely easy to classify. The species complexes of frogs and many polyploid plants, among many other cases, may cause problems. But even if we analyse a community where these „problematic” taxa do not live, we surely will find bacteria and they will stop us to realise the „final aim”. It is not easy to define bacterial species and even the bacterial species concept is questionable.

Even if somebody has a high-resolution web, maybe containing only species, it will probably turn out that many species have exactly the same set of sources and consumers, thus, they can be unified in a single trophic group. Moreover, very importantly, in the case of other species the trophic difference between conspecific individuals may be much larger than the difference between individuals belonging to different species. Thus, sometimes we could stop at higher resolution, but sometimes we need to go below the species level in order to detect reasonable dietary differences (*Fig. 3*). Tadpole and adult frog should be represented by different nodes in the food web graph, but desert spiders may frequently belong to a single or few nodes.

Desert spiders, if tried to sensibly separated to several nodes, will be represented according to their size instead of taxonomic position. In other words, it does not matter which species they belong to, feeding habits depend only on their size class: they eat „everything” smaller that moves around. If functionality is intended to taken into account, the relevance of taxonomy is much smaller if not disappears. Soil nematodes are wisely represented by a bacterivore, a fungivore, a predatory and a parasitic trophic group of species [19, 20]. Another example for the unavoidability of functionality reports on the redundancy of algae in wet ecosystems [93]. Functionality is a key issue in ecology: if a food web is created to represent trophic relationships in a community, it cannot be constrained by „empty” taxonomical classification. In fact, many „bad” food webs are created by taxonomists thinking too rigidly in categories reflecting no function at all. Taxonomists are people without whom food webs cannot be constructed but after they have done their work, ecologists of more functional thinking have to finalise the construction of food webs.

A problem apart of the above ones is that trophic interactions are highly plastic in space and time. If we study a community at the species level, it does matter whether we collect our (feeding) data at night or at daytime, in winter or in summer, and at a particular place or ten meters away. For a trivial example, observing feeding relationships at daytime, we will have no owl in the food web. The spatiotemporal variability of trophic interactions [107, 111, 112] calls for lower levels of resolution: larger trophic components change less, for example, the group of benthic suspension feeders remains functioning even if species come and go [15]. Looking at food webs at the species level may lead to unnecessary complexity.

Of course, lower resolution may also cause problems, for example, indirect interactions between species cannot be detected if they are aggregated into the same trophic group. Thus, as the only robust conclusion, we have to say that the optimal level of resolution (way of aggregation) depends on the context of the actual problem. There is no general recipe, but it is useless to restrict to species. More exactly, it is wise to know a community at the species level, but only for being able to aggregate the species wisely into reasonable larger groups.

From the above, it follows that there is neither qualitative nor quantitative aggregation algorithm accepted widely. However, a practical procedure is to eliminate

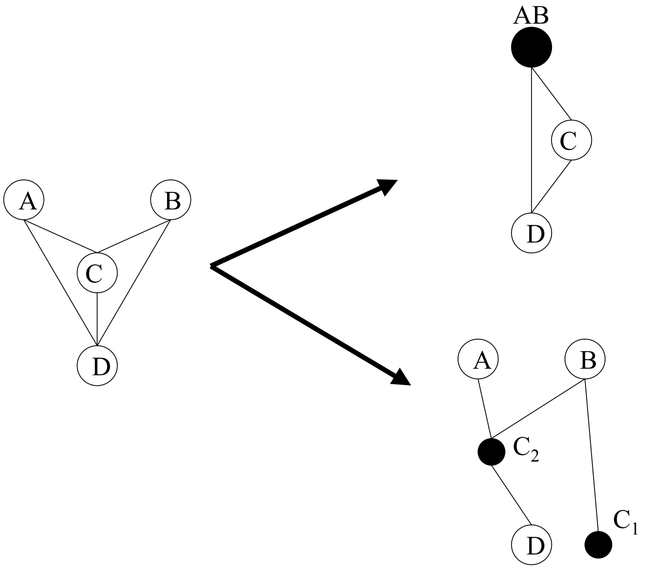

Figure 3. *Whenever the species list of a community is transformed to a list of ecologically reasonable compartments of the ecosystem, functionality can (and need to) be taken into account. The upper graph on the right shows a graph where species „A" and species „B" of an original food web (on the left) have been aggregated into a single trophic component (black circle), since they have exactly the same trophic links („AB" is a trophospecies,* [105]*). But it is not a rule that trophic groups reflecting functionality have always to be above the species level: the lower graph on the right shows a situation where the division of species „C" of the original food web into two smaller trophic components was logical: „C_1" may be a larval form, not eating „D" and eaten only by „B", while „C_2" may represent the adults of „C", eating „D" and eaten by both higher species („A" and „B"). If the feeding habits, i.e. the trophic status, of a species' individuals change fundamentally through their life cycle, this is well reasonable. Differences in feeding between two individuals of the same species belonging to different developmental stages (for example, a tadpole and a frog) can be much larger than differences between two individuals of two species (for example, in the case of desert spiders,* [84]*).*

trophic groups and/or trophic links below certain well-defined biomass and material flow limits, respectively (see [111]). Proposed exact aggregation algorithms [25, 99] criticised for distortions resulted from aggregation [64]. It has been shown that the aggregation of real field data is easier than that of simulated data [92]. Even if we have an exact algorithm, serious problems still remain. An illustrative example is given for that:

Let us assume that our aim is to create larger groups from the species of the broom source web [57], based on nothing else than trophic similarity. The originally described 154 species (more exactly, 153 species and the group of „immature spiders") can be first aggregated into 82 trophospecies [105] containing species with exactly the same set of prey and predators (*Fig. 4*). If we need stronger aggregation (i.e. lower resolution), we may relax a bit the trophospecies criteria: the aggregation step „α" will mean the replacement of an *n*-step chain by an *n*-1 step chain (chain shortening), the step „β" will mean the fusion of two species if they have exactly the same predators but there is a subset relationship between their prey-sets (a relaxed condition), and the step „γ" will mean the fusion of two species if they have exactly the same prey but there is a subset

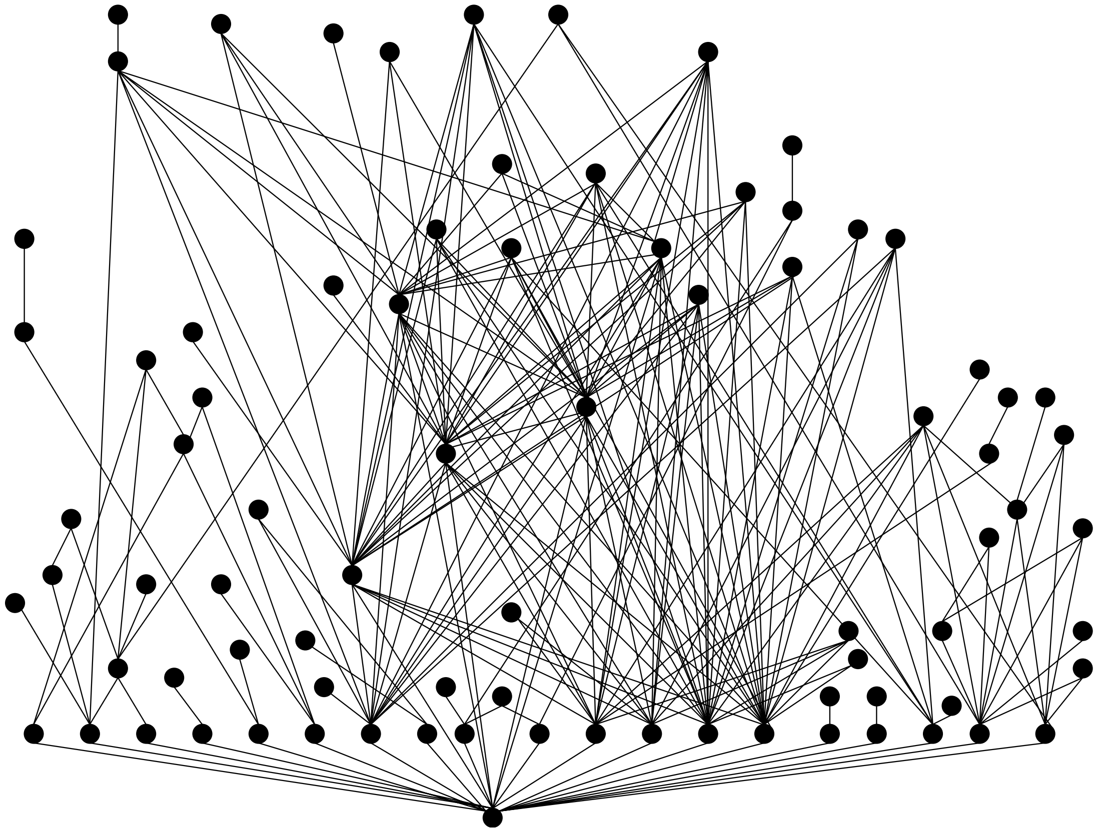

***Figure 4**. The 82 trophospecies living on broom (Cytisus scoparius): they were aggregated from 154 species, based on perfect trophic similarity* [57]. *We do not give the list of species (see it in* [57]*). Higher species always feed on or parasite lower species. The lowest species is broom (this is a source web).*

relationship between their predator-sets (another condition is relaxed now). Combining steps „α”, „β” and „γ”, we can aggregate the original network according to six sequences. The aggregated webs (*Fig. 5*) are of different size, even if the same aggregation steps were made, only their sequence differed. The connectance of the aggregated six webs also differs widely: for the original web, C = 0,06, and the connectance values after aggregation procedures range from 0,11 (α-γ-β) to 0,22 (γ-α-β). This illustrative example only shows that exactly defined rules may still lead to fundamentally different results when applied – and there are no exact aggregation algorithms to date.

Quantitative aggregation methods would provide exactness and objectivity. Aggregation based on field expert would help to save reality. The best solution would be to have a realistic but also quantitative aggregation procedure, but it may not exist considering problem- and context-dependency. But we have seen that some kind of aggregation is necessary, since species-level resolution has its serious limits. So, a skeptical voice would say that there is no way to construct a good food web. If there are no good webs, the minimal criteria of usefulness can be to compare similarly wrong food webs, thus, comparability may be the only key to useful food web research.

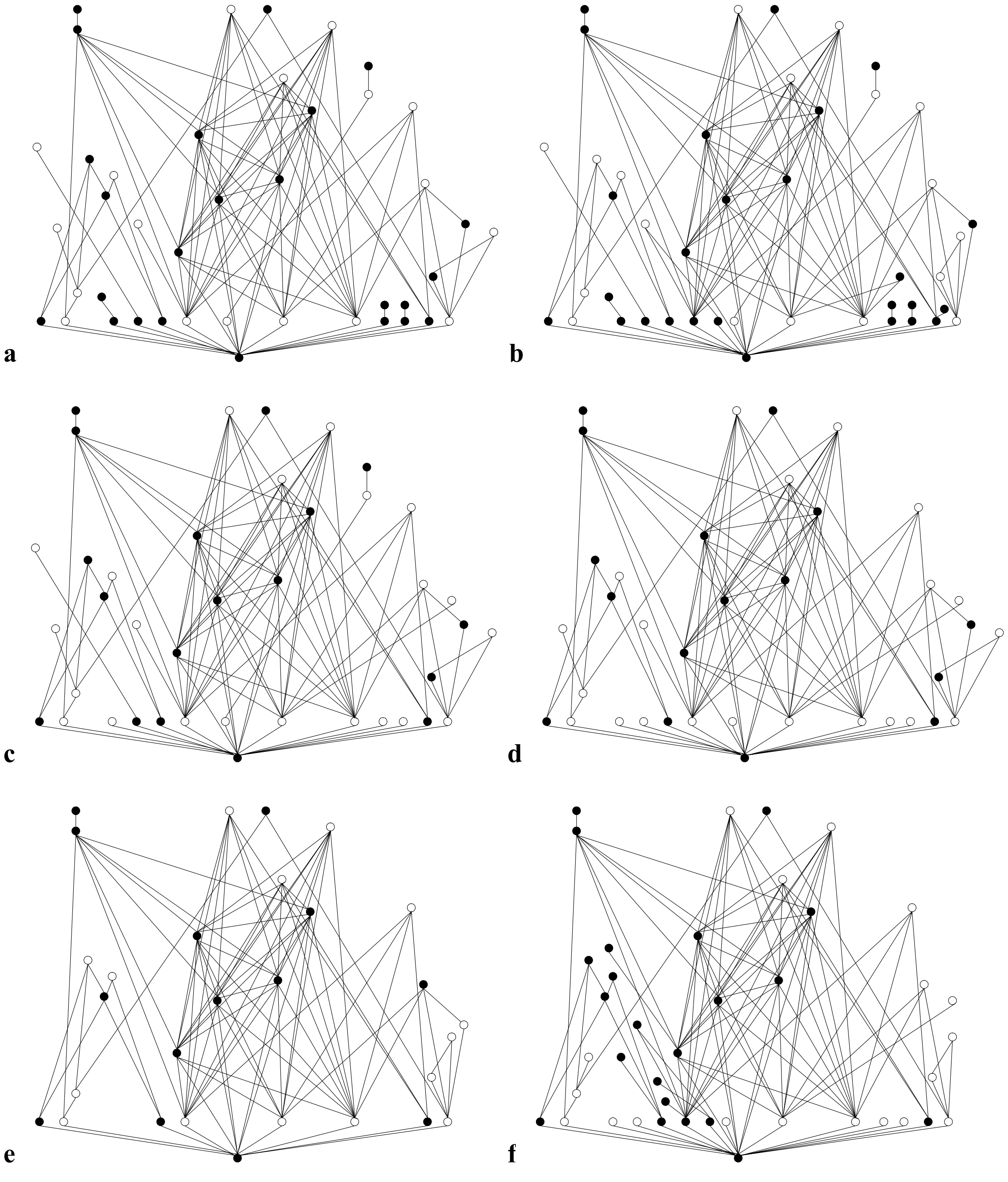

***Figure 5**. The aggregated networks of the original one shown at Fig. 4, according to various sequences of the defined aggregation steps: α-β-γ (**a**), α-γ-β (**b**), β-α-γ (**c**), β-γ-α (**d**), γ-α-β (**e**) and γ-β-α (**f**). Black nodes are not affected by aggregation, while white nodes are aggregated groups of two or more species of the original network. Note that the same three steps lead to different final states, even if only their sequence differs. See more discussion in text.*

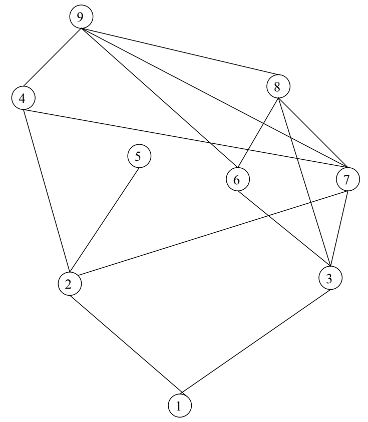

Figure 6. *The food web of the Schlei Fjord ecosystem (N-Germany). In this low resolution web, species are strongly aggregated into large functional groups: 1, Phytoplankton; 2, Zooplankton; 3, Zoobenthos; 4, Planktivores; 5, Temporary planktivores; 6, Whitefish; 7, Small fish; 8, Medium predators; 9, Apex predators (modified after* [11, 34, 62]*). Graph nodes mark functional groups, while links represent trophic interactions: higher groups always feed on lower ones (direction is not marked, for simplicity). The whole community is presented „by and large".*

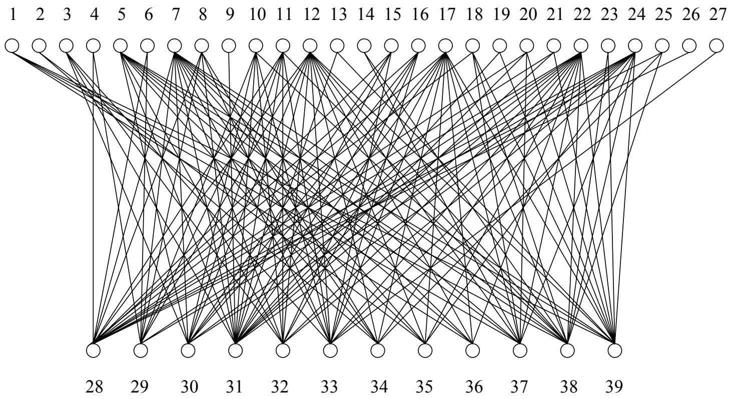

Figure 7. *The food web of a leaf-miner – parasitoid community living on four tree species of a meadow (S-England). In this high resolution web, species are shown with no aggregation: 1, Cirrospilus diallus; 2, C. lyncus; 3, Elachertus inunctus; 4, Pnigalio longulus; 5, P. pectinicornis; 6, P. soemius; 7, Sympiesis gordius; 8, S. grahami; 9, S. sericeicornis; 10, Achrysocharoides splendens; 11, A. niveipes; 12, A. latreillii; 13, A. zwoelferi; 14, Chrysocharis laomedon; 15, C. nephereus; 16, C. phryne; 17, Pediobius alcoeus; 18, P. saulius; 19, Minotetrastichus ecus; 20, Holocothorax nepticulae; 21, H. testaceipes; 22, Colastes braconius; 23, Apanteles sp.; 24, Apanteles circumscriptus; 25, Hormiinae sp.; 26, Scambus sp.; 27, Campopleginae sp.; 28, Phyllonorycter salicicolella; 29, P. dubitella; 30, P. harrisella; 31, P. heegeriella; 32, P. lautella; 33, P. quercifoliella; 34, P. ulmifoliella; 35, P. cavella; 36, P. froelichiella; 37, P. kleemanella; 38, P. rajella; 39, P. stettinensis (modified after* [41, 90]*). Nodes and links represent species and parasitoid interactions, respectively, where the higher 27 species are parasitoids and the lower 12 species are leaf-miner hosts. Only selected species of the whole meadow community are shown but in fine details.*

Comparable food webs

Both the classical [10, 12, 13] and the modern [22, 23, 50, 57, 103] databases of food webs inspired ecologists to compare trophic networks described at quite different places and representing quite different communities. Considering the extreme methodological heterogeneity of field studies and network construction, it is strongly questionable whether the results of any comparison can be useful. For example, Melián and Bascompte [54] compare the food webs of the Little Rock Lake [50] and that of the El Verde tropical rain forest in Puerto Rico [88]. The former database contains nearly exclusively species and genera (i.e. a web of high resolution, 182 graph points), while the latter one contains only 20 trophic components of much lower resolution, such like „birds” (three times), „bats” (twice) and „termites”. I suggest to be skeptical with analyses of this kind, because these webs are completely incomparable.

I believe that two or more food webs can be compared only if they were described for the same purpose, and by the same methodology [33]. If there was any bias or failure in the fieldwork or there was any inconsistency when the web was constructed, then these problems are expected to be minimal as the *differences* between comparable webs are analysed. But if one compares two webs described for different purposes and by different methods, then methodical problems will just grow and give unavoidable artefacts.

Presently, two rich databases of comparable food webs are known; one for systems ecologists and one for population / community ecologists:

Several marine and estuarine habitats are characterized by the energy language popularised by Odum [63]. These give the exact values of carbon flows (in mg C × year^{-1} × m^{-1}) between the identified trophic components of these ecosystems. Respiration losses and recycling pathways are also characterized. Some databases present the trophic flow networks of different elements given to the same ecosystem (carbon: [3]; nitrogen: [6]; phosphorous: [100]). These databases are very robust grounds for analysing quantitatively weighted interactions. These flow networks of energy are of low resolution, i.e. they are highly aggregated (*Fig. 6*).

Recently, Charles Godfray and colleagues are collecting rich databases of host–parasitoid communities from both the tropics and temperate habitats [45, 55, 56, 61, 90, 100]. These webs show less exact weights on links and present only a part of the studied community, however, it is generally known that these subcommunities are relatively well isolated from other species (*Fig. 7*). The great values of these webs are, among others, that they belong to the very few terrestrial food webs, and they constitute a database of similarly described, comparable food webs.

Finally, a colourful database of more or less comparable food webs is the result of a meta-analysis of phytotelmata food webs (describing the fauna of the water-filled pitchers of *Nepenthes* pitcher plants: [42]). These webs roughly satisfy the criteria of comparability, however, they give only a little information on these little communities inhabiting pitcher plants.

Comparing only comparable food webs sounds very logical and I suggest that this is the only right way for future food web research in order to have any chance for applicability.

Applications

However ecologists have recognised very early that purely structural descriptions of food webs are not realistic enough and, thus, should be complemented by dynamical analyses, they had shown only a very limited interest even in possible structural properties. Species were ordered to trophic levels, and they were classified as an omnivore (feeding on different trophic levels, [79]) or not. Food webs were characterised nearly exclusively by their connectance (actual per maximal link number, [12], and see also [108]). These indices were poor structural descriptors of trophic flow networks. It is no wonder that dynamical simulations made models much better. But, as recently we have much more structural indices applied in ecology (for some examples: characteristic path length, [110]; structural equivalence, [29, 46]; clustering coefficient, [109]; keystone index, [37]; network flow reliability, [36]; web diameter, [2], etc.), the original question could be asked again: what does pure structure predict? Of course, dynamical contributions [51, 52, 53, 76] are by no means to forget, but novel structural approaches are beginning to be married with dynamics, again [39, 40]. Attempts have been made also for considering the pattern of flow magnitudes in weighted flow networks [32, 35, 95, 98] and, thus, gaining some information on dynamics.

Food webs are built frequently only for illustrative purposes. These webs do not give quantitative information and have no predictive power. They frequently just help understanding and reviewing existing information. In the following, I list some qualitative and quantitative examples for how to apply food web research in approaching particular problems.

Food webs may be useful in assessing the impact of a poison (e.g. DDT) being transported bottom-up through trophic chains. Here, the simple index of trophic height gives information on bioaccumulation probability and the „time” needed to reach a certain group. Trophic height analysis can help also in assessing and quantifying the problem of fishing down marine food webs [71]. This is in no contradiction with the idea that discrete trophic levels do not exist [85]: it is now generally accepted that there is no reason to order each species or trophic group to an integer trophic level. However, it is clear that it has an ecological meaning that herbivores are closer to plants in a trophic topology, than higher carnivores. A measure of trophic height, if not restricted to integers, provides very important information on organisms.

As food web structure tends to change in a given area, landscape ecological trends may be indicated. Shortening food chains may reflect habitat fragmentation, since top-predators are among the mostly sensitive species to this effect (see Crooks and Soulé [16]). Their large area and particular feeding habits permit them to survive in small, fragmented patches. Habitat fragmentation is rapidly indicated by the loss of higher predators (and, later, by additional changes, such as mesopredator release and secondary loss of herbivores).

Marine (mostly pelagic) food webs help to understand why pelagic ecosystems are so sensitive to the fisheries of some species (e.g. anchovy, hake). Pelagic food webs are frequently of wasp-waist nature [17], meaning that species diversity is very high at the bottom and at the top of the food web, however, the middle region is dominated by a single or a few species (e.g. anchovy). These are the commercially most important species, thus, the effects of fisheries spread easily and rapidly within the trophic network.

Ecologically sensitive network indices of trophic flow networks may help in monitoring ecosystems at the system level. For example, the community-wide effects of thermal stress have been indicated by changes in network ascendency [98] and in the congruency of important flows and important trophic components [32].

High-resolution food webs may help in tracing indirect interaction pathways within ecosystems (of course, only kinds of indirect effects caused by trophic direct effects). The set of affected species can be more or less assessed if a particular species is disturbed [103]. The web tells where to expect responses and helps in predicting the net impact of a pulse perturbation experiment [102]. Methods begin to be developed for quantifying the range of reasonably strong indirect effects of a species, i.e. the strength of its „trophic field" in a topological space [34, 41]. Conservation biology may use these kinds of analyses [104], while as for theoretical interests it can help in understanding the link between species and ecosystems. In general, food web studies may help in clearing the results of experiments (e.g., by calling attention to indirect effects, [9]).

Concluding remarks

If, accordingly to many recently suggested views, we accept that the assembly and functioning of ecological communities is easier to understand from a network perspective [24, 48, 49, 70, 96, 97, 99], questions of central importance are how to create and how to use these networks. Recently introduced terms such as „network algebra" and „network anatomy" are good starting points but approaching reality still depends on, for example, how to incorporate nonlinearity and nonadditivity into these models. This is an area where structural and dynamical models have to meet.

Either local or global network indices can be applied and developed, the basic problem of how to construct food webs from field dietary data remains. If basic methodological problems pervasively exist, „networking" cannot help in better understand ecosystems. There are no universally good food webs, only webs described reasonably in the light of a particular problem. A possible solution is to gain information from the comparison of comparable webs. Thus, databases of food webs described by exactly the same methodology can only help if food web research wants to be applied in future. These groups of comparable webs can be either of low or of high resolution, but similarly described. Both the growing marine and estuarine food web database (e.g. [4,5]) and the collection of mostly terrestrial quantitative host-parasitoid food webs (e.g. [61]) are good examples in this direction. But comparing webs belonging to different groups is meaningless (see [54]). To date, we can skeptically conclude that the predictive power of food web research is probably large but still masked by methodological inconsistencies.

Acknowledgements. I am grateful, for discussions and comments on earlier work, to Professor Gábor Vida, Professor Eörs Szathmáry, István Molnár, András Takács-Sánta, István Scheuring, Professor Henrik Jensen, Professor H. Charles J. Godfray, Wei-Chung Liu, Frank van Veen, Rebecca Morris, and Owen T. Lewis. My research was funded by two grants of the Hungarian Scientific Research Fund (OTKA T 037726 and OTKA D 042189) and a Bolyai Award of the Hungarian Academy of Sciences.

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A REVIEW ON NATURAL STAND DYNAMICS IN BEECHWOODS OF EAST CENTRAL EUROPE

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(Received 4 Jan 2003; accepted 9 May 2003)

Abstract. This paper aims to present a review on the natural stand dynamics as recorded in 'virgin' and other untreated beech forest reserves in East Central Europe. This information can contribute to defining the reference point for nature-based management of beech forests. Topics covered include: distribution of beech, major beech forest types, growth characteristics, seed production and survival, germination and establishment, growth and mortality patterns during development, regeneration cycles, dead wood and herbaceous vegetation dynamics. Based on the analyses of scientific traditions, strengths and weaknesses of available information, recommendations for future research activities are also formulated.

Keywords. *Fagus sylvatica, forest dynamics, virgin forest*

Introduction

This paper is aimed at reviewing information on natural stand dynamics in beechwoods of East Central Europe. The motivation for such review comes from the strong belief that in our region the extremely high biological values of beech forests have become threatened as a result of fast changes in ownership structure and economic forces in this region. The only way to provide long-term solution to this problem is to resolve the challenge of sustainable forest management, which has to be based on natural processes. This means that the knowledge base on natural processes is of utmost relevance for improving beech management, for assisting the multifunctional utilization of these forests.

The area covered includes the Czech Republic, Slovakia, Southern Poland, Ukraine, Romania and Hungary, and covers the Carpathian and Pannonic biogeographic provinces and the southern tip of the Central European province [Meusel 1965/1984 in 28].

This review bears the sign of two important peculiarities:

(1) Limited accessibility of information;
(2) Strong scientific traditions in describing forest stand structures and distinguishing of forest units (e.g. Braun-Blanquet type associations, forest types, site types, ecosystem types).

This latter also means that far less emphasis has been put on studying processes than in countries with different scientific traditions [c.f. 66, 72, 113, 114, 115, 116].

As far as it was possible, information on natural stand structure and dynamics in beechwoods is based on observations and research in unmanaged, near-natural stands.

Most of them are protected as Forest Reserves or National Parks. Besides, several observations and research results from managed beech forests are also used.

The review is based on material we got know about (many publications are not referenced) and we got access to (many are in periodicals not easily available or inaccessible). The papers used were published in Czech, Slovakian, Polish, Russian, Romanian, German, English, French and Hungarian languages.

Early works on the virgin forests of the Carpathians were published from the second half of the 19th century. Some of them are just nice descriptions of the experience of seeing them [15, 46, 63], others contain some basic information on the structure and possible utilization of these forests [17, 18, 20, 21, 22, 23, 62]. Works of Zlatnik [119, 120, 121] and the major books by Prusa [79] and Korpel [43] contain the most substantial information on the structure and composition of virgin forest remnants in the Czech Republic and the Slovakian and Ukrainian Carpathians. In Hungary Czájlik [7, unpublished works] started to conduct systematic forest reserve studies. *Table 1* contains basic information of the unmanaged near-natural reference sites that were used for this review.

Beech in East Central Europe

Status of beechwoods in East Central Europe

Beech is an important tree species in the Carpathian Mts. and also in the Carpathian basin. This area is the easternmost part of its range in Central Europe (*Fig. 1*).

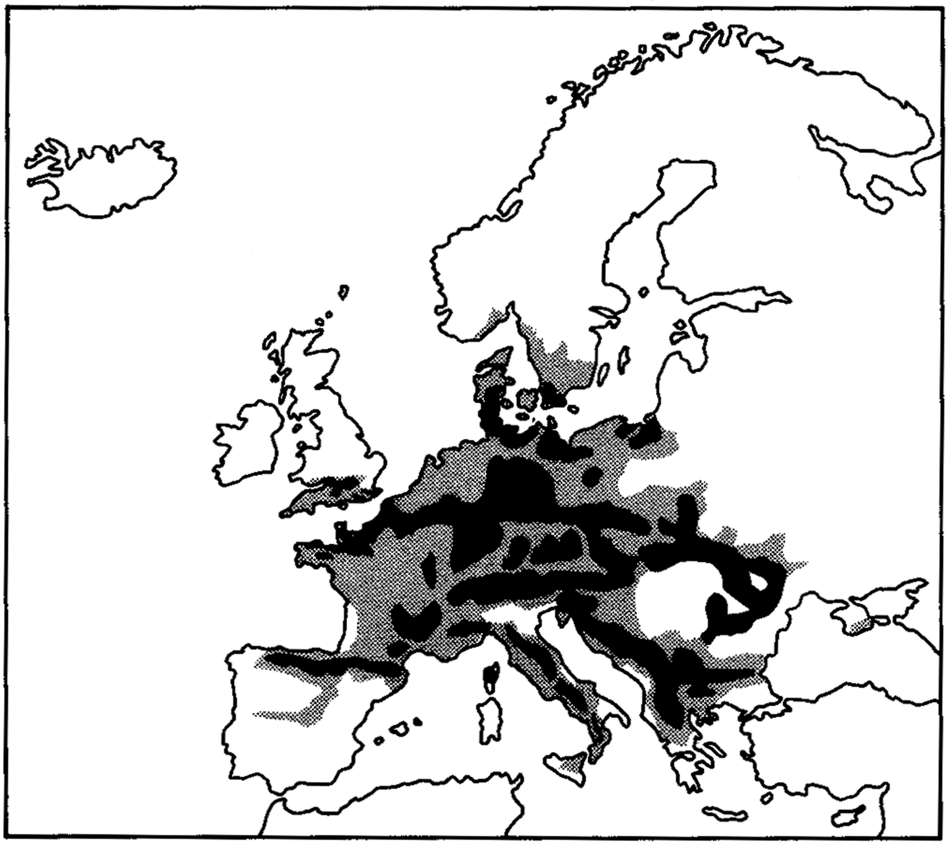


Figure 1. *Natural range of beech (Fagus sylvatica) and major areas of Beech woodland (dark). Source:* [74].

Table 1. *Sites with near-natural beech woodland in which permanent plots have been established to monitor long-term vegetation changes. For tree species: B - Beech; Sp - Spruce; F - Fir; Sy - Sycamore; E - Elm; A - Ash; H - Hornbeam; L - Lime; O - Sessile oak; W - Wild service tree; Bi – Birch. Information is collected from* [79, 80, 105, 106, 107, 108, 109, 110, 111, 112] *for Czech Republic,* [43, 45] *for Slovakia,* [31, 32, 33, 34] *for Poland,* [103] *for Ukraine,* [25] *for Romania, Czájlik (pers. comm.),* [67, 93] *for Hungary.*

Site name	**Major tree species**	**Site characteristics** **S**ize, **N**utrient status; **E**levation; **M**ean **A**nnual **T**emp; **P**recipitation (annual/in growing season); **S**now cover; **L**ength of **G**rowing **S**eason (days warmer 5/10°C)	**Year of recording**
Czech Republic			
Polom	Sp, B, F	**S**: 19.4 ha; **N**: Mesotrophic; **E**: 545-625 m a.s.l; **MAT**: 6°C; **P**: 786 mm/465 mm **LGS**: 210/140 days	1973, 1995
Razula	F, B, Sp	**S**: 23.2 ha; **N**: Mesotrophic; **E**: 600-812 m a.s.l; **MAT**: 6.2°C; 150 freezing days **P**: 1088 mm/613 mm; **LGS**: 205/125 days	1972, 1995
Salajka	B, F, Sp	**N**: Eumesotrophic; **E**: 715-820 m a.s.l; **MAT**: 5.4°C; **P**: 1144 mm **LGS**: 190/133 days	1974, 1994
Zakova hora	B, Sp	**S**: 17.1 ha; **N**: Mesotrophic; **E**: 725-800 m a.s.l; **MAT**: 5°C; **S**: 40 cm; **P**: 916 mm **LGS**: 110-120 days	1888, 1939, 1968, 1974, 1995
Stozec	B, Sp, F	**S**: 16.17 ha; **N**: Mesotrophic; **E**: 750-900 m a.s.l; **MAT**: 5°C;**P**: 793 mm **LGS**: 240/120 days	1974
Zofin	B, Sp, F	**S**: 97.72 ha; **N**: Eumesotrophic; **E**: 735-825 m a.s.l; **MAT**: 4.3°C; **S**: 0.5-1 m; **P**: 915 mm/615 mm; **LGS**: 180/120 days	1974-75
Boubin	B, Sp, F	**S**: 46.66 ha; **N**: Mesotrophic; **E**: 900-1100 m a.s.l; **MAT**: 4.2°C; **S**: 100-140 days; **P**: 867 mm; **LGS**: 115 days	(1847), 1954; 1959; 1964; 1969, 1972, 1984-89, 1996
Milesice	Sp, B, F	**S**: 9.63 ha; **N**: Mesotrophic; **E**: 1070-1125 m a.s.l; **MAT**: 3.7°C; **P**: 757-867 mm	1972, 1996
Mionsí	B, Sy, F	**S**: 5.92 ha; **E**: 620-950 m a.s.l; **MAT**: 6.6°C; **P**: 1228-1370 mm	
Diana	B, Sp, Sy	**S**: 21.9 ha; **E**: 500-532 m a.s.l; **MAT**: 7.5°C; **P**: 723 mm	1991-94
Slovakia			
Boky	O, B, H	**S**: 176.49 ha; **N**: Oligomesotrophic; **E**: 280-590 m a.s.l; **MAT**: 7.5°C; **P**: 720 mm	1974; 1979; 1984
Bujanov	O, B, H	**S**: 88.2 ha; **N**: Mesotrophic; **E**: 420-760 m a.s.l; **MAT**: 7°C; **P**: 675 mm	1966; 1976; 1981; 1992
Sitno	B, O, Sy	**S**: 92.68 ha; **N**: Mesotrophic; **E**: 750-1011 m a.s.l; **MAT**: 6°C; **P**: 850 mm	1977; 1987
Kasivárová and Lesná	O, B, H	**S**: 28.55 ha; **N**: Mesotrophic; **E**: 475-600 m a.s.l; **MAT**: 8°C; **P**: 750 mm	1966/1969; 1972; 1983; 1992
Vihorlat (Kyjov)	B, A, Sy	**S**: 53.4 ha; **N**: Mesotrophic; **E**: 700-820 m a.s.l; **MAT**: 6°C; **P**: 750-800 mm **LGS**: 190-200 days	1963; 1973; 1983
Rozok	B, Sy	**S**: 67.1 ha; **N**: Mesotrophic; **E**: 520-796 m a.s.l; **MAT**: 7°C; **P**: 780 mm; **LGS**: 190 days	1970/1979; 1979; 1989
Havesová	B, Sy	**S**: 171.32 ha; **N**: Mesotrophic; **E**: 500-650 m a.s.l; **MAT**: 7°C; **P**: 700-800 mm	1979; 1989
Stuzica	B, Sy, F	**S**: 659.4 ha; **N**: Mesotrophic; **E**: 650-1220 m a.s.l; **MAT**: 5-6°C; **P**:850-1000 mm	1971; 1981(transsect 4–6); 1991

Table 1. *(continued)*

Site name	**Major tree species**	**Site characteristics** **S**ize, **N**utrient status; **E**levation; **M**ean **A**nnual **T**emp; **P**recipitation (annual/in growing season); **S**now cover; **L**ength of **G**rowing **S**eason (days warmer 5/10°C)	**Year of recording**
Badin	F, B, Sy	**S**: 30.7 ha; **N**: Mesotrophic; **E**: 710-770 m a.s.l; **MAT**: 5.5-6°C; **P**: 850-900 mm	1957/1970; 1970; 1977; 1983/1987
Dobroc	F, Sp, B	**S**: 101.82 ha; **N**: Oligotrophic, acid; **E**: 720-1000 m a.s.l; **MAT**: 4.5-5°C; **P**: 800-960 mm	1958/1968; 1974; (1988)
Hroncokoy grun	B, A, Sy, F, Sp	**S**: 54 ha; **N**: Oligomesotrophic; **E**: 600-950 m a.s.l; **MAT**: 5°C; **P**: 800-850 mm	1962; 1972; 1982; 1992
Pol’ana	Sp, F, B, Sy	**S**: 685.8 ha; **N**: Mesotrophic; **E**: 560-1458 m a.s.l; **MAT**: 4-4.5°C; **P**: 900-1000 mm	1974; 1984
Komárnik	B, F, E	**S**: 733 ha; **N**: Eumesotrophic; **E**: 360-580 m a.s.l; **MAT**: 6.4-8.8°C; **P**: 600-1200 mm	1957-1968
Romania			
Runcu, Zarand	O, B	**S**: 262.6 ha; **N**: Eumesotrophic; **E**: 340-660 m a.s.l; **MAT**: 7.6-9.4°C; **P**: 750-925 mm	
d’Izvoarele Nerei, Banat	B, Sy, E, A, H	**S**: 4816 ha; **N**: Acid mull-moder; **E**: 700-1400 m a.s.l; **MAT**: 3.5-7.3°C; **P**: 1030-1340 mm	
d’Iauna-Craiova, Cerna	B, (F)	**S**: 1545.1 ha; **N**: Acid moder; **E**: 700-1733 m a.s.l; **MAT**: 4.7-7.3°C; **P**: 1000-1250 mm/700-787 mm	
Retezat I.	B (Sp)	**S**: 6630 ha (whole reserve); **N**: Acid, moder; **E**: 940-950 m a.s.l; **MAT**: 4.7-6.8°C; **P**: 950-1280 mm	
Retezat II.	Sp, F, Bi, B	**N**: Acid moder, Oligotrophic; **E**: 1126-1195 m a.s.l; **MAT**: 4.7-6.8°C; **P**: 950-1280 mm	
Hungary			
Kékes	B, Sy-A-L	**S**: 54.8 ha; **N**: Mesotrophic; **E**: 750-950 m a.s.l; **MAT**: 5.7°C; **P**: 840 mm/480 mm; **S**: 113 days	1992, 2002
Őserdő	B, Sy, A	**S**: 59.3 ha; **N**: Eumesotrophic; **E**: 800-900 m a.s.l; **MAT**: 6-7°C; **P**: 800-900 mm	
Alsóhegy	B-H, O, W, L	**S**: 112.8 ha; **N**: Eutrophic; **E**: 300-400 m a.s.l; **MAT**: 8°C; **P**: 700 mm	1994, 2002
Poland			
Babia Gora	Sp, B, F		1976, 1986
Gorce	Sp, F, B		1981, 1991
Bieszczady	B, Sy		
Ukraine			
Ugolsky	B	**N**: Eutrophic; **E**: 710 m a.s.l; **MAT**: 7.1°C; **P**: 1390 mm; **LGS**: 150-160 days	1975
Sirokoluzansky		**E**: 740 m a.s.l; **MAT**: 7.1°C; **P**: 1390 mm; **LGS**: 150-160 days	1975

Beech is one of the most important forest species in the countries covered by this review. *Table 2* shows potential and current share of beech in the forest vegetation of the respective countries.

Table 2. *The importance of beech forests in Central European countries. Source:* [26] *for CZ;* [87] *for SL;* [117] *for PL;* [94] *for UR;* [25] *for RO;* [6] *and* [29] *for H.*

Country	**Forest area (% territory)**	**Potential beech area** (% forest area)	**Actual beech area** (% forest area)
Czech Republic	2 632 000 ha (33.4%)	37.9	5.8
Slovakia	1 920 000 ha (40%)	46.3	30.4
Poland	8 700 000 ha (28.1%)		4
Ukraine			556 800 ha in the Carpathians
Romania	6 370 000 ha (26.7%)	18	30.7
Hungary	1 678 600 ha (18%)	19.5	6.3

Beech forests are associated with the submontane and montane zones of the Carpathians, with beech increasing in frequency above the thermophilous foothill oak forests. Although beech once occupied almost all the montane zone from 600 to 1200 m, apart from in the warmer parts of the Carpathians they have been gradually replaced at higher elevations by coniferous forests of *Abies alba* and *Picea abies*. In general, the limit of beech distribution increases in the inner mountains, for example rising from 550–1100 m at Babia Gora to 800–1200 m at Vysoke Tatry. The analysis of historic data showed that it occurred at many locations even in the Great Hungarian Plain [37]. Details on the altitudinal limits of beech distribution are given in *Table 3*.

Table 3. *Altitudinal limits of beech in the Carpathian and Pannonic floristic provinces. Source:* [19].

Region (as shown in [19])	**Lower limit of trees**	**Lower limit of beech forest**	**Upper limit of beech forest**	**Upper limit of individual trees**
NW Carpathians	339	378	1133	1181 (1220)
N-Central Carpathians	329	330	1246	1258 (1352)
NE Carpathians	254	354	1245	1284 (1335)
E Carpathians			1307	1335 (1396)
S Carpathians			1319	1381 (1441)
Krassó-Szörény Mts.	182	197	1418	1403 (1444)
Transdanubian and Northern Mid-Mts	263	281		
Bihar Mts.	241	360	1301	1351 (1497)
Mecsek Mts.	210	210		
Outer Somogy	200	200		
Sopron-Kőszeg-Szentgotthárd	312	394		
Transsylvanian lowlands (Mezőség)	390	411		
Great Hungarian Plains	82			

Beech forests develop on all types of rocks over a wide area characterized by different climates, so there is no uniformity in the characteristics of beech forest soils [11]. Typical beech forests have slightly acid to alkaline soils, while degraded beech forests have strongly acid soils. The higher the acidity is, the less typical the undergrowth becomes, until finally, forest floor vegetation takes a spruce forest character. As Zlatnik [118] observed, soil acidity rises with increasing humidity of the climate, i.e. with altitude and in deep shaded valley bottoms. In this region podzolization frequently corresponds to the degradation of beech forest soils, i.e. the effects of forest utilization [10].

Climatic and other factors limiting beech in East Central Europe

The climate of Central Europe is largely dominated by the high-pressure system of East Europe. For this reason the climate is generally less humid, colder in winter, and warmer in summer than in the Atlantic region. The degree of continentality increases with the distance from the Atlantic. In the southwestern part of Hungary Submediterranean effect is also considerable. Mountain ranges have considerable effect on the local climates. In the mountains snow cover can last up to five months. *Table 4* shows data on mean monthly temperature and precipitation of selected sites in East Central Europe.

Several indices of „climate goodness" were introduced. Not reviewing those it can be claimed safely, that the length of growing season – though definitions are not straightforward – varies greatly within the area covered. According to data of Mayer [50] it is 170 days in the south Carpathians at 600 m a.s.l., whereas only 115 at 1450 m a.s.l. (see also *Table 1*).

In this part of the world the distribution of beech is limited either by summer drought or winter frost. It is reported in several papers that late spring frost can harm young beech trees. Extreme cold winters like in 1928–1929, when temperature fell to -42 °C, beech forests can be seriously damaged. In 1928–1929 more than 10 000 ha of beech forests were damaged in then Polish, nowadays Ukrainian Carpathians [30, 38, 44, 47]. The upper beech range is often affected by damage caused by wind, snow and ice [1, 24, 39, 40, 86].

For characterizing the lower limit of beech growth, Ellenberg [14] developed an index, the so-called Ellenberg quotient (*Q*) for Central Europe:

$$Q = \frac{Mean\ July\ \ temperature\ \ (°C)}{Annual\ \ precipitation\ \ (mm)} \times 1000$$

Values below 20 indicate pure beech climate, between 20 and 30 its competitive vigour decreases, and above 30 oak becomes more competitive than beech.

Main beech forest types

It is not a simple task to give a short account of beech forest types of the region, since Braun-Blanquet-type phytosociology has developed along partly different paths in the respective countries. Even worse, forest scientists have developed their forest type/forest site type systems rather independently from vegetation scientists, though the level of separation is different in the respective countries (*Table 5*).

To give a short account of the major beech forest types, it is reasonable to consider different substrates (eutrophic, mesotrophic, oligotrophic), altitudinal zones (colline, submontane, montane) and biogeographic provinces (Central European, Carpathian, Pannonian, *Fig. 2*).

In its optimum, beech forms almost pure stands with only scattered associate species. At lower elevations oaks *(Quercus petraea, Q. robur)* and hornbeam *(Carpinus betulus)* are important associates, however, this forest type is not well represented among natural

Table 4. *Mean monthly temperature and precipitation data for selected sites. Source:* [79, 105, 106, 107, 108, 109, 110, 111, 112] *World Climate Database.*

Mean temperature (°C)	**(m a.s.l)**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Year**	**IV-IX**
Polom	590 m	-3.0	-2.0	2.0	6.0	11.0	14.0	16.0	15.0	12.0	7.0	2.0	-2.0	6.0	12.3
Razula	730 m	-4.3	-3.2	1.0	5.2	10.6	13.4	15.7	14.8	11.3	6.4	1.1	-2.2	6.2	11.5
Salajka	722 m	-4.7	-3.5	-0.1	4.8	10.5	13.3	15.3	14.2	11.0	6.2	0.9	-2.7	5.4	14.4
Zakova hora	760 m	-4.7	-3.9	-0.1	4.4	10.2	13.0	14.8	13.9	10.5	5.5	0.1	-3.1	5.0	11.1
Stozec	766 m	-4.0	-3.0	0.0	4.0	10.0	12.0	14.0	13.0	10.0	5.0	0.0	-3.0	5.0	10.5
Zofin	780 m	-4.3	-4.5	-0.4	3.4	8.9	11.8	13.6	12.6	9.3	4.5	-0.3	-3.1	4.3	11.8
Boubin	1003 m	-5.0	-4.0	-1.0	2.0	8.0	12.0	13.0	12.0	9.0	4.0	0.0	-3.0	4.0	9.3
Milesice	1058 m	-5.3	-4.5	-1.3	2.7	8.2	11.1	12.9	12.2	8.7	4.4	-0.5	-3.7	3.7	9.3
Mionsi	530 m	-3.2	-2.3	1.2	6.0	11.5	14.5	16.2	15.3	11.9	7.2	2.4	-1.1	6.6	12.6
Diana	451 m	-2.4	-1.3	2.6	7.1	12.6	15.7	17.6	16.7	12.9	7.6	2.3	-1.1	7.5	13.8
Stuzica		-2.7	-0.6	4.4	10.5	15.6	18.6	20.1	19.6	15.5	9.7	4.8	0.1	9.7	16.6
Kékes	1010 m	-3.9	-3.7	0.6	5.7	11.0	13.1	15.7	15.5	12.2	7.2	0.5	-2.0	6.1	12.2
Alsóhegy	233 m	-2.9	-0.5	4.2	10.2	15.2	18.4	20.1	19.3	15.2	9.4	3.7	-0.5	9.3	16.4

Average rainfall (mm)		**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Year**	**IV-IX**
Polom	590 m	54.0	45.0	46.0	56.0	75.0	82.0	99.0	90.0	63.0	63.0	56.0	57.0	786.0	465.0
Razula	730 m	70.0	73.0	76.0	70.0	88.0	125.0	128.0	120.0	82.0	88.0	88.0	80.0	1088.0	559.0
Salajka	722 m	83.0	76.0	82.0	82.0	92.0	121.0	134.0	127.0	89.0	90.0	89.0	79.0	1144.0	645.0
Zakova hora	760 m	71.0	61.0	58.0	65.0	79.0	88.0	107.0	96.0	76.0	75.0	67.0	72.0	916.0	511.0
Stozec	766 m	55.0	50.0	43.0	57.0	75.0	89.0	100.0	87.0	65.0	60.0	53.0	59.0	793.0	473.0
Zofin	780 m	47.0	48.0	45.0	71.0	94.0	113.0	142.0	116.0	79.0	61.0	47.0	52.0	915.0	615.0
Boubin	1003 m	58.0	61.0	49.0	63.0	88.0	98.0	112.0	96.0	69.0	61.0	51.0	61.0	867.0	526.0
Milesice	790 m	49.0	47.0	41.0	54.0	74.0	84.0	102.0	83.0	61.0	57.0	50.0	55.0	757.0	458.0
Mionsi	730 m	94.0	91.0	89.0	90.0	113.0	139.0	159.0	163.0	111.0	101.0	91.0	89.0	1330.0	775.0
Mionsi	600 m	81.0	73.0	86.0	80.0	117.0	120.0	158.0	156.0	112.0	85.0	82.0	78.0	1228.0	743.0
Mionsi	530 m	78.0	74.0	84.0	100.0	133.0	160.0	179.0	174.0	118.0	106.0	87.0	77.0	1370.0	865.0
Diana	575 m	54.0	45.0	43.0	57.0	60.0	73.0	89.0	76.0	58.0	57.0	53.0	58.0	723.0	413.0
Stuzica		59.0	48.0	47.7	50.8	65.6	92.4	81.3	79.2	61.9	60.4	60.4	66.2	773.9	431.2
Kékes	1010 m	46.0	47.7	48.8	61.4	144.5	101.4	42.2	73.2	55.2	44.4	61.5	44.4	759.4	477.9
Alsóhegy	233 m	29.2	29.7	30.3	40.9	65.0	87.5	66.3	67.6	40.7	35.0	44.8	38.5	576.3	368.0

forest remnants. In the main beech zone sycamore *(Acer pseudoplatanus)*, witch elm *(Ulmus glabra),* mountain ash (*Fraxinus excelsior*), rowan *(Sorbus aucuparia)*, small-leafed lime *(Tilia cordata)* and Norway maple *(Acer platanoides)* are the main associates. At higher elevations silver fir (*Abies alba*) and Norway spruce (*Picea abies*) become important tree species.

Table 5. *Major references for national forest type classifications based on phytosociological and forest/site/ecosystem type approaches of forest vegetation.*

Country	Major phytosociological accounts	Major forest/ site/ ecosystem type systems
Czech Republic	Domin [11] Neuhäusl [64] Neuhäuslova et al. [65]	Zlatnik [122] Pista and Prusa [73] Randuska [81]
Slovakia	Domin [11] Michalko et al. [58]	Zlatnik [122] Randuska [81]
Poland	Szafer [95] Szafer [96]	
Ukraine	Domin [11]	
Romania	Sanda et al. [84]	Pauca-Comanescu [70] Donita et al. [12]
Hungary	Soó [92] Bartha et al. [3] Borhidi [5]	Májer [52]

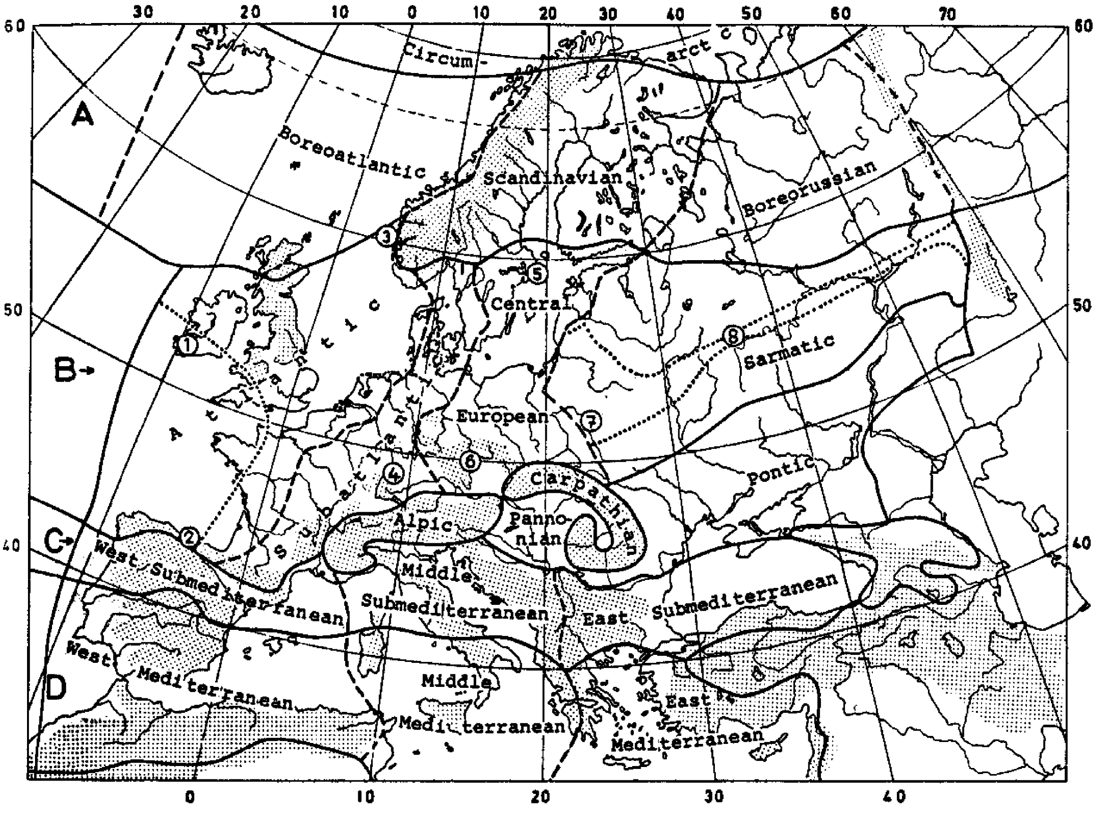


Figure 2. *Biogeographic Provinces of Europe. Source: after Meusel in* [28].

Carpathian Province

The largest tracks of beech forests belong to the Carpathian Province. Vegetation scientists distinguished many associations for this area. A simplified picture is given in Michalko et al. [58] where beech forests are grouped into 7 units for mapping the potential natural vegetation of Slovakia.

For the same country Zlatnik distinguished 46 major forest type groups, with many more subgroups, intergroups and geographic variants. Of these, 22 contain beech as a major component [81, 122].

In Romania Pauca-Comanescu [70] and Donita et al. [12] published detailed accounts of major beech forest ecosystem types. The 15 beech ecosystem types in Donita et al. [12] are distinguished on the bases of phytosociological associations, forest types, soil types and climatic characteristics. These main groups also cover beech forests of the Polish and Ukrainian Carpathians. East of the Carpathians beech reaches the limit of distribution to the east. Szafer [95] and Stojko [94] described forest types of this region.

Central European Province

Only a small part of the area covered by this review belongs to this province, namely the middle and western part of the Czech Republic. In addition to the Carpathian beech forest types this area is characterised by the acidophilous Hercynian beech forests belonging to the *Luzulo-Fagion* alliance, and the beech-fir woods characteristic in the montane belt of the Sudeten and the Sumava Mts (*Dentario enneaphylli-Fagetum*).

Pannonic Province

In the Pannonic Province beech forests grow in the low mountains of Transdanubia and northeastern Hungary, and at low altitudes in the westernmost part of Hungary. Beech wood in the northeastern part resemble to the submontane-beech woods of Slovakia, whereas those in Transdanubia (west of the river Danube) contain more atlanto-mediterranean species. Special beech forest associations (e.g. *Vicio-oroboidi-Fagetum* Borhidi, *Helleboro odor-Fagetum*) were described in the southern part of Hungary, where illyric (West-Mediterranean) floristic effects (e.g. *Knautia drymea, Lathyrus venetus, Asperula taurina, Tamus communis*) are strong.

Characteristics of beech and its associates

In this chapter main characteristics of beech are discussed, in some cases important associates are also included.

Growth performance

Depending on site conditions, beech trees can grow to a considerable size (40–45 m height, over 1 m dbh) and age (over 350 years). Standing volume can be as high as 1195 m^3/ha, and basal area can reach 67 m^2/ha (*Table 6*). Annual average productivity varies greatly according to site types, and variation among years is also considerable. Kosut [45] carried out a detailed study in the Komárnik region in East Slovakia. He showed, that the mixed stand produced 27.56 m^3 (beech – 20.30, silver fir – 6.12, sycamore – 0.94, ash – 0.18, hornbeam – 0.02) between 1958 and 1968 on the 0.5-hectare sample plot, so the average annual productivity was 5.6 m^3/ha. Tree ring analyses showed great variations among years, especially for silver fir.

Table 6. *Density, basal area and volume of major tree species in selected Romanian natural forests. Species: S - Spruce; F - Fir; B - Beech. Source:* [9, 76].

Site name	**Tree number (N/ha)**				**Basal area (m^2/ha)**				**Volume (m^3/ha)**			
Species	**S**	**F**	**B**	**Sum**	**S**	**F**	**B**	**Sum**	**S**	**F**	**B**	**Sum**
E Carpathians												
Cosna	189	58	111	358	27	15	8	50	364	199	81	644
Cosna	194	64	93	351	24	13	7	44	324	176	71	571
Stulpicani	80	109	93	282	10	20	8	38	132	297	111	540
Ostra	105	102	98	305	13	18	7	38	151	242	75	468
Ostra	399	159	15	573	31	13	1	45	262	155	8	425
Tomnatec	350	150	170	670	42	22	3	67	649	350	28	1027
Rebra	146	—	244	390	34	—	19	53	564	—	314	878
SE Carpathians												
Viforata	68	242	118	428	9	37	14	60	125	533	222	880
S Carpathians												
Cheia	73	190	98	361	3	16	6	25	31	197	69	297
Cheia	—	457	365	822	—	31	15	46	—	363	164	527
Cheia	—	151	211	362	—	11	18	29	—	116	246	362
Cheia	—	56	265	321	—	2	27	29	—	21	360	381
Cheia	—	300	153	453	—	21	12	33	—	267	162	429
Cheia	—	134	140	274	—	14	12	26	—	180	158	338
Glodeasa	—	178	130	308	—	18	22	40	—	257	347	604
Piatra Arsa	—	190	82	272	—	37	16	53	—	538	263	801
Piatra Arsa	—	173	89	262	—	37	13	50	—	503	198	701
Piatra Arsa	5	131	110	246	—	32	11	43	3	485	166	654
Piatra Arsa	4	168	196	368	—	10	23	33	5	129	388	522
Piatra Arsa	3	147	130	280	—	13	20	33	3	192	353	548
Piatra Arsa	—	240	84	324	—	23	6	29	—	278	80	358
Piatra Arsa	4	183	164	351	1	17	11	29	6	206	131	343
Piatra Arsa	—	229	101	330	—	21	8	29	—	244	95	339
Zgarbura	—	258	128	386	—	17	3	20	—	—	—	—
Zgarbura	—	174	90	264	—	16	1	17	—	—	—	—
Curtea de Arges	—	203	237	440	—	22	21	43	—	302	301	603
Romani	—	38	282	320	—	3	35	38	—	35	498	533
Romani	618	—	9	627	38	—	1	39	385	—	11	396
Romani	—	108	163	271	—	17	23	40	—	232	346	578
Parang	—	—	—	660	—	—	—	—	—	—	—	1013
Ponor	220	—	262	482	13	—	31	44	143	—	460	603
Ponor	287	—	307	594	19	—	33	52	153	—	484	637
Nera	—	—	373	373	—	—	—	—	—	—	1195	1195

Popescu-Zeletin and Petrescu [75] found that diameter increment was ca. 1 cm in 6 years for the majority of trees, higher rates (4–6 cm) being confined to medium-sized trees.

Table 7 shows data on tree size and growth characteristics for selected reference sites.

In managed forests the correlation between age and size, and also between dbh and height is rather consistent, so growth tables for different site types were developed. However, in natural forests these relationships are strongly influenced by the history of individual trees. Abrupt height and radial growth can follow decades of suppression in shade tolerant species, like beech and silver fir, when they have been released from the shade of overstorey trees [43].

Productivity is highest on well-aerated and well-drained soils with slightly acidic to neutral chemistry. Sandy substrates and temporary water saturation can decrease growth potential and competitive vigour of beech (c.f. data in *Table 1*). Beech usually forms the upper canopy layer, though in certain forest types (e.g. mixed beech-fir on acid substrate, mixed beech-spruce on mesotrophic sites) silver fir or Norway spruce give the dominant layer and beech gives the secondary canopy layer [70].

Competition and disturbances can reduce growth or they can lead to mortality of trees. Competition is strongest in younger stages especially when dense regeneration develops over larger patches. However, this situation is rather rare in natural beech forests. In a Romanian virgin stand Popescu-Zeletin and Petrescu [75] showed that competition was strongest at the „pole stage" (dbh 3–10 cm), since 56–92% of conifers and 82–98% of beech trees died in the 6-year period of investigation. Beech is extremely flexible even at older ages, so canopy growth can follow and utilize resources opened up by the death of other trees.

Data on the strength, frequency and biological effects of disturbances are rather scarce, and in many cases incomplete to judge their importance in forest dynamics [16, 72]. This is especially true for natural forests of East Central Europe. Under prevailing climatic conditions wind, ice and snow are the major abiotic disturbance factors in the beech forests of the region.

Wind was reported for several „virgin forest" as important disturbance agent. Badin Virgin Forest in Slovakia suffered from serious wind damage in 1947, but recording of stand structure started only 10 years later [43, 86]. A heavy gale impacted the surroundings of the Boubin Virgin Forest in Czech Republic on 26 October 1870, which caused extensive - though not quantified - wind breakages [79, 112]. Popescu-Zeletin reported in a Romanian virgin forest site, that many trees (13–32% of conifers and 18–67% of beech) had been destroyed by windthrow between 1949 and 1955.

Table 7. *Exemplary data of dbh, tree height, standing volume and basal area for selected reference sites. Data are given by species indicated as B - beech, F - silver fir, S - Norway spruce, Sy - sycamore, Source:* [43, 79, 80, 110, 111, 112].

Site name	Age	Dbh	Height
Zofin F	425	176	45.3
Badin F	350-400	148	49.5
Badin B	210-230	108	45
Boubin S	440	162	57.6
Boubin F	450	145	51.8
Boubin B		91	45.5
Milesice S		105	45
Milesice F		87	40
Milesice B		68	37
Kyjov B	250	112	
Razula S		94	53.5
Razula F		148	41
Razula B		100	44.5
Dobroc S		134	54
Dobroc F	450	193	58
Dobroc B		118	

In Slovakia Konopka [40] studied the volume of salvage cutting caused by wind, snow and ice between 1961 and 1995 in Slovakian forests. Salvage cutting caused by wind, snow and ice during 1985–95 was 800 000, 180 000, and 35 000 m^3, respectively. Norway spruce and silver fir were the species most frequently damaged by wind, Norway spruce and Scots pine by snow, and Scots pine and European beech by ice. However, these data mostly relate managed, often planted (e.g. spruce on beech sites) forests. The same limitation is valid for the study of the causes of wind and ice damage in the Börzsöny Mts, Hungary [1]. The authors studied a 70 km^2 area, where serious ice and wind damages occurred in 1996 and 1999, respectively. Unfortunately pre-disturbance measurements are missing, so only the area affected could be studied in detail. As *Table 8* shows, ice created more large gaps than wind.

Adult beech trees are usually not seriously affected by biotic disturbances. Fungi are the most important biotic agents causing damage to beech, since the anatomical and chemical makeup of tree trunks make it rather susceptible [27]. Mechanical wounds caused by abiotic factors or forestry operations can open places for successful infection. Species that might attack beech trees are shown in *Table 9*. Szontágh investigated 188 beech trees in a 1 ha plot in the Őserdő Reserve in Hungary. He found that in the mixed-aged (0-150 years) stand fungi attacked 49 trees (26%). Of the 553 m^3 volume 172 m^3 (31%) were affected [Szontágh in 27]. Leaf-miners (e.g. *Rhynchaenus fagi,*) can attack up to 20% of beech trees [98, 99].

Table 8. *Comparison of sizes of canopy gaps created by severe ice or wind-damage in beech forests near to Királyrét, Börzsöny Mountains, Hungary.*

	Gaps created by severe ice-damage in 1996 (n =)	**Gaps created by severe wind-damage in 1999 (n = 33)**
Size		
Maximum size (m^2)	80756	66579
Average size (m^2)	19162	15803
Minimum size (m^2)	627	663
Area	**N**	**n**
<5000 m^2	20	10
5000–<10000 m^2	6	8
10000–<15000 m^2	0	5
15000–<20000 m^2	2	2
20000–<50000 m^2	12	5
50000–<85000 m^2	5	3

Regeneration characteristics

Beech generally regenerates by seeds, which are produced periodically. Frequency of seed production and success of establishment is greatly affected by site characteristics and weather conditions. Density and spatial distribution of established seedlings is strongly affected by disturbance patterns in the overstorey. In natural beech forests regeneration is rather patchy, since canopy gaps are usually small.

Table 9. *Fungi affecting the growth of adult beech trees. Source:* [27, 88].

Species name	Organ affected
Microsphaera alphitoides Griff. et Maubl.	leaf
Phyllactinia suffulta (Rebent.) Sacc.	leaf
Nummularia bulliardi Tul.	branch
Nectria galligena Bres.	trunk
Nectria ditissima Tul.	trunk
Fomitopsis pinicola (Sw. ex Fr.) Gill.	trunk
Fomes fomentarius (L. ex Fr.) Gill.	trunk
Inonotus radiatus (Sw. ex Fr.) Karst.	trunk
Laetiporus sulphureus (Bull.) Bond. ex Sinq.	trunk
Ganoderma applanatum (Pers.) Pat.	trunk
Inonotus obliquus (Pers.) Pil.	trunk
Daedalea quercina (L.) Fr.	trunk
Grifola gigantea (Pers.) Pilát	trunk
Oxyporus populinus (Fr.) Donk.	trunk
Pholiota squarrosa Huds. ex Fr.	trunk
Polyporellus squamosus Huds. ex Fr.	trunk
Pleurotus ostreatus (Jacq. ex Fr.) Kummer	trunk
Xanthochorus obliquus (Pers.) B. et G.	trunk
Xanthochorus cuticularis (Bull.) Pat.	trunk

Seed production and dispersal

Beech is characterized by periodic seed production starting when beech trees are 40–50 years old, but in closed dense stands they start producing fertile seeds only at the age of 60–80 years [4]. Periodicity of seed production is rather irregular. However, observations show that individual beech trees can produce seeds in consecutive years [56]. In general mast years are followed by lower seed production [8], and on optimal sites seed production is more frequent and more reliable (regular) than on suboptimal sites where certain environmental factors (precipitation, soil moisture content, etc.) can be limiting [56]. In the eastern part of its distribution beech flowers more often than in e.g. West Europe, but this phenomenon does not lead to more frequent seed production. For this reason detailed studies were carried out to investigate the factors affecting successful fructification. It was shown that both meteorological and biotic factors (pests) affect successful seed production. Best fructification occurred when temperature was between 15 and 25 °C, and relative humidity did not fall below 26–33% [56]. Phaenology of individual trees (early or late flowering) and social position within the stand (height class of Kraft) also affected seed production. In Hungary mast years occur every 6–8 years on the average, but even within such a small country, seed production is more frequent in the western part where climatic condition are more favourable [52, 83]. Májer [53] published the results of a historical study on beech seed crops in the Bakony Mts., Hungary, over the last 242 years. A heavy crop can be expected (on average) once every 14 years, an average crop every 7 years, and a poor crop every 3–4 years. However, heavy crops can occur at short intervals (1948, 1951). In the Ukraine several authors studied the amount and periodicity of beech seed production. They also showed that seed years are more frequent in the Carpathians (optimal sites) than at lower elevations east of the Carpathians [35]. In Opolia Tretjak [102] reported beech seed years of different intensity using a 5-scale system (1: 1–2 million seed/ha, 2: 2–3 million, 3: 3–4 million, 4: 4–5 million, 5: more than 5 million): 1916–5; 1922–4; 1936–3; 1931–5; 1934–1; 1936–4; 1941–2; 1943–4; 1945–4; 1947–5; 1951–5. Kaplunovszkij

[36] reported four „better than average" seed years between 1960 and 1969, which means that 54–77% of mature trees produced seeds. In 1962 all trees with dbh >40 cm produced seeds. In Romania Papava [68] found that fructification is extremely variable, is strongly correlated with altitude, and mast years occur once in every 3–4 to 6–8 years. Badea et al. [2] published a comprehensive account of studies carried out in 1957-64 on seed production, effects of climatic factors and of methods of regeneration felling on the establishment and development of regeneration.

The number of seeds produced shows high spatial variability within a single stand. Márkus [54] studied the number of beech seeds in a 100 year old beech stand in the Bakony Mts, Hungary. He set up a grid with 25 m intervals, and sampled beech seeds at each grid points. Using the data collected in 91 sample plots he showed that at edges seed numbers per unit area were higher than within the stand. This effect could be traced as far as 1.5 tree height from the edge. Not only absolute numbers, but also the proportion of vital seeds decreased from the edge to the inner stand. He also observed that beech seeds were almost always found in groups of a few. Mendlik [57] compared seed numbers at the edges and in the centre of a stand where he found much lower numbers (5-10 nuts/m²), than at the edges (40-50 nuts/m²). In 1964 Márkus and Mátyás [55] carried out a country-wide survey of seed production in Hungary. They collected data from 611 forest ranges from all over the country representing all forest regions where beech occurs. They found large variation within each forest region, but the average differences in the amount of beech seeds produced in different forest regions could be explained by the climatic differences of previous year. In the western part of the country, where June and July of 1963 were cool and rainy, much less seeds were produced than in the northeastern part of the country.

Korpel [42] and Saniga [85] studied the dynamics of seed shedding and got similar results. Korpel found that on the average, of the 399 seeds shed on 1 m^2, 18.7% germinated. Saniga [85] found that the amount of seeds shed until September 25, October 20 and October 31 were 465.3, 321.3 and 274.5 kg/ha, respectively. Based on thousand-seed-weight data he estimated that on the average 399 seeds per m^2 were shed. Average proportion of fertile seeds was 53%, 71%, 65% for the three sampling period, so the average number of fertile seed per m^2 was 244.

Seed size also shows natural variation. Parpan et al. [69] collected seeds in 1982 from 45 locations within the natural range of beech in the Ukraine. The heaviest and most elongated seeds were from Podolia and the lightest and least elongated from the mountains of Transcarpathia. Results suggest a clinal variation from the [eastern] lowlands to the [western] mountains. Smelkova [90, 91] carried out biometric studies of 14 seed samples collected from beech stands aged 70–130 years in 11 localities throughout Slovakia at altitudes between 290–940 meters. Negative correlation was found between stand age, altitude and the dimensions and weight of seeds and embryos. Stand density and topographical aspect had no significant effect.

Beech is a species with poor dispersal. Large nuts fall beneath the mother trees, only topography can play a role in short distance dispersal. Certain bird species eat beechnuts. Turcek [104] studied the retrieval of beechnuts collected and hidden by jay *(Garrulus glandarius*) and nutcracker (*Nucifraga caryocatactes*) in Slovakia, including a brief discussion of the silvicultural importance of the seeds not retrieved.

Seed predation and mortality of young seedlings

Mortality of beechnuts and seedlings is very high. Many animals, e.g. wild boar, roe deer, red deer, rodents and birds use beech seed for food. Mortality caused by rodents is less dramatic in years when seed production is low, because gradation of rodents can not arise [36, 101].

Exact studies are almost lacking on the dynamics and exact causes behind this dramatic mortality. One important factor is infection by fungi. Prochazkova [77, 78] studied infection of seeds for several tree species. Based on the analysis of 466 seed samples collected from Czechoslovakia, 44 species of fungi were found on beech seeds. Beechnuts were most frequently attacked by *Trichothecium roseum* (79%), *Penicillium* (76%), *Rhizopus stolonifer* (61%) and *Alternaria alternata* (51%). Pathologically important species, especially *Fusarium* spp. *(F. avenaceum, F. oxysporum, F. sporotrichoides* v. *sporotrichoides)* were determined in 12% of samples. 43% of seed samples originating from Slovakia were infected (up to 5% of seeds/sample) by *Fusarium* species. In addition to the *Fusarium* species, isolated pathogens included *Phytophthora cactorum, Rhizoctonia solani, Cyclindrocarpon magnussianum*. In Poland Skrzypczynska [89] studied the fate of 2100 seeds that had fallen under beech trees in the Ojcow National Park, Poland. Damaged seeds constituted 8.3% of the total, and the agent responsible was identified as *Cydia fagiglandana*; 40.6% of seeds were viable and 51.1% were empty. In Slovakia Saniga [85] found that 90% of first year's mortality was caused by mould and mice.

Germination and initial establishment

Beechnuts usually germinate in April or May depending on snow cover. Young seedlings are often infected by *Phytophora cactorum* (Leb. et Cohn.) Schroet [88]. In Hungary Mendlik [57] published data on the number of seedlings in the first year after seed production. In spring 1981 he found 110–170 thousand seedlings/ha. By autumn the numbers decreased to 30–70 thousand. Germination success and the number of surviving seedling were higher at forest edges. The main cause of seedling mortality was damage caused by aphids. Domin [11] made the interesting observation that partly decomposed litter impeded successful germination in nudum beech forests with thick litter layer. The few individuals that survive out of thousands help to weaken the litter layer, and then a new generation of young beech trees can establish themselves under these sparse groups.

Dead wood can provide appropriate establishment site for tree species in certain forest types. The importance of nursery logs is well known from boreal forests, where soil is covered by thick carpet of mosses that impedes successful establishment. In mixed or deciduous forest this role of logs has received less attention, although the presence of characteristic stilt roots have been observed in several Central European natural forests (Standovár personal observation). Szewczyk and Szwagrzyk [97] studied regeneration on soil and on decaying wood in a natural mixed stand in Babia Gora National Park, in the Western Carpathians, S. Poland. They found that logs covered around 6% of the forest floor. Regeneration was co-dominated by beech and fir seedlings, while spruce was less numerous. Average seedling density on the soil with herb layer (240/100 m^2) was higher than on the logs (even on the strongly decayed ones) at 177/100 m^2. However, the density of fir and spruce seedlings was higher on the rotten wood than on soil. Seedling survival of all species was better on the logs, especially for conifers. Because of the total dominance of beech among saplings, the presence of fir and spruce in the next generation of canopy trees depends strongly on their regeneration on decaying wood.

Development of seedling

Information from managed forests

Most of the studies dealing with growth and success of beech regeneration are carried out in managed beech stands, using experimental plots with different treatments. Standard silvicultural textbooks deal with the problems of how fast and intensively old stands should be opened to provide beech regeneration with appropriate environment and to avoid competition from herbaceous weeds and other tree species like ash. These works are not reported here.

However, the results of a detailed study that was carried out in semi-natural beech forests of the Carpathians are briefly summarized as an example. Saniga [85] made observations on beech natural regeneration over a 10-year (1981–1991) period in three plots (87%, 73%, 70% canopy closure) in a 85 years old beech stand. He found that seedling survival was the lowest in the most shaded plot for all time steps studied. But even in this most shaded plot the number of eleven-year old seedlings was 27 000 per hectare in 1991. The other two plots contained 43 700 and 53 200 seedlings, respectively. Height growth was not different in the first five years, but later the effect of light could be traced.

Besides light, soil water can also limit the success of regeneration. Coping with too much water is as problematic for young beech trees as surviving too dry periods. For this reason, silvicultural systems, like uniform shelterwood, can destroy regeneration by causing soil water saturation at moist sites, and by drying out less humid sites. In the first case competition of tall herbs (e.g. *Impatiens noli-tangere, Dryopteris filix-mas*) and appearance of mould can be detrimental. In the latter case competition from old trees and drought can impede successful regeneration. Special cutting protocols were developed to overcome these problems. In Hungary Török [100] published a method that was developed in the Bakony Mts. He applied uneven cutting regimes taking into account the direction of shade that old trees shed.

Game browsing is one of the major problems of nature-based forest management throughout Europe. In spite of its overwhelming importance there are hardly any exact study on the effects of browsing. Instead, foresters in many regions have set up demonstration exclosures. However, these plots are usually without measured controls and even within the exclosure young trees are not counted or measured.

Information from unmanaged natural forests

Permanent plot studies in unmanaged forest reserves usually record trees above certain dbh, usually above 7, 10 or 20 cm, hence missing the most dynamic part of the regeneration processes. However, there are studies, where regeneration was also recorded and followed in time. There is one study in which regeneration succession is followed after a serious wind disturbance. One of the permanent plots set out by Korpel in the Badin Forest Reserve was placed in that part of the reserve, which was felled by a serious wind. Korpel made recordings on the tree stand in a 0.5 ha plot every 10 years from 1957. All trees larger than 7 cm dbh were recorded. In 1986 and 1996 Saniga repeated the measurements, but he also measured young trees in 9 age and size classes. He showed that the number of large trees (>7 cm) was 2589 and 2410 per hectare in 1986 and 1996, respectively. The proportion of goat willow + aspen decreased from

71.6% to 66.5%, whereas the proportion of beech increased from 26.1% to 31.1%. Among small trees the number of goat willow sprouts are very high (650/ha) because of strong deer browsing, which also affected silver fir [86].

Regeneration dynamics in small patches created by the death of individual old trees could be followed in those reserves where tree mapping is accompanied by more detailed (usually transect) sampling of crown projection, regeneration and herbaceous species [41]. This could provide the basis for studying the relationships among different vegetation layers. Understanding the dynamics of early phases of regeneration would also require more frequent than usual (once in every 10–20 years) sampling. Another approach was followed in the study of several Czech forest reserves. There they mapped the patches where regeneration was abundant, but trees did not reach 10 cm dbh [79, 105, 106, 107, 108, 109, 110, 111, 112]. In this way the total area and pattern of regeneration groups could be followed. This kind of information is available for the Polom, Razula, Zakova Hora, Boubin, Milesice, Mionsi and Diana Forest Reserves. The general message of these studies is that the success of regeneration is as much dependent on stand dynamics as on game pressure. In several reserves fencing was necessary to initiate the growth of advanced browsed regeneration and to make the establishment for new generations possible.

The effects of game species are usually assessed indirectly by the possibilities of natural regeneration without fencing, or by setting up demonstration exclosures. Miscicki and Zurek [59] presented an example of the rare quantitative studies. They studied damage to natural regeneration in the Gorce National Park in Poland, where killing of deer had been banned since the establishment of the park in 1981. Regeneration and browsing/stripping damage were assessed by species. Fir (*Abies alba*) was stripped most and heavily browsed, followed by sycamore (*Acer pseudoplatanus*) and rowan (*Sorbus aucuparia*). Beech (*Fagus sylvatica*) and spruce (*Picea abies*) were only slightly damaged. The proportion of fir and sycamore decreased in successively larger diameter classes. The level of browsing in the park was assessed as 280% of the admissible value, while damage to the stem surface (stripping and other) was assessed as 580% of the admissible value.

Regeneration cycles in natural forests

The aim of studying natural forest dynamics has been to describe and understand the nature and length of the developmental cycles of forests throughout Europe. Major scientists in the field recognized different stages of development, and saw these natural forests as mosaics of patches in different development stages [41, 42, 43, 48, 49, 51, 60, 79, 123]. However, there are several obstacles to drawing general conclusions from these results.

Major characteristics of existing researches

Naturalness of sites

It is important to bear in mind that the reference sites used in these studies differ greatly in their naturalness. Each site has their own management history from no management to grazing and non-intensive timber extraction (e.g. only dead wood). They also differ in their sizes. It is hard to compare an isolated reserve of up to 100 hectares in a cultural landscape with a vast near-natural forest area of several thousands hectares in a forested landscape of 100 000 hectares. These differences could affect the pattern of disturbance, propagule source, the presence of large predators and many other factors that influence forest development. As it was observed in several reference sites, the density of large herbivores had overwhelming effect on development, so differences in game pressure should be taken into consideration.

Scientific approaches

An interesting aspect of Central European forest dynamics research is that it developed in countries where the dominant view on biological communities was based on the equilibrium theory. Classic Braun-Blanquet-type phytosociology typically described characteristic patches of mature managed forests. Emphasis was put on distinguishing distinct vegetation units (associations).

Another important feature is that the major emphasis has been put on the tree component from mensurational viewpoint. Most results show dimensions, productivity, standing crop and their changes through the regeneration cycle. Effects of site quality have always been in the focus in these investigations.

These studies had to face the problems of the incompatibility between thinking in homogenous types (associations, site types, forest types) and experiencing heterogeneity, i.e., complex fine-grained mosaic structure in naturally dynamic forests. This problem was clearly seen by early phytosociologists [e.g. 11], but later got mostly forgotten.

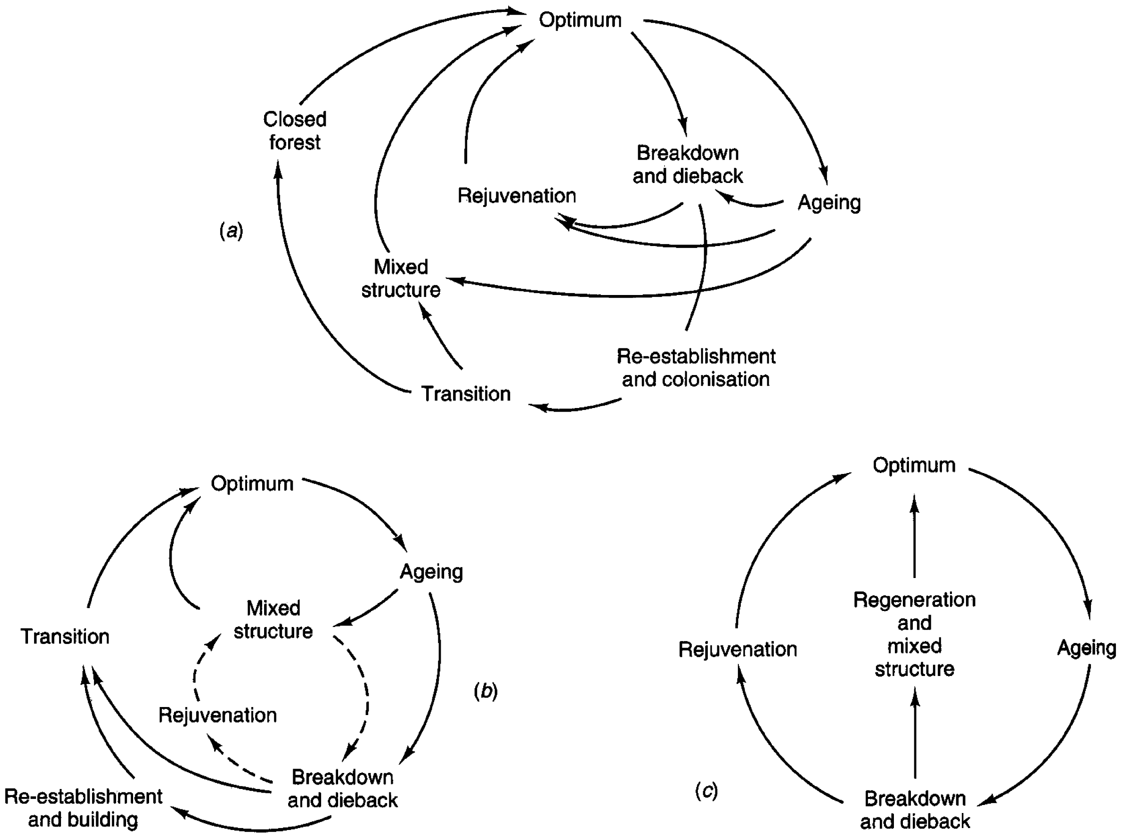


Figure 3. *Development phases of virgin forests (**a**) as recognised by Leibundgut* [48] *for Central Europe, with alternative versions by (**b**) Zukrigl et al.* [123] *and Mueller-Dombois* [61]. *Dashed lines in (**b**) indicate uncommon transitions. Source:* [71].

A major tool in understanding forest dynamics was the concept of forest cycles described by forest development stages. The systems developed by different authors are not completely compatible (examples are shown in *Fig. 3*), the categories used are loosely defined, the mapping units of the mosaic might be of different size, so the perceived mosaic might have different spatial resolution (grain-size) according to the system used. Another consequence is that the recognition of stages and phases is observer-dependent, which might cause problems for long-term observations.

Important results

In this section examples are given for the most typical type of results that were published in the scientific literature.

Stand development

Most efforts have been put into studying changes of tree species composition, tree dimensions (height, dbh, basal area, distribution by size-classes) along the forest cycle. Models of the stages and length of the cycles were constructed and the equilibrium share of stages in the forest mosaic was defined (*Figs. 4–7*).

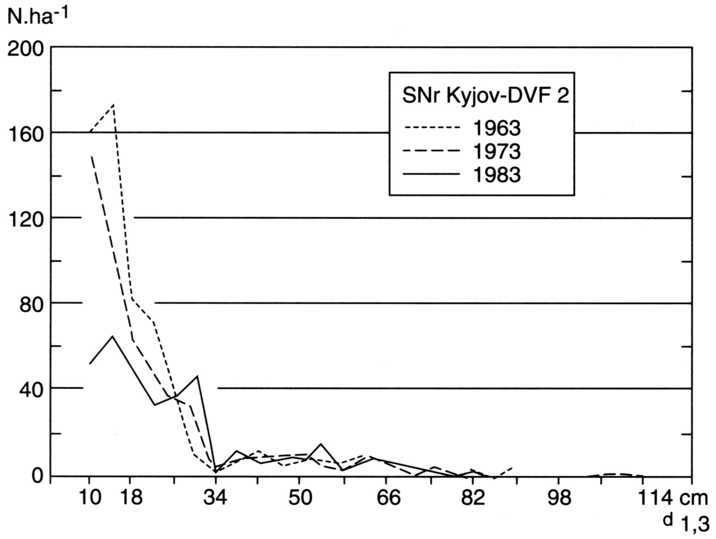


Figure 4. *Diameter distribution of trees in permanenet plot 2 in the Kyjov Forest Reserve in 1963, 1973, 1983. Source:* [43].

Patterns of natural mortality caused by competition and natural disturbance was compared in some cases. Dziewolski and Rutkowski [13] studied a 26.88 ha patch of the Wladiyslaw Orkan Forest Reserve in the Gorce Mts., southern Poland. Patterns of mortality were studied between 1969 and 1986 in 20 sampling plots, 0.05 hectare each. After the second measurement in July 1986, serious wind damage occurred on 12/13 August 1986. With the next measurement in September 1986 they could compare species and size distribution of dying trees. As *Fig. 8* shows, most of the 219 trees that died between 1969 and 1986 were small, whereas the wind in August 1986 killed more large trees.

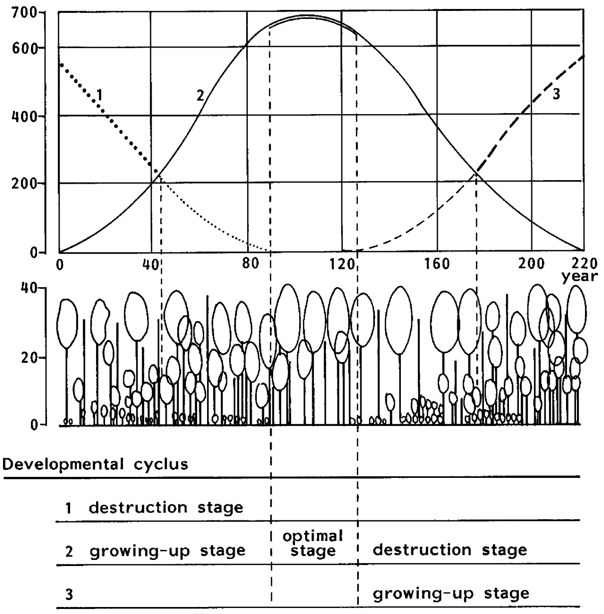


Figure 5. *Korpel's model of beech forest cycle, simplified by Koop* [41].

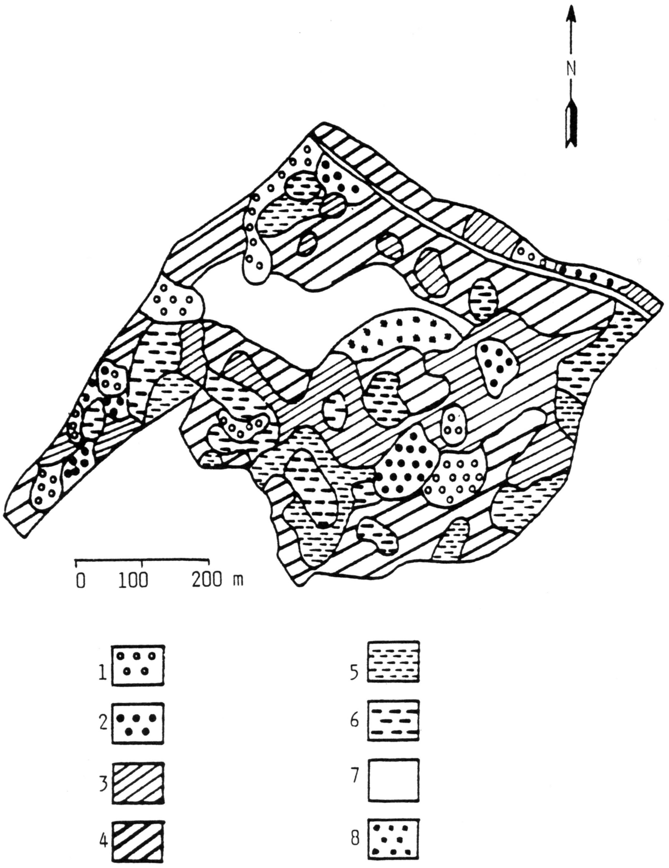
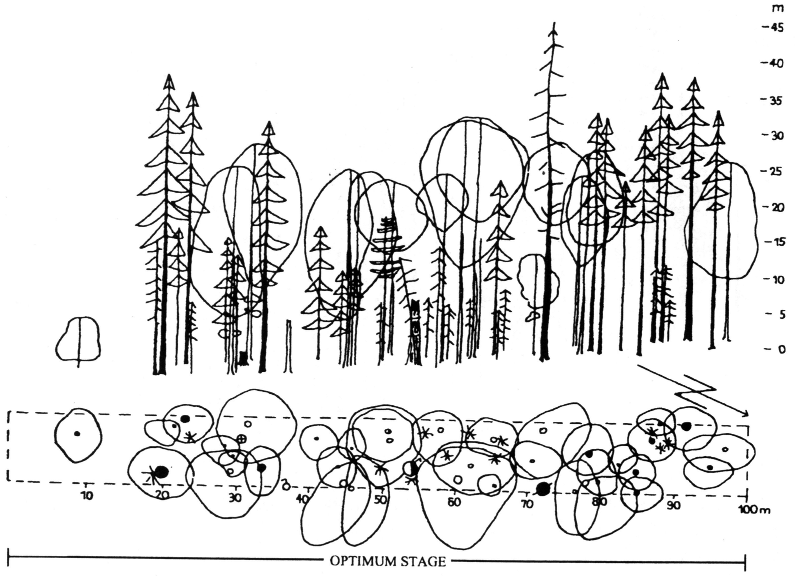


Figure. 6. *Mosaic of forest developmental phases in the Badin Forest Reserve. Source:* [43]. *1. Early growing-up phase; 2. Late growing-up phase; 3. Early collapsing phase; 4. Late collapsing phase; 5. Early optimal phase; 6. Late optimal phase; 7. Initial phase; 8. Transition phase.*

BOUBÍN 1960



BOUBÍN 1996

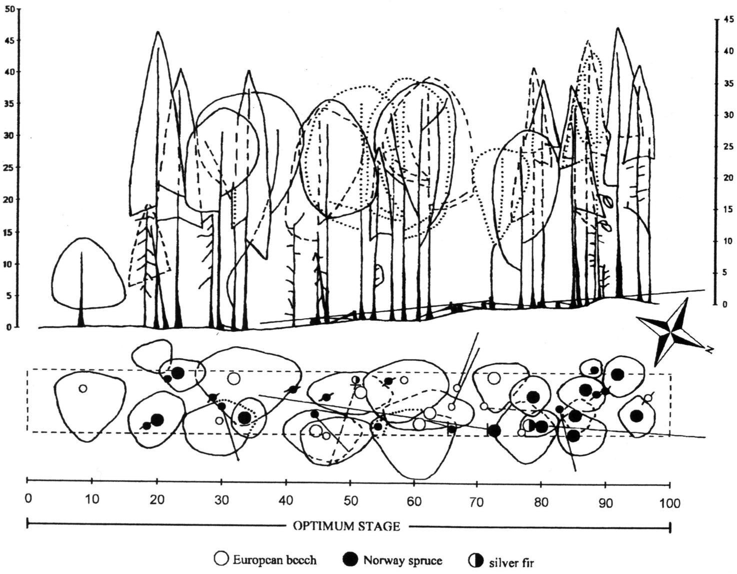


***Figure** 7. Changes of stand structure in the Boubin Forest Reserve illustrated by transect profiles drawn in 1960 and 1996 Source:* [112].

Dead wood

Dead woody material is an important component of natural forests, which is often missing from managed forests. So, several studies described the amount and very rarely also the decay stage of dead wood through the forest cycle. A typical example is shown for the Milesice Forest Reserve in the Czech Republic. The total volume of dead timber increased from 751 m^3 to 851 m^3, whereas the number of dead trees from 324 to 684 in the whole reserve from 1972 to 1996 [110]. The distribution among species is shown in *Table 10*. If dead trees are distributed among developmental stages and different types

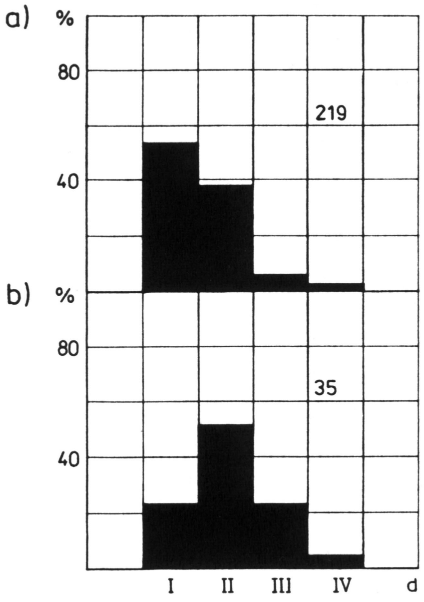


Figure 8. *Trees that died between 1969 and 1986 in the Wladiyslaw Orkan Forest Reserve* [13]. *Distribution of trees into diameter classes: I: 7–15 cm; II: 15–35 cm; 3: 35–55 cm; IV: 55–75 cm; a) natural loss 1969–1986 (21 trees); b) windfall in August 1986 (35 trees).*

of dead wood (standing dead tree, snag, log) then other aspect of dead wood dynamics can be traced. As *Table 11* shows, there are much more standing dead trees in the optimal stage than in the destruction stage, where fallen logs are more numerous.

The ecological role of dead wood is much less intensively studied in Central European beech forests than in the boreal zone [e.g. 67].

Table 10. *Distribution of the number and volume of dead trees among species in the Milesice Forest Reserve. Source:* [110].

	Number of trees		**Timber volume (m³)**	
	1972	**1996**	**1972**	**1996**
Spruce	211	423	437.74	613.97
Fir	53	156	217.31	469.44
Beech	40	105	95.79	144.09

Table 11. *Distribution of the number of dead wood among developmental stages and dead wood types in the Milesice Forest Reserve. Source:* [110].

	Stage of growth		**Optimum stage**		**Stage of disintegration**	
	1972	**1996**	**1972**	**1996**	**1972**	**1996**
Standing	9	13	151	136	43	136
Snag		14		32		32
Log	14	23	20	117	87	117
Total	23	50	171	285	130	285

Herbaceous vegetation

The composition of forest floor vegetation is widely used for recognizing forest types with different site quality. Forest floor vegetation can also be a serious competitor for young tree seedlings. For these reasons studying herbaceous vegetation in natural forests has always been an important task. Several authors studied the reaction of vegetation to changes in light conditions in forest reserves [e.g. 79, 93]. Resmerita [82] made a thorough analysis of herbaceous species occurring in Romanian beech forests. Of the 562 species known from beech sites 185 were grouped on the basis of their reaction to light. The system distinguishes 13 shade tolerant species, 25 shade-semishade species, 50 semishade species, 42 semishade species that tolerate light, 50 semishade-light species and 5 light species. Of the 5 light species *Chamerenion angustifolium* and *Rubus idaeus* are always present in clearings. Real shade species always disappear after large gaps have been created, whereas others can survive for several years: *Athyrium filix femina, Dryopteris filix-max, D. carthusiana, Geranium robertianum, Euonymus latifolia, Festuca drymea, Luzula luzuloides, L. sylvatica, Lysimachia nummularia, Polygonatum verticillatum.* Light tolerating semishade species can survive very long in large gaps: *Campanula persicifolia, Dactylis polygama, Melampyrum nemorosum, Poa nemoralis, Solidago virga-aurea, Thalictrum aquilegifolium, Vaccinium myrtyllus et vitis-idaea, Veronica officinalis.* The first species that recolonize gaps after canopy closure are: *Pulmonaria mollissima, P. officinalis, Symphytum tuberosum, Geum urbanum, Geranium robertianum, Polygonatum odoratum, Brachypodium sylvaticum, Dactylis polygama, Plathanthera bifolia, Epipactis helleborine, Athyrium filix-femina, Dryopteris filix-mas.*

Future tasks

To be able to get better ecological understanding of natural beech forests, this research area needs several improvements in our region. Among others:

- It is of utmost importance to clarify our definitions and sampling methods used for describing forest development stages so that different observers can collect comparable data.
- More specific analyses are needed to study relationships among different strata of forest vegetation. For this purpose spatially explicit individual-based approaches should also be used.
- Besides species and size distributions of trees, spatial structure of the stands should also be studied in more detail.
- The role of environmental heterogeneity in regeneration processes should be specifically addressed. Types, frequency and ecological role of microsites created by natural disturbances should be studied.
- Especially for conservation applications, it is essential to carry out specific studies on the relationships between certain forest-dwelling species and forest developmental stages or structural elements. This requires the inclusion of several animal groups into our studies.

Acknowledgements. The authors wish to express their thanks to all those people who helped in the collection or the translation of the material used. Among others we are grateful to Gabriella Magyar, Eszter Ruprecht, László Gálhidy, Zoltán Boda, Ildikó László, Stefan Stojko, Tamas Vrska, and Jozef Fanta. This work was financed by an EU 5th Framework Programme (Nat-Man No QLRT1-CT99-1349), which is greatly acknowledged.

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AN AGRO-ECOLOGICAL SIMULATION MODEL SYSTEM

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(Received 15th April 2002; accepted 15th June 2003)

Abstract. In this paper five different models, as five modules of a complex agro-ecosystem are investigated. The water and nutrient flow in soil is simulated by the nutrient-in-soil model while the biomass change according to the seasonal weather aspects, the nutrient content of soil and the biotic interactions amongst the other terms of the food web are simulated by the food web population dynamical model that is constructed for a piece of homogeneous field. The food web model is based on the nutrient-in-soil model and on the activity function evaluator model that expresses the effect of temperature. The numbers of individuals in all phenological phases of the different populations are given by the phenology model. The food web model is extended to an inhomogeneous piece of field by the spatial extension model. Finally, as an additional module, an application of the above models for multivariate state-planes, is given. The modules built into the system are closely connected to each other as they utilize each other's outputs, nevertheless, they work separately, too. Some case studies are analysed and a summarized outlook is given.

Keywords: *food web, population dynamical model, activity function, spatio-temporal simulation model, multivariate state-planes*

Introduction

The need to apply computer science and electronics in agricultural production for a targeted region has become increasingly urgent. By 'precision and sustainable agriculture', we mean not only a new production method, but also a complex system that

- integrates biological, technological and economic factors, and
- joins the natural circumstances flexibly.

This form of agriculture aims to optimize proficiency and environmental protection, by assessing together forecasts for risk, damages and profit.

In order to get to know better how the examined agro-ecosystem is functioning, we need correct simulation models of the complex food web system, as well as continuous monitoring of the processes [24, 31, 32, 37].

This simplified food web model accounts for seasonal weather aspects [74, 75], the nutrient content of soil and biotic interactions (*Fig. 1*). On the first level, K denotes the water and nutrient content of soil, as the input of the system. The input comes from a simplified nutrient-in-soil model [54] described below. Above the nutrient-in-soil term K, are cultivated plants, denoted by N, and two kinds of weed, denoted by G_1 and G_2, respectively. On the third level, monophagous M_1 consumes the cultivated plant N, while monophagous M_2 eats one of the weeds. P denotes a polyphagous pest which consumes the cultivated plant N, as well as weed G_1. Additionally, there is a predator, denoted by P, that consumes pests M_1, P and M_2.

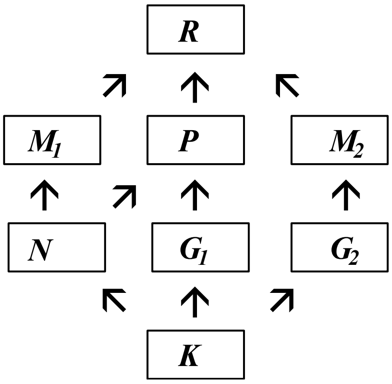


Figure 1. *A food web model. The interactions amongst nutrient-in-soil (K), cultivated plant (N), weeds (G_1 and G_2), monophagous (M_1 and M_2) and polyphagous (P) pests, as well as predator (R). (The arrows run from the nutrient to the consumer.)*

In this paper five different models, as five modules of a complex agro-ecosystem are investigated, furthermore, an extra module is constructed:

- The water and nutrient flow in soil is simulated by the *nutrient-in-soil model.*
- The biomass changes according to the seasonal weather aspects, the nutrient content of soil and the biotic interactions amongst the other terms of the food web, are simulated by the *food web population dynamical model.* The model is constructed specially for a piece of homogeneous field.
- The *activity function evaluator model* expresses the effect of the daily average temperature on the activity of the individuals.
- The numbers of individuals in all phenological phases of the different populations are given by the *phenology model.*
- The food web model is extended for a piece of inhomogeneous field by the *spatial extension model.*
- The last module gives an application of the above models for *multivariate state-planes.*

Although the modules built into the system are working separately, too, they are closely connected to each other, as they can utilize each other's outputs:

- The *food web model* is based on the *activity function evaluator model* and on the *nutrient-in-soil model* and it can immediately be followed by the *phenology model.*
- The *nutrient-in-soil model* applies the outputs of the *food web model* as its own inputs.
- The *food web model* and the *spatial extension model* can directly be linked.
- The *multivariate state-planes module* is built on the results of the *food web model* completed with the *phenology model* and on the ones of the *spatial extension model.*

To simulate the interactions, a discrete difference equation system with daily scale is used. As in the literature, there are plenty of excellent models which describe certain parts of the processes quite exactly, our aim was to create a model that describes the whole interaction process, in order to be able to apply it also in cases when detailed data are missing and to extend it in cases when more complex data are available.

The pattern analysis and the investigation of spatio-temporal inhomogeneity of agricultural fields are also of great significance, especially in the precision and sustainable agriculture. Additionally, it is important to elaborate the methodology of the information and data handling and the optimal decision making. Our aim is to go ahead in these problems. In former works the agro-ecosystem models (soil–plant–weather–pest systems) and pattern analyses were operated separately. By a spatial extension of the agro-ecosystem model a space specific complex ecological model is obtained.

Some case studies are analysed and a summarized outlook, amongst others, of possible ways to develop and apply the models, is given.

Review of literature

After the first food web model was described by Shelford in 1913, the most popular early monography became Bird's book from 1930 (In Jordán, [42]). Since that time, several theories have been appeared investigating the food web from several different points of view such as from energetical aspect [56], from population dynamical aspect [41], from stability, graph theory or information theory aspects [69, 70, 81, 82]. The structure of a food web and its interactions are characterized by Jordán [42, 44], while its reliability has been investigated by Jordán and Molnár, 1999; Jordán et al, 1999; Jordán, 2000 [43, 45, 46]. In the past, there have been few papers published on food-web researches applied for Hungary.

Models have been constructed for ecosystems with food web simulations [65] that, nevertheless, are based on classical Lotka-Volterra interactions, ignoring either abiotic effects or phenological aspects. Crop–weed competition is investigated e.g. in Kropff and Laar [50] and a population–phenology simulator is applied by Mols [60, 61].

Agricultural modelling and empirical survey deal mainly with soil–plant–weather systems with different additional main points, such as climate change impact studies [10, 58], mineralisation and heat, water and nitrate transfer [18], soil heat and water dynamics [27, 79], non-homogeneous cropped soil profile [47, 64], management impact [27, 77], environmental conditions [51, 62], water and nutrient dynamics in a plant [68] , fertilization [14], physiological and physical processes [8], water run-off and erosion in soil [49], phenology [48], planning and decision support [2, 3, 8], cropping systems [77] and informatics [19, 20, 21]. Investigations of food web sytems are, however, not involved in the above studies. Comparisons of cropping systems can be found in Francaviglia and Marchetti [17] and in Giardini et al. [25]. A valuable review of methodologies to evaluate simulation models is given by Martorana and Bellocchi [59].

There have been published some recent papers on zoocoenological explorations of fresh-water patterns [4, 12, 13, 36, 81]. Investigations on agro-ecosystems can be found in Hufnagel et al. [32], in Ferenczy et al. [16] and in Nyilas et al. [64] for pest populations. Methodological questions of the ecosystem surveys are discussed e.g. in Hufnagel et al. [33, 34, 35] and in Gaál and Hufnagel [22, 23, 24], while the ones for agrosystem researches can be found in Harnos [28].

Results

Water and nutrient flow in soil

In order to minimize the difference between the optimal and the real results in agriculture, water and nutrient flow in soil have been observed yet from several aspects [5, 9, 83]. There was created a special, drastically simplified nutrient-in-soil model by

Erdélyi [15], with the special aim that it can be built into the food web population dynamical model to complete it with the most important abiotic effects.

The differential equation system of the nutrient-in-soil model consists of three equations: they follow the change of water, ionic nutrient and organic matter.

Water content of soil

As the plants can absorb ionic nutrient solution only, water content of soil plays as important role in vital processes as the ionic nutrient content of soil. The water content of soil is

- reduced mainly by evaporation (of soil and plant), by take-up and water run-off;
- increased mainly by the precipitation and watering.

These factors are depending, amongst others, on temperature, global radiation, the relative water holding capacity and the growing rate of the plant, as well as the water holding capacity and the current water content of the soil. These effects are involved in our model, nevertheless, other properties of soil such as the amount of carbon dioxide, the effect of wind, etc. are ignored.

Water content of soil V_{t+1} at the (t+1)th point of time can be calculated with the help of the water content of soil V_t at the tth point of time multiplied by an evaporation term Π_t, a take-up term Ω_t and, moreover, added to a precipitation – watering – and water run-off term Ψ_t:

$$V_{t+1} = V_t \cdot \Pi_t \cdot \Omega_t + \Psi_t .$$

Evaporation term Π_t is derived from the potential evapotranspiration formula due to Turc (in: Szász, [79]), that is given for the case water content is not limited and is corrected for the case water content does be limited which is the real case in Hungary. Evaporation term Π_t is depending on the daily temperature, the daily global radiation value and the current water content of soil. The more the water content is, the greater the rate of evaporation is, thus the less the evaporation term Π_t is; $0 < \Pi_t < 1$, and it is tending to 1 as the water content tends to zero.

Take-up term Ω_t is depending on the daily biomass growth dB_t and on the relative water holding capacity of the plant. The more the daily growth dB_t of the biomass is, the less take-up term Ω_t is and with $dB_t \to 0$, take-up term Ω_t tends to 1.

Precipitation – watering – and water run-off term Ψ_t is depending on the daily precipitation, the daily amount of watering and the water holding capacity of soil.

Ionic nutrient and organic matter content of soil

Denote by K_t the daily ionic nutrient solution content of soil that depends, of course, on the daily water content of soil V_t. Ionic nutrient solution content of soil K_{t+1} at the (t+1)th point of time can be calculated by ionic nutrient solution content of soil K_t at the tth point of time multiplied by a take-up term I_t, an erosion term E_t, and added to a decomposition term D_t and an artificial fertilizer term $K_{art,t}$:

$$K_{t+1} = K_t I_t E_t + D_t + K_{art,t} .$$

Take-up term I_t ($0<I_t<1$) is depending on the relative nutrient content of the plant derived from its need for ionic nutrient and on the daily biomass growth dB_t. It is obvious that the more the daily biomass growth dB_t is, the less take-up term I_t is, and as the daily biomass growth dB_t tends to zero, take-up term I_t goes to 1.

Erosion term E_t ($0<E_t<1$) expresses the fact that in case water is limited in soil, ionic nutrient solution is also limited by it, while in case water is unlimited, ionic nutrient solution is limited by ionic nutrient that is unable to be taken up by the plant. Erosion term E_t depends on the solubility of the different kinds of ionic nutrient. The greater amount of ionic nutrient is erosed the less amount of it is erosable, so erosion term E_t tends to 1.

Organic decomposition term at the t^{th} point of time D_t can be expressed by the formula

$$D_{t+1} = (1-\xi)D_t + D_{biom,t} + D_{of,t},$$

where $\xi<1$ denotes the daily percent of the decomposed organic matter, $D_{biom,t}$ denotes the amount of the developed organic matter in soil and $D_{of,t}$ denotes the amount of utilizable organic fertilizer added.

The artificial fertilizer term $K_{art,t}$ is equal to the amount of the utilizable artificial fertilizer added.

A food web seasonal population dynamical model

An agro-ecosystem is directed mainly by the interactions amongst the populations living in the agro-ecosystem together. Several indirect or hidden types of interactions that can not be expressed as different kinds of material flow such as competition, the indirect interactions that can be derived from the escape from or the defence against a common predator, as well as the so-called 'top down and bottom up regulations' are involved in our food web population dynamical model. To simulate the interactions, a discrete difference equation system is used. The general equation of the web model is based on three elements: the first one is to express the activity of the individual depending on the temperature, the second one is to describe the effect of the quality and the quantity of nutrient of plants and/or pests and the third one is to display the effect of the predators. The model is based on the nutrient-in-soil model defined above.

To describe the interactions in the food web a discrete difference equation system with seven equations is used, each equation is for a certain element N, G_1, G_2, M_1, M_2, P, or R of the system at the $(t+1)^{\text{th}}$ point of time. The general form of the difference equation is

$$X_{t+1} = X_t \cdot R_{X,t} \cdot F_{X,t} \cdot P_{X,t},$$

where

- the current amount of the biomass of one of the populations N, G_1, G_2, M_1, M_2, P, or R at the $(t+1)^{\text{th}}$ and at the t^{th} points of time are denoted by X_{t+1} and X_t, respectively;

- the activity term of the individual X is denoted by $R_{X,t}$ and is depending on the daily average temperature T;
- $F_{X,t}$ denotes the so-called nutrient term;
- $P_{X,t}$ denotes the so-called predation term.

In what follows the terms of the general equation are characterized.

Activity term $R_{X,t}$

To forecast the time and the mass of the local appearance of pest generations, the so-called 'classical temperature-sum' method is widely used, however, it is often unreliable and in these cases the errors can rush quite high. To avoid this, a parametric activity function that uses the data of the National Light-trap Network and the daily average temperature data as input, has been created by a special optimisation process by Révész [73]. Our model is based on the idea that was applied by Révész, namely, the agro-ecological process for each individual *X* is defined not by the temperature, itself, but by the so-called 'activity function' r_X that is a non-linear function of the daily average temperature *T*:

$$r_X : T \mapsto r_X(T) = \frac{1}{2}\left(\left|s_X(T)\right| + s_X(T)\right)^{f_X},$$

$$s_X : T \mapsto s_X(T) = \frac{1}{\exp(a_X(T-b_X)) + \exp(-c_X(T-d_X))} - \frac{1}{\exp(-a_X b_X) + \exp(c_X d_X)},$$

where a_X, b_X, c_X, d_X and f_X are suitable constants relative to individual *X*.

Activity function r_X expresses that the individuals do not develop under low temperature circumstances; while the temperature increases, the individuals develop at an increasingly rapid rate up to a certain point; at higher temperature as it is optimal for the individuals, the development is impeded peculiarly to the individuals' sensitivity.

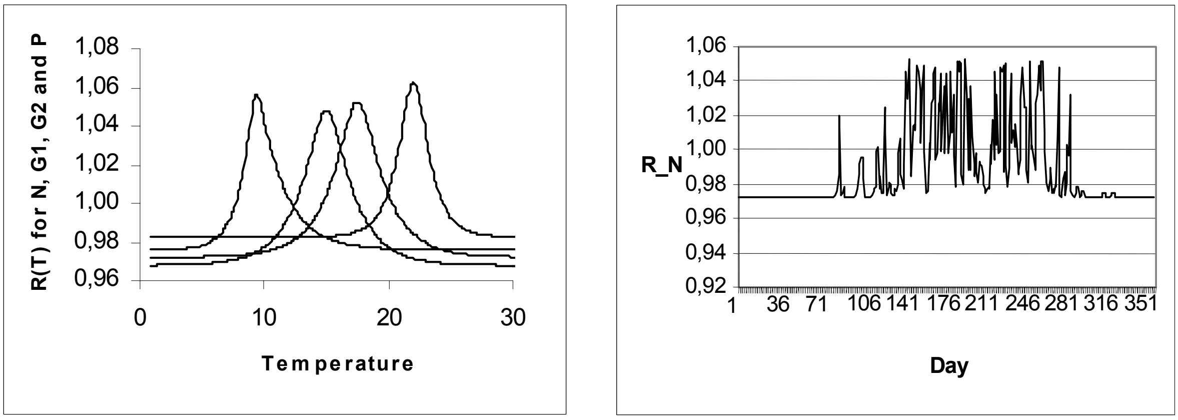
Activity term R_X is derived from the activity function r_X by a linear transformation:

$$R_X : T \mapsto A_X r_X(T) + B_X .$$

The range of term R_X is a narrow interval around number 1:

- In the case the temperature is unfavourable, $R_X < 1$, the effect of the term is impedimental.
- In the case the temperature is favourable, $R_X > 1$, the effect of the term is supporting.

Term R_X is continuous, monotonously increasing until the temperature is optimal and monotonously decreasing if the temperature is higher than it is optimal (*Figs. 2* and *3*).



2 **3**

Figures 2–3. 2: *Activity term of temperature (°C) for the cultivated plant N, weeds* G_1 *and* G_2 *and polyphagous P.* 3: *Activity term of day for cultivated plant N.*

Nutrient term $F_{X,t}$

Nutrient term $F_{X,t}$ is due to performance the following properties of the individuals in the model:

- In the case nutrient is unlimitedly available (under fixed all other circumstances), the biomass of *X* is increasing at a maximal rate denoted by K_X.
- In the case nutrient is limited, the biomass of *X* is increasing more slowly, stagnating or decreasing.
- In the case nutrient is just as much as needed, the amount of the biomass is nearly constant ($F_X \approx 1$).
- In the case nutrient decreases excessively, the individual is going to die ($F_X \to 0$).
- In the case the individual is in competition with another consumer, the change of biomass is influenced by the amount of the biomass of the other consumer together with some weight parameters.
- A polyphagous (*P* or *R*) consumes from the different populations in proportion to the amounts and the nutritive values of its nutrient-biomasses.

Term F_X that satisfies all the properties above will be constructed step by step the following way. First, we give the proportion of the daily amount of total available nutrient reduced by the amount of necessary nutrient, and the amount of total available nutrient, more exactly the proportion X_F

$$\boxed{\frac{(-1)\cdot(\textit{total available nutrient} - \textit{necessary nutrient})}{\textit{total available nutrient}}}$$

as follows:

$$N_F = G_{1\,F} = G_{2\,F} = -\frac{K - a_{KN}N - a_{KG_1}G_1 - a_{KG_2}G_2}{K+\varepsilon},$$

$$P_F=-\frac{N-a_{NM_1}M_1-a_{NP}\dfrac{P}{P+1}\cdot\dfrac{P}{N+\varepsilon}\cdot\dfrac{1}{G_1+1}+G_1-a_{G_1P}\dfrac{P}{P+1}\cdot\dfrac{P}{G_1+\varepsilon}\cdot\dfrac{1}{N+1}}{N+G_1+\varepsilon},$$

$$M_{1\,F}=-\frac{N-a_{NM_1}M_1-a_{NP}\dfrac{P}{P+1}\cdot\dfrac{P}{N+\varepsilon}\cdot\dfrac{1}{G_1+1}}{N+\varepsilon},$$

$$M_{2\,F}=-\frac{G_2-a_{G_2M_2}M_2}{G_2+\varepsilon},$$

$$R_F=-\left(\frac{M_1-a_{M_1R}\dfrac{R}{R+1}\cdot\dfrac{R}{M_1+\varepsilon}\cdot\dfrac{1}{P+M_2+1}+P-a_{PR}\dfrac{R}{R+1}\cdot\dfrac{R}{P+\varepsilon}\cdot\dfrac{1}{M_1+M_2+1}}{P+M_1+M_2+\varepsilon}\right)+$$

$$-\left(\frac{M_2-a_{M_2R}\dfrac{R}{R+1}\cdot\dfrac{R}{M_2+\varepsilon}\cdot\dfrac{1}{P+M_1+1}}{P+M_1+M_2+\varepsilon}\right).$$

Coefficients a_{XY} denote the weights of the narrows runnung from population X to Y, constant $\varepsilon>0$ is a tiny number due to avoid numerical errors during division. It is obvious, that $X_F>-1$.

As the next step we introduce function

$$f:x\mapsto f(x)=\left(\frac{2}{2+x}\right)^{\nu}\qquad (x>-1)$$

that – substituting x by X_F – satisfies all the properties above but the first one because its limit remains under K_X even in case nutrient is unlimitedly available. Note that we choose $\nu>0$ such that $\nu<\ln K_X/\ln 2$ holds.

Consider function

$$g:x\mapsto g(x)=\max\left\{\left(1-\frac{K}{2^{\nu}}\right)x+1,\ 1\right\}$$

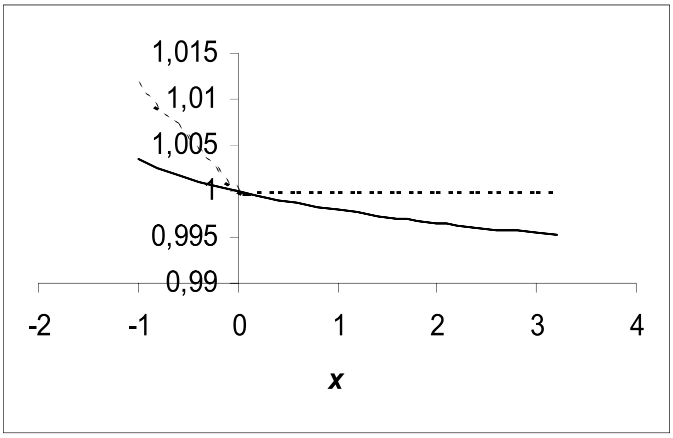


Figure 4. *Functions f (smooth line) and g (dotted line).*

that is linear, continuous, strictly monotonously decreasing whenever $x < 0$ and takes constant 1 if $x \geq 0$.

Function

$$F_X : X_F \mapsto F_X(X_F) = g(X_F) \cdot f(X_F)$$

satisfies all the properties above including (i):

- If $-1 < X_F < 0$ that is to say, if nutrient is unlimitedly available:

$$F_X : X_F \mapsto F_X(X_F) = \left\{ \left(1 - \frac{\mathrm{K}}{2^{\nu}}\right) X_F + 1 \right\} \cdot \left(\frac{2}{2 + X_F}\right)^{\nu}.$$

- If $X_F \to -1$ then $F_X \to \mathrm{K}$, so substituting K by K_X, we get that property (i) holds.
- If $X_F \geq 0$, that is to say, if nutrient is just enough or short

$$F_X : X_F \mapsto F_X(X_F) = \left(\frac{2}{2 + X_F}\right)^{\nu}$$

so, in the case nutrient is just enough ($X_F \approx 0$) then $F_X \approx 1$, thus (iii) is satisfied.

- Function F_X is monotonously decreasing, thus (ii) holds.
- In case $X_F \to +\infty$, that is to say the individuals are starving, $F_X \to 0$, as a consequence, they are going to die, so (iv) holds.
- Property (v) follows from the construction of X_F, as we see that the decrease of the biomass of the nutrient-population is caused by the consumers-in-competition, together.
- Property (vi) follows from the construction of X_F, again, with the brake effects

$$\frac{1}{G_1 + 1}, \frac{1}{N + 1}, \frac{1}{P + M_2 + 1}, \frac{1}{M_1 + M_2 + 1} \text{ and } \frac{1}{P + M_1 + 1}.$$

ISSN 1589 1623

Predation term P_X

Predation term P_X satisfies the properties of the biomass-change as follows:

- While the biomass of the consumer-population is increasing, the nutrient-population is decreasing at a slower and slower rate and, at the same time, the decreasing amount of the biomass of the nutrient-population is an impeding factor for the consumer-population. While the consumer-population is increasing slower, stagnating or decreasing, however, the amount of the biomass of the nutrient-population is going to stagnate or even to increase.
- Consider the case of polyphagy. From the one nutrient-population's aspect the effect of the other nutrient-population is, on the one hand, positive (while the other is being consumed, the one can escape), on the other hand, is negative (the other nutrient-population is making the consumer-population stronger by nourishing it).

The above effects of the interactions are quite complex. Our aim was to give the simplest model ever which describes the above properties as exactly as possible. It can be proved that terms

$$P_N = \frac{1}{\left(1 + a_{NP} \frac{P}{P+1} \cdot \frac{P}{N+\varepsilon} \cdot \frac{1}{G_1+1} + a_{NM_1} \frac{M_1}{M_1+1} \cdot \frac{M_1}{N+\varepsilon}\right)^{\mu}}$$

$$P_{G_1} = \frac{1}{\left(1 + a_{G_1P} \frac{P}{P+1} \cdot \frac{P}{G_1+\varepsilon} \cdot \frac{1}{N+1}\right)^{\mu}}$$

$$P_{G_2} = \frac{1}{\left(1 + a_{G_2M_2} \frac{M_2}{M_2+1} \cdot \frac{M_2}{G_2+\varepsilon}\right)^{\mu}}$$

$$P_{M_1} = \frac{1}{\left(1 + a_{M_1R} \frac{R}{R+1} \cdot \frac{R}{M_1+\varepsilon} \cdot \frac{1}{P+M_2+1}\right)^{\mu}}$$

$$P_{M_2} = \frac{1}{\left(1 + a_{M_2R} \frac{R}{R+1} \cdot \frac{R}{M_2+\varepsilon} \cdot \frac{1}{P+M_1+1}\right)^{\mu}}$$

$$P_P = \frac{1}{\left(1 + a_{PR} \frac{R}{R+1} \cdot \frac{R}{P+\varepsilon} \cdot \frac{1}{M_1+M_2+1}\right)^{\mu}}$$

satisfy all the above properties where μ denotes a speed factor and $\varepsilon > 0$ is a tiny number due to avoid numerical errors during division.

Multipliers

$$\frac{1}{G_1+1}, \frac{1}{N+1}, \frac{1}{M_1+M_2+1}, \frac{1}{P+M_2+1} \text{ and } \frac{1}{P+M_1+1}$$

are to express the breaking effect in case more predators are in competition. The other poperties can be derived in a similar way we did before for nutrient term $F_{X,t}$.

The connection of the nutrient-in-soil and the food web models

Input data applied by the models can be devided into four groups:

- Daily data such as precipitation, temperature, watering, global radiation, fertilization etc. These kinds of data have been available in Hungary for tens of years.
- Constants related to the plant, soil, ionic nutrient or speeds of bioprocesses etc. These kinds of data can be obtained by estimation or fitting.
- Staring values like V_0, K_0, D_0, etc. These kinds of data can be gained by e.g. soil survey.
- Other kinds of data such as the growth of biomass dB_t defined by

$$dB_t := \max\left\{ \sum_{\text{for all populations } X} (X_t - X_{t-1}),\ 0 \right\},$$

organic matter $D_{biom,t}$ developed in soil defined by

$$D_{biom,t} = \left| \min\left\{ \sum_{\text{for all populations } X} (X_t - X_{t-1}),\ 0 \right\} \right|$$

etc. that are the outputs of the food web model and inputs of the nutrient-in-soil model, on the other hand, the available nutrient in soil $K_{X,t}$ that is the output of the nutrient-in-soil model and the input of the food web model. It is realized such that one step is taken by the nutrient-in-soil model, its output would be input into the food web model, one step is taken by which right after. Having the output of the food web model, the nutrient-in-soil model can be started again.

A case study for the population dynamical model.

Simulated results based on daily average temperature and precipitation data measured in 1980, Debrecen, Hungary

The models described above was tested with real temperature and precipitation data together with fictious but real proportional starting values K_0, V_0, S_0, N_0, $G_{1,0}$, $G_{2,0}$, $M_{1,0}$, $M_{2,0}$, P_0, and R_0 . The parameters of the activity terms as well as the coefficients a_{ij} and the constant K_X were set such that they can demonstrate the different temperature sensitivity and some other properties of the different populations. In *Fig. 3*, it can be seen that for the different populations, the advantageous effect of activity term $R_X > 0$ appears at different points of time in spring and, furthermore, that at about the 220th day of the year, there was a period with extremely high temperature and no precipitation, which was more or less impeding for every population.

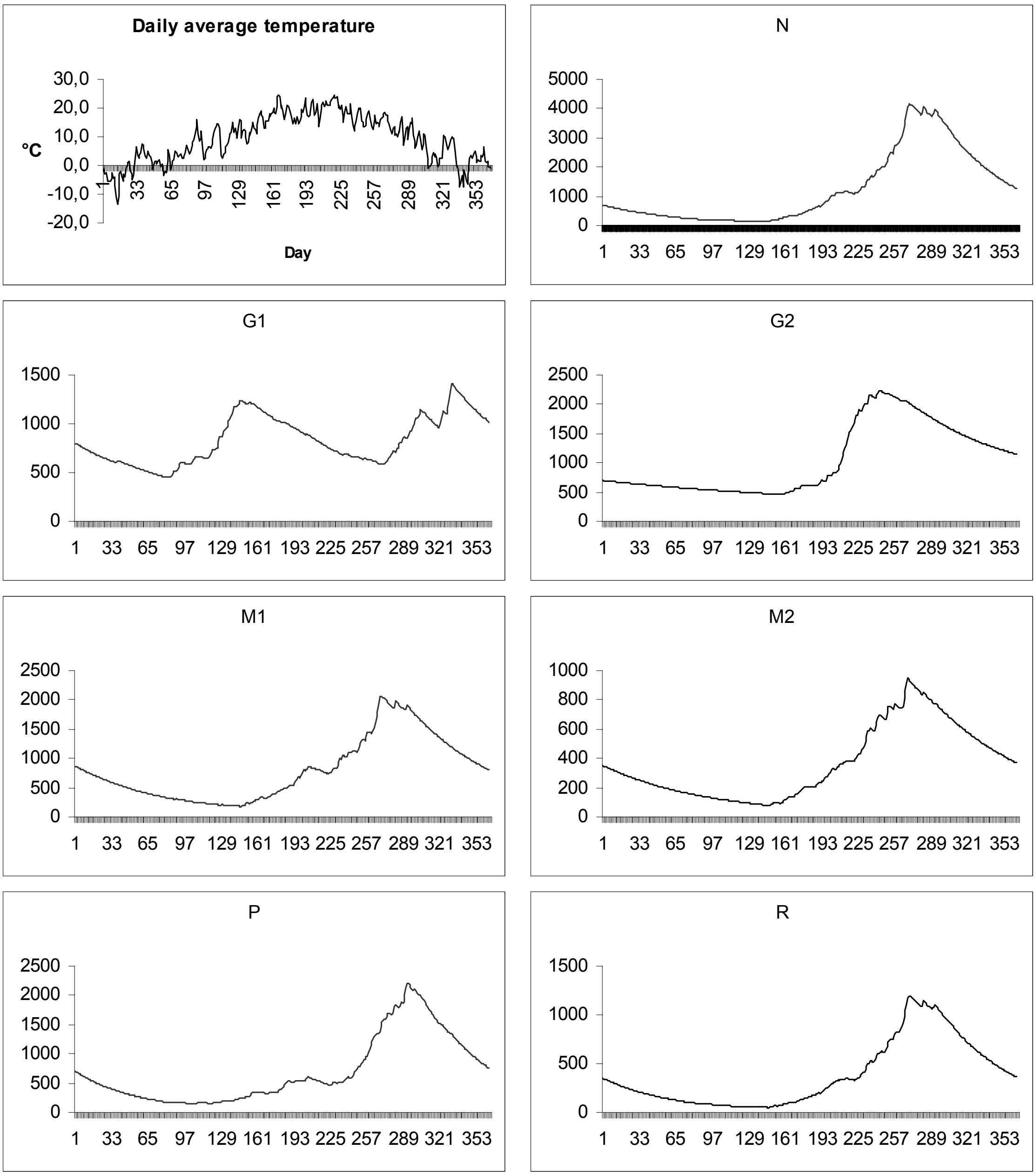


Figure 5. *Biomass change of cultivated plant N, weeds G_1 and G_2, monophagous M_1 and M_2 and polyphagous P, as well as predator R; a simulated result based on the daily average temperature measured in 1980, Debrecen, Hungary.*

Compare temperature data with biomass data of the different populations in *Fig. 5.* (For the activity terms see *Figs. 2* and *3*.)

The biomass of cultivated plant *N* (from the last year) had been slowly decreasing till spring, then after having reached its optimal daily average temperature (in June) it was acceleratingly increasing. The growth came to a point of standstill at about the 220th day and after it reached its extended maximal rate, it was quickly decreasing.

Weed G_1 prefers low temperature. It started to increase quite early, rather intensively. In the middle of summer it was decreasing because of high temperature. After the average daily temparature fell below 15 °C, it increased again and started, again, to decrease quite late in autumn. In its graph, one can see the effect of fluctuating temperature in late autumn.

Weed G_2 prefers higher temperature. It started to grow very quickly earlier than cultivated plant *N*. After the 250th day it was decreasing quite fast but the speed of decrease was lower and lower.

The activity term of monophagous M_1 is similar to the one of its nutriant, thus their biomass graphs are similar, too, just with a short time shift.

Monophagous M_2 consumes the weed that prefers higher temperature, though its optimal temperature is slightly lower. Therefore, it started to increase a bit later and slowlier than weed G_1 and the same is for its biomass decrease.

Polyphagous *P* consumed from the early weed very few as it dislikes low temperature, however, it started to grow slowly. The decrease of the early weed left its mark on the graph of the pest. As the biomass of the cultivated plant started to increase quickly, the one of the polyphagous followed it and it started to decrease just after the cultivated plant's biomass subsided.

Predator *R* can choose from three kinds of nutrient. It started to grow at about the 150th day at a stable rate, it reached its extended maximum with the marks of fluctuating temperature in late autumn/early winter which is followed by a very quick decrease.

Simulated results based on the daily average temperature and precipitation data measured in 1980-84, Debrecen, Hungary

In *Fig. 1*, the seasonality relative to the populations can be seen well. While year 1983 was the most favourable for the cultivated plant *N*, yield in 1980 was quite poor (*Fig. 6*).

The effect of the mild winter in 1981–82 is considerable on the graph of the early weed G_1.

Besides seasonality, it can be seen in the graph of the weed G_2, which prefers warm weather, that the different conditions in different years imply graphs with different maximum, slope and convexity properties.

Notice the effect of a warmer (1981) and a cooler (1984) summer on monophagous G_1 that prefers warm weather.

The graph of monophagous G_2 that consumes the less sensitive weed seems to be the most stabile one.

Similarly to weed G_1, polyphagous *P* prefers cool weather, thus years 1980–81 were more favourable than the ones after.

The graph of predator *R* can be said to be the less changeable.

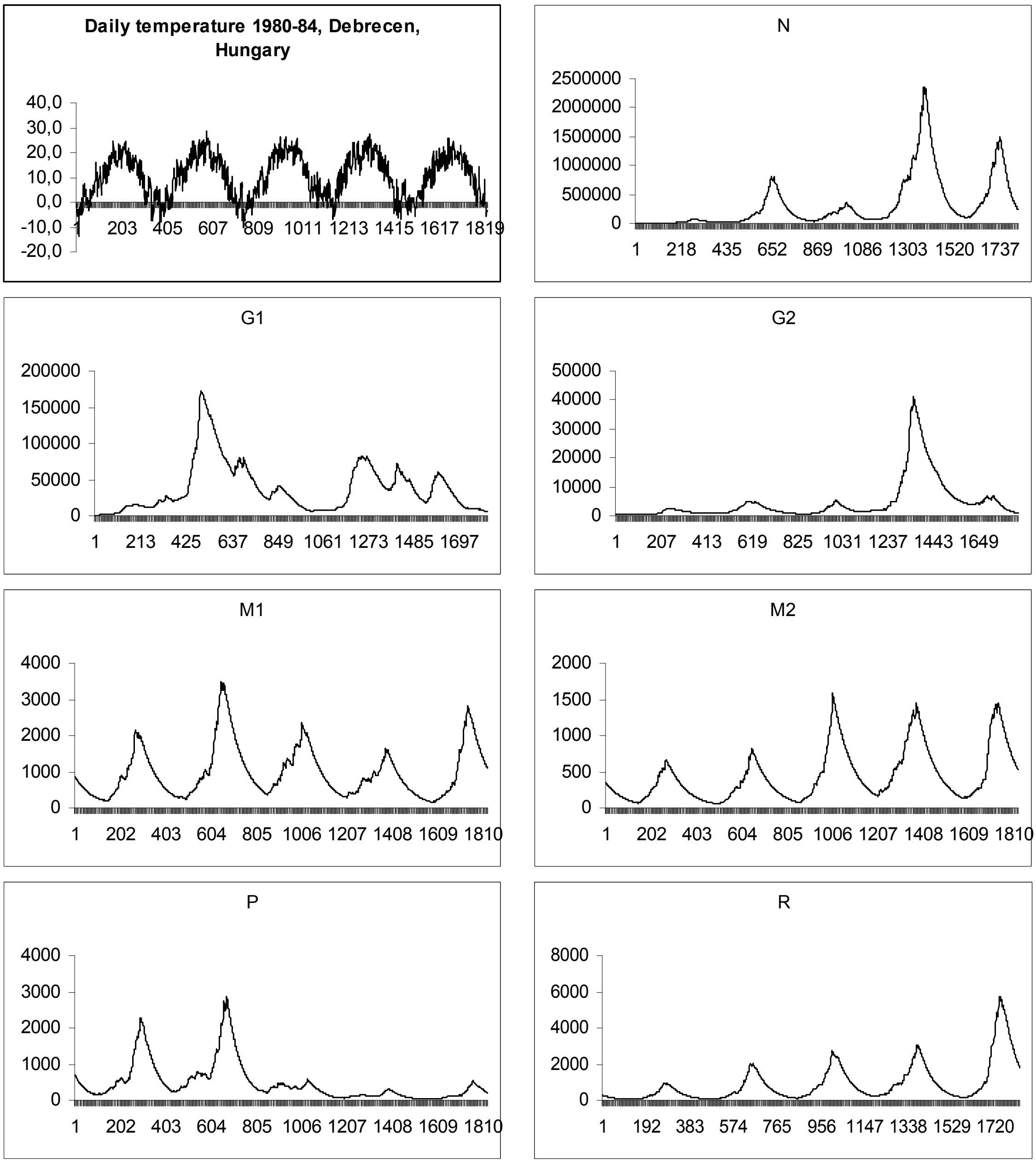


Figure 6. *Five-year (1980–84) simulation results of the food web model for each element of the web.*

Phenology model

Applying the above models, the obvious question is how the number of individuals can be derived from a given amount of biomass. More exactly, if the phenological phases of the population, together with their biological properties, are known, how can one define the number of the individuals in the phases at a given point of time? The following model solves this problem.

Recall the idea mentioned in the section activity term $R_{X,t}$ was introduced, namely, that the agro-ecological process is not defined by temperature, itself, but by the so-called 'activity function', since the effect of the same temperature on the individuals is very different in different phenological phases. Thus, instead of cumulative temperature, we introduce cumulative activity

$$\underset{t \geq t_{0,X}}{cum}\, R_{X,t}^{Ph} = \sum_{i=t_{0,X}}^{t} R_{X,i}^{Ph} \cdot SW_{X,i}^{Ph}$$

with the help of which the entering dates of the phenological phases can be defined. Cumulative activity $\underset{t \geq t_{0,X}}{cum}\, R_{X,t}^{Ph}$ cumulates the values of activity terms $R_{X,t}^{Ph}$ of individual *X* from a starting point of time $t_{0,X}$ relative to *X* (let us say 'the first spring point of *X*'), in the case phase *Ph* holds, where *Ph* denotes one of E_i (for the egg state of the i^{th} generation,
$i = 1, 2, \dots, g_X$), L_{ji} (for the j^{th} larva state of the i^{th} generation, $j = 1, 2, \dots, l_X$) and I_i (for the imago state of the i^{th} generation).

To express the phase *Ph* holds we introduce function $SW_{X,t}^{Ph}$ for a population of *X* in a phenological phase *Ph* at a point of time *t*:

$$SW_{X,t}^{Ph} := \begin{cases} 0 & if \quad t = 0 \quad and \quad Ph > E_1 \\ \prod\limits_{Ph > E_1} \left(1 - SW_{X,t}^{Ph}\right) & if \quad Ph = E_1 \\ \min\left[\max\left\{\left(CumR_{X,t} - T_{m,X}^{L_1}\right), 0\right\}, 1\right] \prod\limits_{Ph > L_1} \left(1 - SW_{X,t}^{Ph}\right) & if \quad t > 0 \quad and \quad Ph = L_{11} \\ \min\left\{\min\left[\max\left\{\left(m_{X,t-1}^{Ph} - k_X^{Ph}\, \overline{m}_X^{Ph}\right), 0\right\}, 1\right] + \min\left[\max\left\{\left(CumR_{X,t}^{Ph} - T_{m,X}^{Ph_1}\right), 0\right\}, 1\right], 1\right\} * & \\ \quad * \prod\limits_{Ph > L_1} \left(1 - SW_{X,t}^{Ph}\right) & if \quad t > 0 \quad and \quad Ph > L_{11} \end{cases},$$

where

- $T_{m,X}^{Ph}$ denotes the minimum of cumulated activity of *X* that is necessary to enter phase *Ph*;
- $m_{X,t}^{Ph}$ denotes the current average mass of an individual *X* in its state in phase *Ph*;
- $\overline{m}_X^{Ph}$ denotes the average mass of an individual *X* at entering phase *Ph*;
- g_X and l_X denote the numbers of generations and larva phases related to *X*, respectively;

- k_X^{Ph} is a proportion constant $\overline{m}_X^{Ph}$ is multiplied by which in order to obtain the maximum mass of an individual *X* in phase *Ph* and, finally,
- relation $>$ for phases means „later phase than".

Function $SW_{X,t}^{Ph}$ equals to 1 if and only if the population of *X* has more than zero number of individuals in phase *Ph* at a given point of time *t*, and equals to 0, else. The change of the values of function $SW_{X,t}^{Ph}$

- from 0 to 1 is caused by the fact cumulated activity has reached the minimum that is necessary for an individual *X* to enter phase *Ph* and/or by the one the mass of individual *X* has reached the maximum an individual in phase *Ph* can even have;
- from 1 to 0 is caused by the fact the next phase has been entered.

With the help of function $SW_{X,t}^{Ph}$, a corrected food web biomass model can be created as follows:

$$X_{t+1}^{corr} = X_{t+1}\prod_{i=1}^{g}(1-SW_{X,t}^{E_i})(1-SW_{X,t}^{I_i}) + W(X_t)\sum_{i=1}^{g}SW_{X,t}^{E_i} + I(X_t)\sum_{i=1}^{g}SW_{X,t}^{I_i} - LS_X^{Ph}\chi_{X,t}^{Ph}.$$

The corrected food web biomass model above satisfies the following properties:

- In winter there is no growth; in this case, function *W* of X_t expresses the biomass-waste caused by winter weather.
- During the imago phase consumption is suspended; in this case, function *I* is the same as X_{t+1} of the original food web biomass model, except term F_X, which is now identically equal to 1.
- There is a loss in biomass at entering a new phase; function LS_X^{Ph} of X_t denotes the amount of it, with characteristic function $\chi_{X,t}^{Ph}$, that is equal to 1 if and only if *t* is the point of time phase *Ph* entered, and is equal to zero, else.

It is obvious that there must be a point of time a phase is entered first, and, at the same time, there must be another one at which the process of metamorphosis is finished for the whole population. This means that function $SW_{X,t}^{Ph}$ that 'switches' on/off the phases has to be smoothed as follows:

$$SSW_{X,t}^{E_1} = SW_{X,t}^{E_1} + p_{X,t}^{L_1},$$

$$SSW_{X,t}^{Ph} = SW_{X,t}^{Ph} * (1 - p_{X,t}^{Ph}) + p_{X,t}^{Ph+1},$$

where

$$p_{X,t}^{L_1} = \left\{1 - \min\left[\max\left(\frac{cumR_{X,t}^{L_1} - MT1_X^{L_1}}{MT2_X^{L_1} - MT1_X^{L_1}}, 0\right), 1\right]\right\} \cdot SW_{X,t}^{L_1},$$

$$p_{X,t}^{Ph} = \left\{1 - \min\left[\max\left(\frac{m_{X,t}^{Ph} - c1_X^{Ph}\cdot \overline{m}_X^{Ph}}{(c2_X^{Ph} - c1_X^{Ph})\overline{m}_X^{Ph}}, 0\right), 1\right]\right\} \cdot SW_{X,t}^{Ph} \quad \text{for every } Ph > L_1.$$

This means that $p_{X,t}^{Ph}$ is equal to zero until phase *Ph* is entered. In the case the minimal value of activity, that is necessary to enter phase *Ph* has been reached, it monotonously decreases from 1 to zero. At the point of time at which the whole process of metamorphosis is finished, $p_{X,t}^{Ph}$ becomes to be equal to, and also keeps to be, zero.

It is easy to see that

$$\sum_{for\ all\ phases} SSW_{X,t}^{Ph} = 1.$$

Finally, the numbers of individuals in all phases will be calculated as follows. Set out from an estimated starting value of the number of individuals at a starting point of time t_0 in phase E_1:

$$NoI_{X,t_0}^{E_1} = \frac{X_{t_0}}{\overline{m}_X^{E_1}},$$

from which the numbers of individuals of later phases can be derived if $Ph \neq E_i$:

$$NoI_{X,t}^{Ph} = NoI_{X,t_0}^{Ph-1} p_{X,t}^{Ph} + \left[\min\left(\frac{X_t}{w_X^{Ph} \cdot \overline{m}_X^{Ph}}, NoI_{X,t-1}^{Ph} \right) \chi_{X,t}^{s} + \min\left(\frac{X_t}{\overline{m}_X^{Ph}}, NoI_{X,t-1}^{Ph} \right) (1 - \chi_{X,t}^{s}) \right] SSW_{X,t}^{Ph}$$

where $0 \leq \chi_{X,t}^{s} \leq 1$ denotes a function to express the rate of starving of a population of *X* at a point of time *t*, calculated with the help of

- the available amount of nutrient (denoted by $NU_{X,t}^{av}$), as well as
- the necessary amount of nutrient (denoted by $NU_{X,t}^{ne}$) as follows:

$$\chi_{X,t}^{s} = \min\left(\frac{NU_{X,t}^{av}}{NU_{X,t}^{ne}}, 1 \right).$$

Constant $0 < w_X^{Ph} < 1$ denotes the rate of maximum amount of weight that can be loosed without dying.

This formula is suitable to express the following properties of the populations:

- The sum of the numbers of individuals does not increase in any phase except if $Ph = E_i$ for $i = 1,2,...,g_X$.
- During the metamorphosis from a phase *Ph* into the next one, denoted by *Ph*+1, the number of individuals in phase *Ph* is decreasing tending to 0, while the number of individuals in phase *Ph*+1 is increasing.
- The decrease of the biomass of *X* can be caused, on the one hand, by the fact that in case nutrient is short the individuals are losing their weights, and, on the other hand, by the one the population is consumed by another population. The number of individuals, in the first case, does not change, while, in the latter case, it is decreasing.

In case nutrient is shorter than it is necessary for the individuals even to keep being in existence, the number of individuals is decreasing because of starvation.

Note that the loss of biomass during the metamorphoses has been yet subtracted from the biomass of *X*.

The current average mass of an individual *X* in a phase *Ph* at a point of time *t* can be obtained as:

$$m_{X,t}^{Ph} = \begin{cases} m_{X,t}^{Ph} = \dfrac{X_t}{NoI_{X,t}^{Ph}} & \textit{if} \;\; Ph \neq E_i \;\; \textit{and} \;\; Ph \neq I_i \\ m_{X,t}^{L_{ji}} & \textit{if} \;\; Ph = I_i \;,\; j = l_X \\ \overline{m}_X^{E} & \textit{else} \end{cases} ,$$

where *E* is belonging to the same generation as *Ph*. Therefore, the number of eggs of a later generation than the first one is

$$NoI_{X,t}^{E_i} = \frac{dB_X^{L_{ji}}}{\overline{m}_X^{E_i}} \qquad (i = 2,3,\ldots,g_X \,,\, j = l_X),$$

that is to say, the number of eggs can be derived from the whole biomass growth $dB_X^{L_{ji}}$ during the very last phase just before imago phase, which is, practically, equal to the biomass of eggs.

The spatial extension model

In what follows, a simplified spatial extension model of the above agro-ecosystem model, with the help of which a space specific complex ecological model can be obtained, will be discussed. The modules of the spatial system are strongly connected to, and dependent from each other, however, each of them works independently, too.

The model introduced in this paper describes just an only prey–predator or plant–pest relation and is based on two assumptions:

- Populations have a great number of individuals (hypothesis of abundance).
- Individuals belonging to the same populations are identical in every dynamically relevant aspects (hypothesis of uniformity).

There is no need to consider the third assumption known in population dynamics, namely the hypothesis of ergodicity. Every individual perceives the same environment around itself. This statement is true exclusively in the homogeneous parts inside in an inhomogeneous piece of field.

An inhomogeneous piece of field was divided into 5×5 parcels and it was considered to be separately homogeneous. In all the parcels, the number of plants (*Z*) and the number of pests (*H*) are known. Simulate the parcels with a neighbour model. The quantities of the elements of the food chain in the different parcels are varying dynamically in time.

At the $(t+1)^{\text{th}}$ point of time, the quantity of pests in cell *i* depends on the quantity of the nutrient available there and the number of the pests invading from the neighbourhood. There are individuals of two kinds of pests represented in the model, the first one is attacking frontally (locally), the second one attacks globally.

$$H_{i,t+1} = \left\{ H_i \cdot F_i^{w} + \sum_j H_j \cdot (1 - F_j) \cdot Q_{ij} \cdot W_{ij} \right\}_t ,$$

where:

$$F_i = \begin{cases} \dfrac{1}{1+\dfrac{a\cdot H_i + b}{Z_i + c}} & \text{if } \dfrac{a\cdot H_i + b}{Z_i + c} \geq 1 \\ 1 & \text{else} \end{cases} .$$

- H_i denotes the quantity of the pests in the i^{th} parcel (kg),
- Z_i expresses the quantity of the plants in the i^{th} parcel (kg),
- coefficient a sets the proportion $\frac{a\cdot H_i + b}{Z_i + c}$ such that $F_i = 1$ if the quantity of the plant is just enough for the pest. If the situation is unfavourable, $F_i < 1$, while in case $F_i \ll 1$, all the pests intend to depart from the parcel. Setting coefficient a is of great importance from the aspect of the model, because this factor determines principally whether a pest should abandon the parcel or the parcel is considered as suitable or even ideal to remain there.
- Parameters b and c are to avoid numerical errors during the calculations. They denote the quantities of the so-called 'surviving individuals' that are staying for a (short) while in cells without suitable living circumstances. It is obvious that $b \ll H_i$ and $c \ll Z_i/a$.
- w is a speed factor of compulsion to emigrate that sets the strength of will to leave a cell. With the help of this factor the pests can be characterized according to the differences in their ways of emigration. For example, some of them depart very quickly if the conditions change to a bit unfavourable, while others would abandon the territory later, not so rapidly.

If

$$\frac{a\cdot H_i + b}{Z_i + c} < 1,$$

then function F_i takes the value of 1. In this case the quantity of the plants is sufficient for the pests, the pests do not intend to depart from the territory. The quantity of the pests that are going to stay in the next cycle is expressed by $H_{i,t} \cdot F_i^{\,w}$. It is obvious, that the greater the proportion

$$\frac{a\cdot H_i + b}{Z_i + c}$$

is, the closer to zero function $F_{i,t}$ is, which means that some of the pests might be going to stay in the parcel, but more of them try to abandon. If the territory is ideal ($F_i = 1$), they would not want to leave the parcel. By the sum

$$\sum_j H_j \cdot (1 - F_i^{\,w}) \cdot Q_{ij} \cdot W_{ij}$$

it can be calculated, how many pests arrive from the rest of the parcels j to the observed parcel i, where

$$Q_{ij} = \left(\frac{1}{(x_i - x_j)^2 + (y_i - y_j)^2} \right)^v .$$

- The coordinates of the examined parcel are denoted by (x_i , y_i).
- The coordinates of that particular parcel, from where the pests are arriving are denoted by (x_j , y_j).
- The rate of attacking ability that describes how far a pest can go is denoted by v. It was necessary to build this factor into the model, because the measure of infection depends greatly on the distance of the parcels. In the case $v \gg 1$, the attacker can be considered as the only one attacking frontally. If $v \cong 0$, the pest can appear everywhere sooner or later.

Finally,

$$W_{ij} = \frac{\dfrac{(Z_i + c)^2}{a \cdot H_i + c}}{\sum_j \dfrac{(Z_j + c)^2}{a \cdot H_{ji} + c}} .$$

Factor W_{ij} shows how „desirable" a given parcel is. If W_{ij} is great, a pest would more likely go towards the parcel. It is possible, that a parcel is highly desirable, but it is too far, in this case the pests are going to choose a less favourable, but closer parcel.

A case study for the spatial model

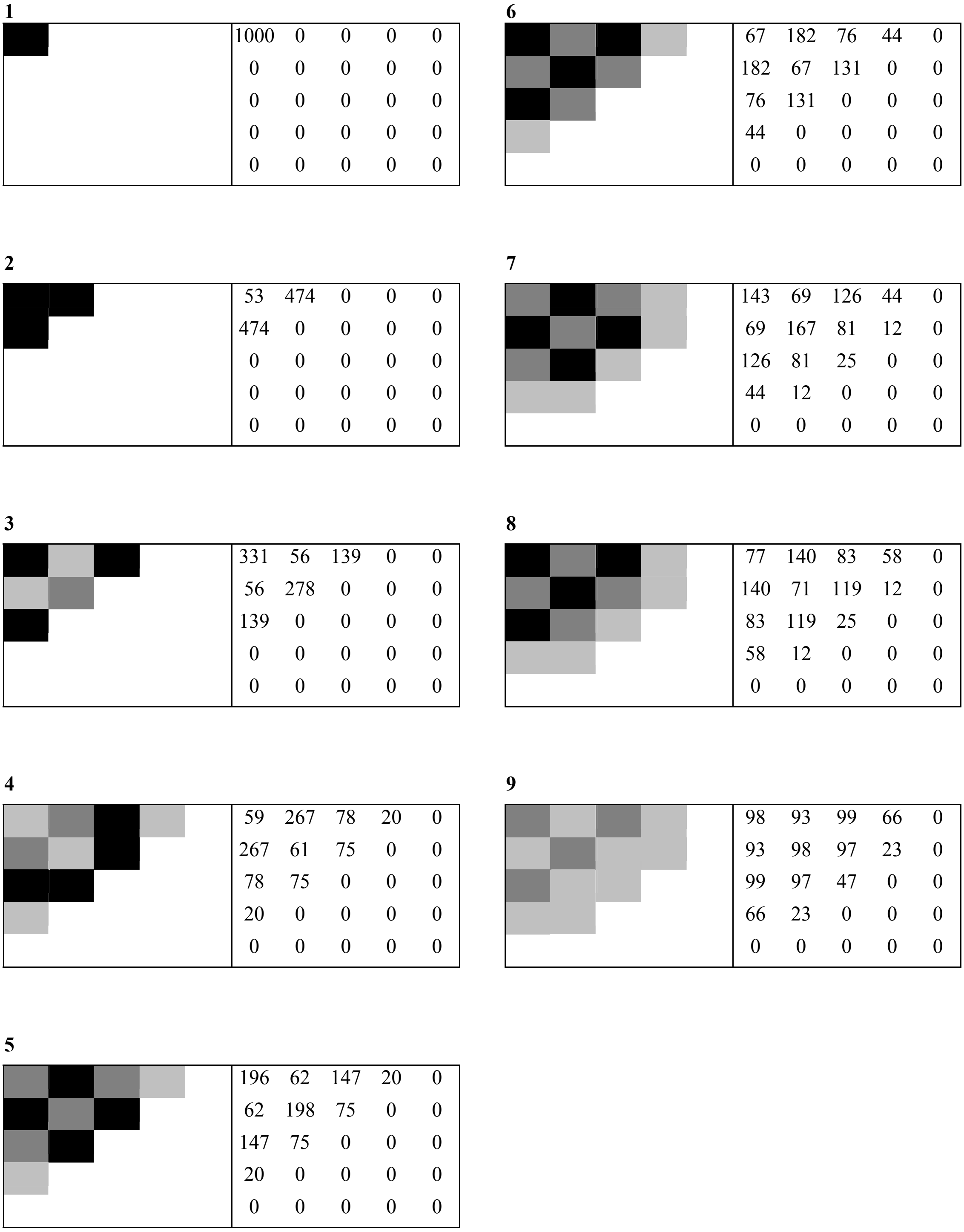
A very simple case study, in which there are completely the same quantities of available nutrient in every parcel of the 5×5 field, is demonstrated as follows. In one of the corner parcels, there appear some pests. This sample is set for a pest with a medium emigration ability. The tables below show the changes till a stable situation is set in.

In *Fig. 7* a spreading process can be seen, where 1000 pests appeared in the upper left corner. All the parcels contained 100 units of plants as aliment. The quantities of the pests are shown on the left side, graphically, on the right side, numerically. It can be seen, that the pests moved every time in the direction with the more ideal (greater) proportion of plant nutrients per pests. In the current situation the value of a is set to 1. The process of spreading will continue until the value of function F_i reaches 1, so the proportion

$$\frac{a \cdot H_i + b}{Z_i + c}$$

falls below 1.

This model has many possibilities of progress in it. Not only the plant aliment but also the simultaneous presence of more pests and plants can be described. Even the effects of the relief can be built into this model.



1

1000	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0

2

53	474	0	0	0
474	0	0	0	0
0	0	0	0	0
0	0	0	0	0
0	0	0	0	0

3

331	56	139	0	0
56	278	0	0	0
139	0	0	0	0
0	0	0	0	0
0	0	0	0	0

4

59	267	78	20	0
267	61	75	0	0
78	75	0	0	0
20	0	0	0	0
0	0	0	0	0

5

196	62	147	20	0
62	198	75	0	0
147	75	0	0	0
20	0	0	0	0
0	0	0	0	0

6

67	182	76	44	0
182	67	131	0	0
76	131	0	0	0
44	0	0	0	0
0	0	0	0	0

7

143	69	126	44	0
69	167	81	12	0
126	81	25	0	0
44	12	0	0	0
0	0	0	0	0

8

77	140	83	58	0
140	71	119	12	0
83	119	25	0	0
58	12	0	0	0
0	0	0	0	0

9

98	93	99	66	0
93	98	97	23	0
99	97	47	0	0
66	23	0	0	0
0	0	0	0	0

Figure 7. *Temporal-spatial quantity of pests in dates 1–9.*

Application of the state-planes

The above mentioned spatio-temporal simulation models offer new possibilities to use the multivariate state-planes. Executing the ecosystem food web model for one year, we took out data of every tenth day to obtain the reference database and to make the indirect ordination. For a simple visualisation of the state-plane we can use Excel diagrams. For a more detailed representation and further analysis of the objects (places / dates) and other related information in many point of views the use of a GIS program is recommendable. In the followings we demonstrate two case studies, which simulate the temporal changes of different parcels in an inhomogeneous field.

The effects of different nutrient amounts

The amount of the available nutrients can significantly influence the states of an agro-ecosystem. In *Fig. 8*, we can examine it in a simulated situation. The simulation shows the results of parcels with different available nutrients at the same period in spring and at the beginning of summer. The moderate and high nutrient levels come from an additional nutrient dosage after 15 days of the simulation, so the three trajectories have the same origin.

In the figure we can see that the trajectories more and more differ from each other. As the nutrient amount is increasing, the trajectories go to the left and down. We know from other results that this area means the better conditions for the cultivated plant. The observed changes in the states help the impact assessment of fertilizing.

The effect of different plant protection methods

Similarly to the fertilizing the different plant protection methods can be considered as agrotechnical treatments. In this case we simulated the use of pesticides decreasing the density of the affected populations on a given day. All other parameters kept their values. M1 means a selective insect control against a monophagous pest, the other treatment was a general zoocide (*Fig. 9*). In this case the changes are not continuous as in the former example, steps from a point to the other can be observed in accordance with our expectation.The results change in the same direction, but with different rates. Of course, the general zoocide, which effects all the four insect populations, proved to be most drastic, compared with the original state. In both examples we can observe that the trajectories are similar to a pipe. This shape comes from the seasonal dynamics (Hufnagel and Gaál [38]), which proved to be a very strong effect.

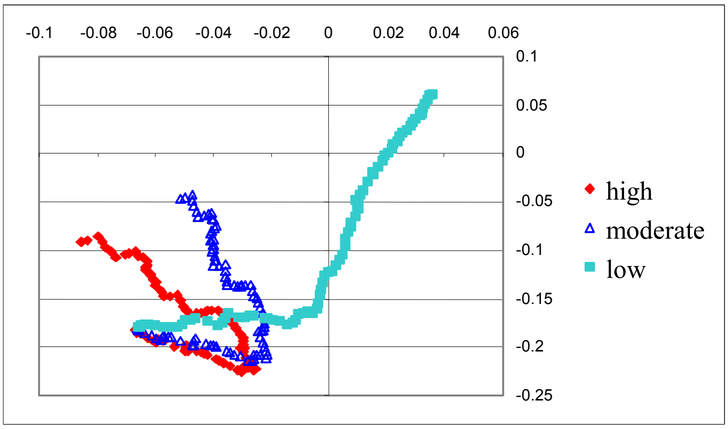


Figure 8. *The effects of different nutrient amounts.*

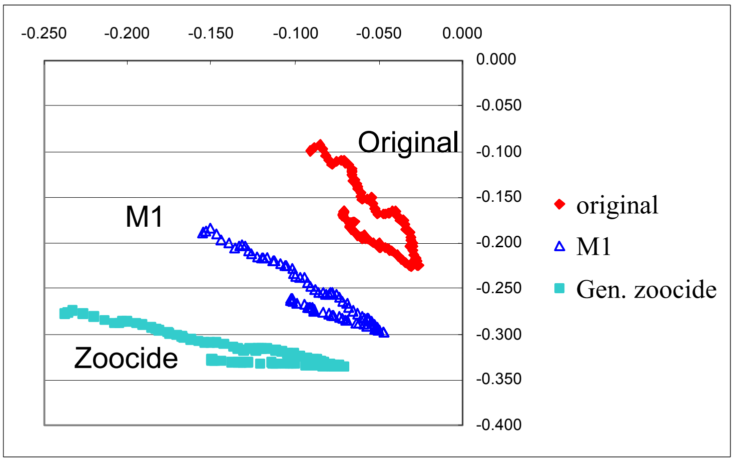


Figure 9. *The effect of different plant protection methods*

Discussion

(1) During the simulation of the food web model the effects of some extremal events were examined, as well, such as the extinction of a population that might cause the extinction of the monophagous that consumes it. Our further plans are the surveys of the exhaustion of soil, the manual intervention like fertilization, plant protection, watering, ploughing, sowing, harvesting (e.g. in Hufnagel and Gaál [38]), the long-term time series the risk and stability analysis of the above effects, the effect of extreme weather conditions and global change. The models are intended to be generalized for highly complex food web systems with great volumen populations and to extend and validate them for special food web systems.

(2) The phenology model that was introduced above was created originally with the following aims:

- To switch on/off certain elements of the food web model [53] that describes the biomass dynamics of populations in an ecosystem. In this way, the seasonal changes of both biotic and abiotic interactions of the examined individual can be followed more exactly.
- To convert the measure of biomass for the number of individuals. In this way, the reasons of biomass change can be seen well.
- Above all, a methodical development of the general model was intended to give through an example for pest populations. The model can be embedded in simulation models with discrete difference equations. Similar models in literature have probably not yet been appeared.

The phenology model can be applied in studies of phenological events of pests even independently of the food web model. In addition to in modelling ecosystems, it is expected to be applied in plant protection prognostics as well to improve the phenology model, further investigations are planned, such as:

- a stochastic generalization,
- a spatial generalization [29, 30, 73],
- an application for pest populations with different phenologies,
- a validation and fitting for real data,

- an investigation of the validated model for quite different weather conditions,
- a study of the effects of extreme weather conditions and global change.

The systems presented in this paper are used for modelling the spatio-temporal patterns of agricultural ecosystems. The joint application of the simulation models and the state-planes could help us to survey the effects of the ecological and agrotechnical conditions in the same system. If we can fit our model to real field monitoring data, too, a wider range of interpretations and conclusions will be obtained. In this case the reference database, itself, should contain both real and simulated data that can generalize the application possibilities of the state-plane systems.

Based on the case studies, our systems seem to be suitable to solve the problems mentioned in the introduction, so the systems are still under development.

Acknowledgements. We would like to express our thanks to Professor Zs. Harnos for supporting our work at Szent István University, Department of Mathematcs and Informatics.

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SENSITIVITY OF 4M MAIZE MODEL TO THE INACCURACY OF WEATHER AND SOIL INPUT DATA

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(Received 14th May 2003; accepted 26th June 2003)

Abstract. The accuracy of a crop model is judged mostly by how precise it is in estimating the production. The preciseness of a crop model is determined on one hand by the authenticity of the algorithms describing the processes of the real world, while on the other hand by the quality of its input data. The goal of this study was to test how sensitive crop models are to errors occurring in the measurement of key weather and soil inputs. The key weather and soil related input data for most crop models are air temperature, solar radiation, precipitation, saturated water content, drained upper limit and wilting point. The level of error in air temperature, radiation, and precipitation measurements were reported to be ±0.2 ^{o}C, ±2% and ±3% respectively by the Hungarian Meteorological Service. An other study reported 0.008 cm^3/cm^3 level of error in determining the drained upper limit. The question we asked was: 'To what extent do the yield and biomass change due to this level of inaccuracies in weather and soil inputs?' The uncertainty caused by the errors of the measured weather elements was found to be 4.7 and 6.9% for the calculated biomass and yield, respectively. The soil parameter errors caused smaller uncertainties in the simulation results. On an average we got 2.3% uncertainty for the biomass and 3.2% uncertainty for the yield. The effect of weather and soil data uncertainties can both strengthen and weaken each other. In certain cases the uncertainty of the simulation could be over 15% due to errors in weather and soil data.

Keywords: *crop modelling, error of measurement, uncertainty of simulation*

Introduction

For a long time models have played a very important role in the scientific research. The primary purpose of crop models is to describe the processes of the very complex atmosphere–soil–plants system using mathematical tools and to simulate them with the help of computers. The ultimate aim of using crop models however is to answer such questions that otherwise could only be answered by carrying out expensive and time-consuming experiments.

It was only in the 1970's that developments in information technology enabled scientists to create the first crop model software using the accumulated scientific knowledge. Since then crop models have been used in numerous educational and scientific projects.

In the year 2001 a new workshop, called 4M, was set up within the Hungarian Soil Science Society with the specific purpose of creating an easy to use package for modelling cropping systems. The 4M package was developed by Hungarian scientists from various institutes in the country. The CERES model was chosen to be a starting point for this project, since it has an open source code and several studies have proved its competence in describing the soil–plant–atmosphere system [3, 4, 5]. 4M is continuously being developed. During the past one and a half years more than ten new subroutines have been incorporated into the model, for instance a new water balance module and a simple weather generator.

The accuracy of a crop model is judged mostly by how precise it is in estimating the production. It is especially significant in cases when crop models are used in decision support. The preciseness of a crop model is determined on one hand by the authenticity of the algorithms describing the processes of the real world, while, on the other, hand by the quality of its input data. Even the 'perfect' model would not be able to simulate the real processes precisely if inaccurate input data were fed into it.

The goal of this study was to test how sensitive crop models are to errors occurring in the measurement of key weather and soil inputs. The key weather and soil related input data for most crop models are air temperature, solar radiation, precipitation, saturated water content, drained upper limit and wilting point. For the test we needed a model, quality weather and soil input datasets, as well as studies on the measurement errors.

Materials and methods

4M crop model [2] was used for the test. Since the basis of 4M is the well-known CERES model that was used as a starting point for several other crop models in the world, the result of this test gives relevant information for a wide range of scientists. The effect of inaccuracies of the two input data groups were investigated separately, followed by an examination of some error combinations.

Inaccuracies of weather inputs

The weather input was a carefully selected quality dataset of 20 years (1968–87) from a weather centre near the city of Budapest, Hungary. In the past 10 years MILOS 500 and QLC 50 automated equipments were set up at more then 60 different stations of the Hungarian Meteorological Service. A study on the measurement error of these equipments was published recently [6]. The level of measurement errors of air temperature, radiation, and precipitation are presented in *Table 1.*

Table 1. *Level of error of different weather measurements.*

Data	Level of error
Global radiation	± 2%
Temperature	± 0.2 ^{o}C
Precipitation	± 3%

The question we asked was: 'To what extent do the yield and biomass change due to this level of inaccuracy in weather input?'. For setting a reference point, we supposed that the measured dataset ('base dataset' in the following) had no measurement error. Twenty-six additional, 20 year-long weather datasets were created by modifying the components of the base dataset with the corresponding level of errors (*Table 2*).

For example, one weather dataset was created of which daily global radiation data were 2% higher, temperature and precipitation data were 0.2 ^{o}C and 3% respectively lower than in the base dataset (combination No. 18 in *Table 2*).

***Table 2.** Characteristics of the modified weather datasets (combinations).*

Combination No.	Supposed level of errors with which the daily values of the base dataset were modified during model simulations		
	Global radiation (%)	Temperature (^oC)	Precipitation (%)
1 (base)	0	0	0
2	0	0	+3
3	0	0	-3
4	0	+0.2	0
5	0	+0.2	+3
6	0	+0.2	-3
7	0	-0.2	0
8	0	-0.2	+3
9	0	-0.2	-3
10	+2	0	0
11	+2	0	+3
12	+2	0	-3
13	+2	+0.2	0
14	+2	+0.2	+3
15	+2	+0.2	-3
16	+2	-0.2	0
17	+2	-0.2	+3
18	+2	-0.2	-3
19	-2	0	0
20	-2	0	+3
21	-2	0	-3
22	-2	+0.2	0
23	-2	+0.2	+3
24	-2	+0.2	-3
25	-2	-0.2	0
26	-2	-0.2	+3
27	-2	-0.2	-3

For the required soil inputs, data of a chernozem profile was used that was selected from the database of RISSAC [7, 8]. The genetic parameters of the Pi3978 cultivar (maize) were used as crop specific inputs.

First, the model was run for the 20 years (1968–87) using the base dataset. The calculated biomass and yield outputs were recorded and the results of the following runs were compared to them. Then the model was run with the modified weather datasets. The calculated yearly biomass and yield values were compared to the ones that were obtained by using the base dataset.

Inaccuracies of soil inputs

In a study on in situ measurement of soil hydraulic parameters [1] we have found 0.008 cm^3/cm^3 uncertainty of the drained upper limit of the samples coming from the very same profiles and from the very same horizons. In the present study we used this level of error for modifying the saturated water content, drained upper limit and wilting point values of the base soil input file to create input files that are loaded with ‘measurement error’. Data of the above mentioned chernozem profile was used as a base input file (*Table 3*).

Twenty-six additional soil input files were created by modifying the base dataset. Each modification was applied for all of the horizons of the profile (*Table 4*).

Table 3. *Characteristics of the chernozem profile.*

Horizon	Thickness (cm)	Saturated water content (cm^3/cm^3)	Drained upper limit (cm^3/cm^3)	Wilting point (cm^3/cm^3)
A_p	23	0.442	0.327	0.146
A	20	0.454	0.314	0.135
B	22	0.506	0.295	0.131
BC	15	0.504	0.306	0.131
C	100	0.473	0.282	0.118

Table 4. *Characteristics of the modified soil datasets (combinations).*

Combination No.	Supposed level of errors with which the base dataset were modified for model simulations		
	Saturated water content (cm^3/cm^3)	Drained upper limit (cm^3/cm^3)	Wilting point (cm^3/cm^3)
1	-0.008	-0.008	-0.008
2	-0.008	-0.008	0
3	-0.008	-0.008	+0.008
4	-0.008	0	-0.008
5	-0.008	0	0
6	-0.008	0	+0.008
7	-0.008	+0.008	-0.008
8	-0.008	+0.008	0
9	-0.008	+0.008	+0.008
10	0	-0.008	-0.008
11	0	-0.008	0
12	0	-0.008	+0.008
13	0	0	-0.008
14 (base)	0	0	0
15	0	0	+0.008
16	0	+0.008	-0.008
17	0	+0.008	0
18	0	+0.008	+0.008
19	+0.008	-0.008	-0.008
20	+0.008	-0.008	0
21	+0.008	-0.008	+0.008
22	+0.008	0	-0.008
23	+0.008	0	0
24	+0.008	0	+0.008
25	+0.008	+0.008	-0.008
26	+0.008	+0.008	0
27	+0.008	+0.008	+0.008

The genetic parameters of the Pi3978 cultivar (maize) were used as crop specific inputs. The weather input was the above mentioned quality dataset of 20 years (1968–87) from Budapest, Hungary. First, the model was run using the base soil dataset and then using the modified soil datasets. The model was run for the 20 year-long period with every soil setting. The calculated yearly biomass and yield values were compared to the ones that were obtained by using the base dataset.

Finally we investigated four cases where the worst error combinations were applied both to the weather and the soil data, causing the largest differences (‘extreme’ combinations) compared to the run that used the base weather and soil dataset. The aim was to find out whether the errors of different types of input data strengthen or weaken each other’s effect. We selected two ‘extreme’ weather combinations (*Fig. 4*). Using combination No. 20 we got consistently lower yields than using the base weather dataset, and using combination No. 18 we got consistently higher yields than using the base weather dataset. Similarly we selected two ‘extreme’ soil combinations (*Fig. 8*) with which the model gave consistently lower (No. 21) and higher (No. 25) yields than using the base soil dataset. This resulted in four extra combinations. We compared the model results obtained with these extra combinations to those that were obtained by using the base weather and soil datasets.

Results

Effects of inaccuracies of weather inputs

The differences between the model results obtained by using the base dataset and the modified datasets were calculated for every year and for every combination. Yearly (*Figs. 1–2*) and the overall (for the 20 years) average values (*Figs. 3–4*) of these differences were also calculated.

The simulated yield was more sensitive to errors of the weather measurements than the biomass. If one has no prior knowledge of the weather and of the measurement error, which is usually the case, the expected error/uncertainty of the model results would be 6.0 ± 0.9% ($\alpha = 0.05$) considering the yield, and 3.2 ± 0.3% ($\alpha = 0.05$)

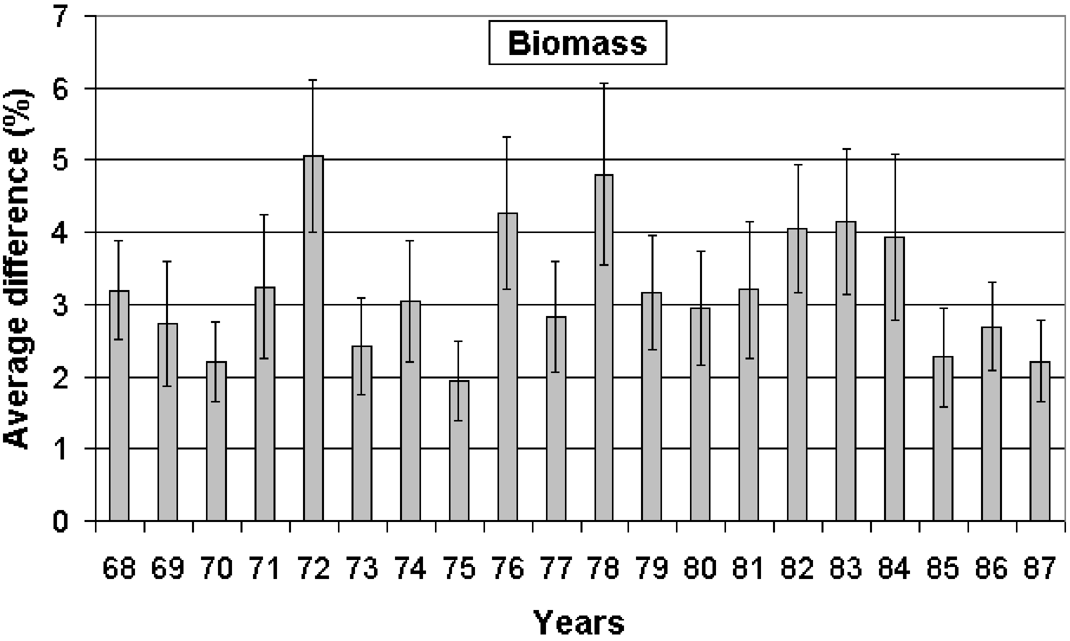

Figure 1. *Yearly averages of the differences between the model results obtained by using the base weather dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.*

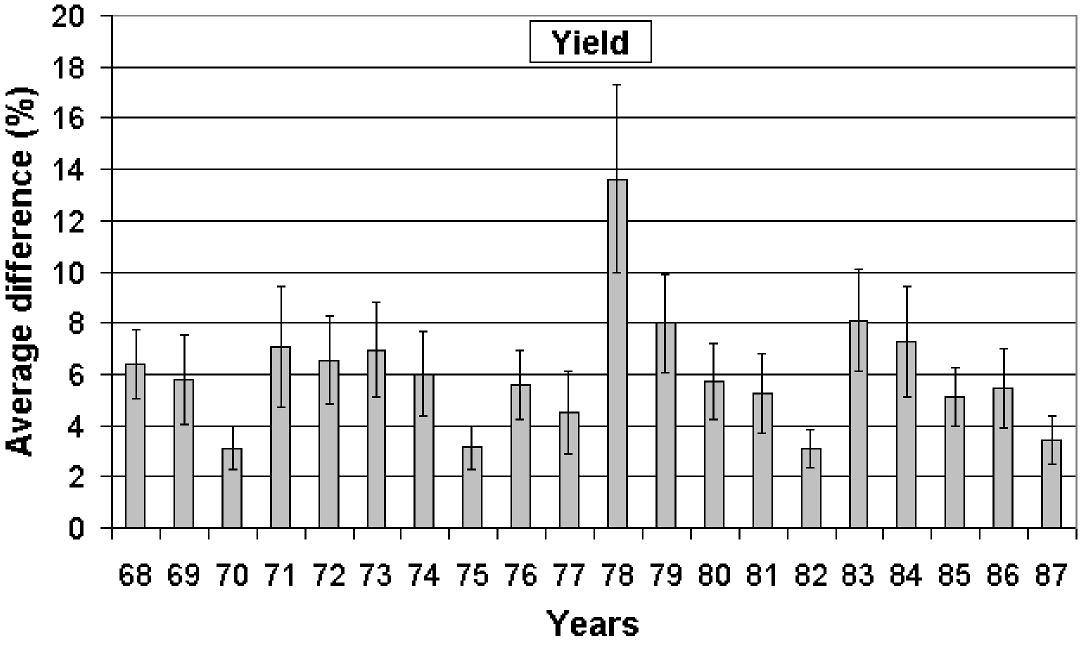

Figure 2. *Yearly averages of the differences between the model results obtained by using the base weather dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.*

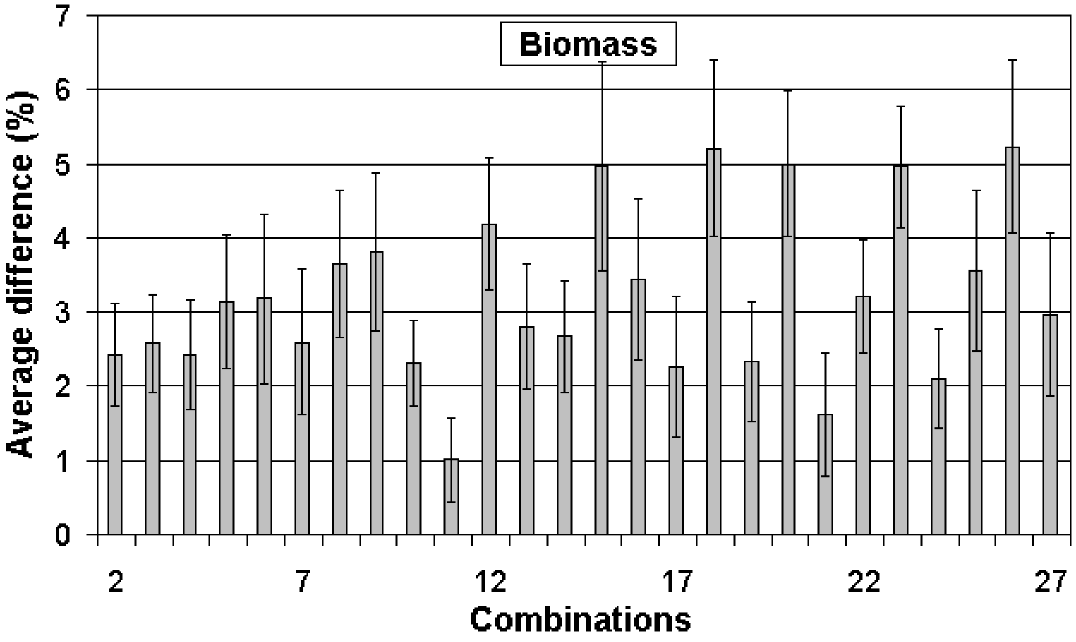

Figure 3. *Average differences (for 20 years) between the model results obtained by using the base weather dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.*

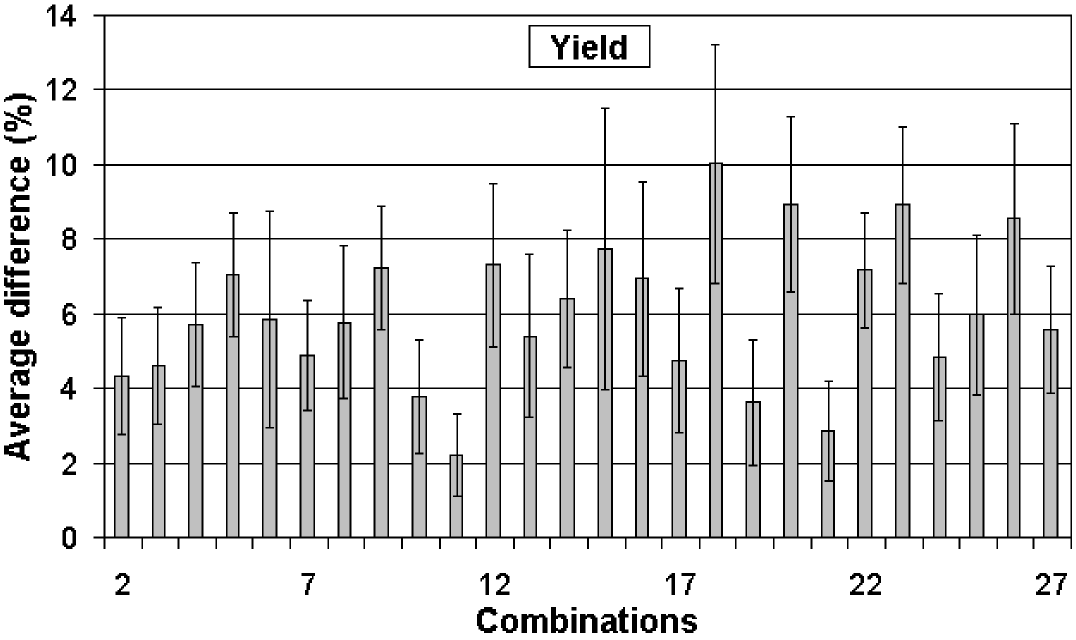

Figure 4. Average differences (for 20 years) between the model results obtained by using the base weather dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.

considering the biomass. For the simulated yield this uncertainty is 4.7 ± 1.2% ($\alpha = 0.05$) and 6.9 ± 1.4% ($\alpha = 0.05$), in high yielding and low yielding years, respectively. For the simulated biomass this uncertainty is 3.1 ± 0.8% ($\alpha = 0.05$) and 3.3 ± 0.4% ($\alpha = 0.05$), in high yielding and low yielding years respectively. The inaccuracy of the calculated yield caused by the errors of the measured weather data is significantly larger in low yielding years than in high yielding years.

There might be years when the expected value of error of the calculated yield is around 10% or even higher (1978, 1979 and 1983 in *Fig. 2*). Furthermore some combinations of measurement errors in certain years could cause more than 20% ‘shift’ in the calculated yield compared to the ones that were obtained by using the ‘errorless’ base dataset (*Table 5*). Even in 20 year average, there was a combination (No. 18) found to cause more than 10% error in the model calculations (*Fig. 4*). This and three other combinations (No. 20, 23 and 26) were found to be quite ‘extreme’. That implies that simultaneous over measuring of the radiation and under measuring of the temperature and of the precipitation (combination No. 18) can cause huge errors in calculating the yield if such weather datasets are used in modelling. If feasible these combinations must be avoided in measuring weather data.

***Table 5.** Largest differences between the calculated yield using the base dataset and a modified one (combination).*

Year	Combination	Difference (%)
1971	6	23.3
1977	20	20.2
1978	18	36.1
1979	15	22.2

Table 6. *Smallest differences (20 year average) between the calculated yield and biomass using the base dataset and a modified one (combination).*

Combination	Difference (%)	
	Biomass	Yield
11	1.0	2.2
19	2.3	3.6
21	1.6	2.8

On the other hand, there are combinations that were found to cause relatively small errors in the calculations in 20 year average (*Table 6*). This means that the combinations – when the radiation and the precipitation are simultaneously over measured (combination No. 11) or under measured (combination No. 21) – cause only very small errors in calculating the biomass or the yield.

Effects of inaccuracies of soil inputs

The differences between the model results obtained by using the base dataset and the modified datasets were calculated for every year and for every combination. Yearly (*Fig. 5–6*) and the overall (for the 20 years) average values (*Fig. 7–8*) of these differences were also calculated.

The simulated yield was more sensitive to errors of the soil parameters than the biomass. The soil parameter errors/uncertainties caused smaller uncertainties in the simulation results than the weather measurement errors. The expected error/uncertainty of the model results would be 3.2 ± 0.6% ($\alpha = 0.05$) considering the yield, and 2.3 ± 0.4% ($\alpha = 0.05$) considering the biomass. For the simulated yield this uncertainty is 2.7 ± 1.4% ($\alpha = 0.05$) and 3.6 ± 0.7% ($\alpha = 0.05$), in high yielding and low yielding years, respectively. For the simulated biomass this uncertainty is 2.6 ± 0.5% ($\alpha = 0.05$) and 2.0 ± 0.9% ($\alpha = 0.05$), in high yielding and low yielding years, respectively.

The five most 'extreme' error combinations that caused more than 3% difference in biomass, and more than 5% difference in yield calculations compared to the base dataset had one thing in common. Their drained upper limit values were lower and their wilting point values were higher than in the base dataset (combinations: No. 3, 12 and 21) or their drained upper limit values were higher and their wilting point values were lower than in the base dataset (combinations No. 16 and 25). For these combinations – for the whole profile – the extractable water capacity was 28.8 mm smaller or larger than in the base dataset. This difference resulted in relatively big differences in the simulated yield and biomass. For the rest of the combinations – except for No. 7 – the extractable water capacity was the same as in the base dataset. This result shows the sensitivity of the model to the extractable water capacity.

Combined effects of inaccuracies of weather and soil inputs

Effects of weather and soil data inaccuracies and their combined effect are presented in *Table 7*.

The errors of weather and soil measurements can either strengthen or weaken each other's effect during model simulations. The bad news is that there can be error combinations (weather: 21 combined with soil: 25) where the average difference for 20 years is over 15% compared to the results obtained by using the base weather and soil datasets.

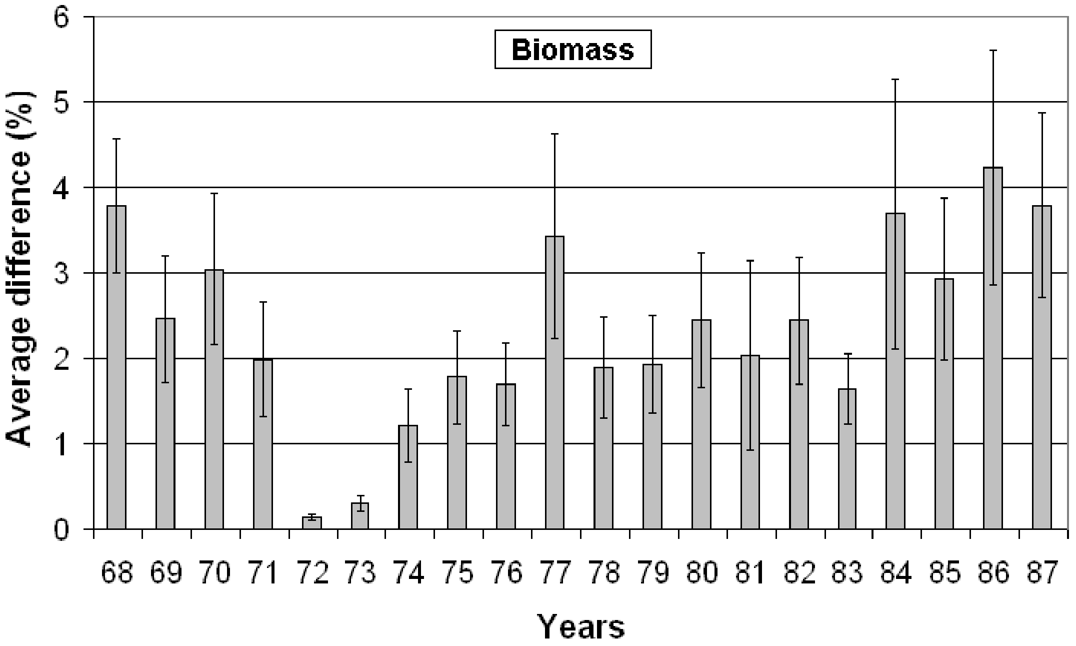

Figure 5. Yearly averages of the differences between the model results obtained by using the base soil dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.

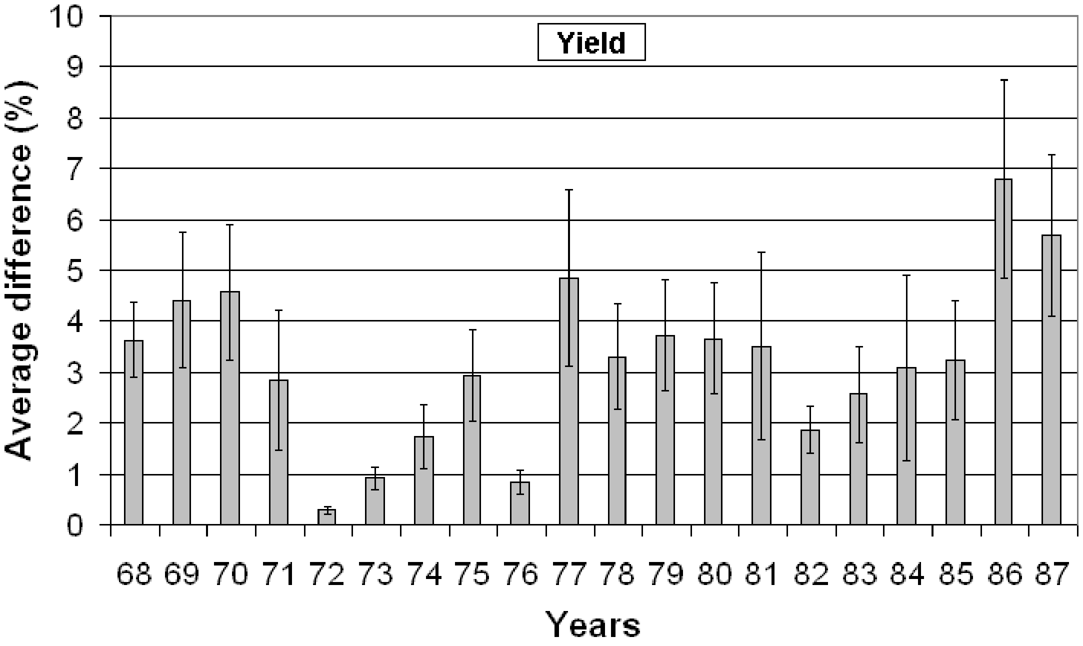

Figure 6. Yearly averages of the differences between the model results obtained by using the base soil dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.

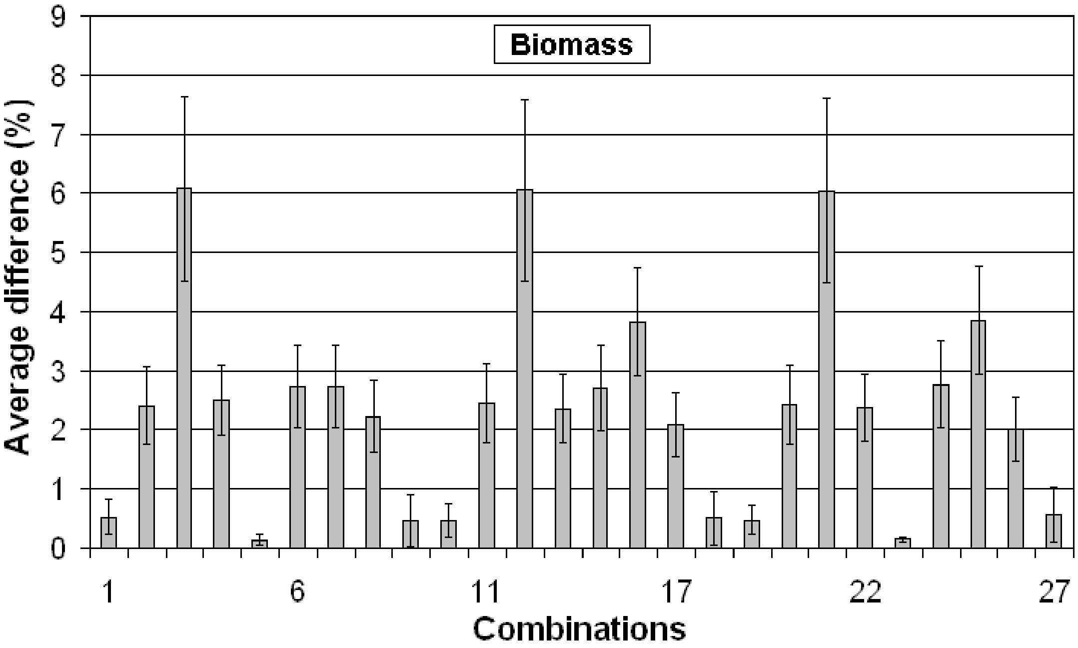

***Figure** 7. Average differences (for 20 years) between the model results obtained by using the base soil dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.*

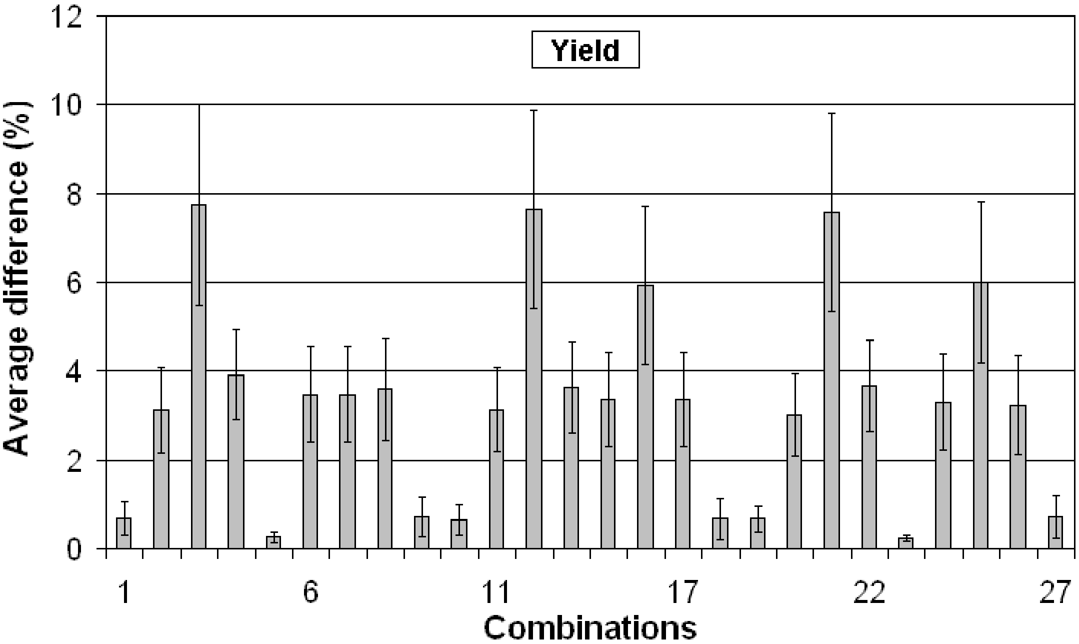

***Figure 8.** Average differences (for 20 years) between the model results obtained by using the base soil dataset and the 26 modified datasets (combinations). Error bars stand for the 95% confidence interval.*

Table 7. *Effects and combined effects of input data inaccuracies. Average differences (for 20 years) between the simulated yields that were obtained by using the given input data combinations and the yield that was obtained by using the base weather and soil datasets.*

Combinations	Direct effects	Weather: 21	Weather: 18
	▼ ►	8.9%	10%
Soil: 21	7.6%	6.4%	12.8%
Soil: 25	6%	15.1%	7.1%

Based on this study we can say that it is not only the level of error of the model input data that needs to be given in modelling papers but the uncertainties of the model estimations caused by the errors of the input data, as well. The uncertainty caused by the errors of the measured weather elements was found to be 4.7 and 6.9% for the calculated biomass and yield, respectively. The soil parameter errors/uncertainties caused smaller uncertainties in simulation results. We got 2.3 and 3.2% for the simulated biomass and yield, respectively. Since these two effects can both strengthen and weaken each other we can conclude that the inaccuracies of weather and soil measurements can cause 5–6% uncertainty in the simulated yield on an average. In certain cases the uncertainty of the simulation could be over 15% due to errors in weather and soil data.

Acknowledgements. This study was supported partly by grants of OTKA T032768 and T042996.

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USE OF SIMULATION TECHNIQUE TO DISTINGUISH BETWEEN THE EFFECT OF SOIL AND WEATHER ON CROP DEVELOPMENT AND GROWTH

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(Received 17th May 2003; accepted 26th June 2003)

Abstract. Environmental factors significantly influence the development and growth of plants. The main factors are soil and weather conditions. In real world it is not possible to segregate these influences. Using simulation models there are ways to analyse the effects of the changes of soil characteristics or weather elements separately. This way all the soil characteristics and weather elements can be changed one by one or different combinations of them can be used as input series.

In this study real Hungarian soil and weather scenarios were used that are significantly different from one another. Maize and wheat – the two main crops of Hungary – as well as field pea were used. Pea is known as a sensitive crop to weather. 4M-simulation package was used as a modelling tool. Our group at RISSAC based on CERES and CROPGRO models has developed it.

The results showed that the weather differences caused more significant changes in yields then soil differences though soils could moderate the effects of the extreme weather scenarios. The measure of reactions is meaningfully different depending on the species and cultivars. Analysis of separated effects of soil and weather factors has not only theoretical and methodological importance, but useful for the practice, too. When new plant species or cultivars are introduced in a country the optimal habitats can be found. The optimal structure for crops (where to seed different crops, and what sequence should be applied) and technology for crops (sawing time, fertilizer application and timing, etc.) can be estimated.

Keywords: *crop models, soil, weather, plant development and growth*

Introduction

The development and growth of plants in a given habitat is controlled by the soil and weather conditions as the main environmental factors. In real world it is not possible to segregate the influences of the soil and the weather on the crop production.

Many aspires were made but few attain has been achieved to separate the effects of the soil from the weather factors on crop yields. Statistical analysis failed to lead us a conclusion. Simulation modelling of weather–soil–plant is the proper means to analyse the effects of the changes of soil characteristics or weather elements separately. This way all the soil characteristics and weather elements can be changed one by one or different combinations of them can be used as input series. A more practical approach is when the role of local soils and weather are compared by a series of runs applying observed weather data from different years and real soil profiles from different fields of the selected farm.

The models of the two main crops of Hungary – maize and wheat – were applied, plus the model of pea crop as an addition. Weather – as many authors has shown – is the most obvious controlling factor of the development and growth of a given year at a changeable temperate climate [2, 4, 7, 9, 11], but pea is known as one of the most sensitive crop to weather [10, 12, 13, 14]. In this paper the environmental demands of crops and varieties were evaluated using real and simulated weather data.

Materials and methods

The DSSAT simulation model families (CERES and CROPGRO) have been adapted at our Institute for the Hungarian conditions. PEAGRO [9] model has been developed by our research group at RISSAC based on CROPGRO models [5] and CERES models [6]. These made us able to analyse the effects of the changes of soil characteristics or weather elements separately.

The data observed

For the simulation experiments several selected weather data observation series were used from Hungary. Each of these included maximum and minimum temperature, rain and radiation. The selected weather data sets were the followings: Nagyhörcsök (1976, 1988), Újmajor (1993-1996), Tápiószele (1993, 1995), Kompolt (1993, 1995). The selected soil data sets were two series of loam from Nagyhörcsök and Debrecen, two series of clay loam from Újmajor and Kompolt, a silty loam series from Tápiószele.

Conditions of simulation experiments under controlled environment

Controlled environment were simulated as follows: two levels of temperature as: $T_{\min} = 22\ ^{o}C$, $T_{\max} = 34\ ^{o}C$ and $T_{\min} = 16\ ^{o}C$, $T_{\max} = 25\ ^{o}C$, four levels of radiation as 20, 25, 30, 35 $MJ \cdot m^{-2}$, four levels of precipitation as 5, 10, 20, 40 $mm \cdot day^{-1}$ given in a sequence of 5 days.

Crops included

Three traditional food and feed crops of Hungary were included in the simulation experiments: winter wheat, maize and pea. These species were selected since they have different demands concerning soil and climatic conditions. Some of the reasons of the divergent reactions (influences on the development and growth) of the used species to the environmental conditions are as follows:

- Different climatic demands (i.e. base temperature 2 ^{o}C for wheat, 4 ^{o}C for pea and 8 ^{o}C for maize).
- Different length of life (winter wheat and summer crops like maize and pea).
- Different CO_2 assimilation types (C3 like maize and pea, and C4 like wheat).
- Different transpiration coefficients (250–300 $l \cdot kg^{-1}$ for maize, 500–600 $l \cdot kg^{-1}$ for wheat, 700–800 $l \cdot kg^{-1}$ for pea).
- Different demands to soil conditions (i.e. pea has nitrogen absorbent capability while the other two species do not, but as a result pea is more sensitive to soil moisture conditions).

Hungarian varieties of these species were selected with different characteristics: e.g. breeding season in case of maize, cold resistance and food quality in case of wheat, leaf morphology in case of pea. At the decision of selection of varieties it was considered whether or not the variety played a role in the National Fertilizer Experimental Network, or the National Breeding Test or in our own experiments.

Results and analyses

Simulation experiments using observed data sets

In field experiments it is not possible to separate the influence of soil conditions and weather conditions. One of the advantages of simulation modelling is that these conditions can be freely exchanged, and the cause and effect relationships can be studied. Applying the same soil and different weather scenarios can separate weather-generated changes. In the contrary, applying the same weather and different soils can separate soil-generated changes.

Pea development and yield was the most sensitive among the studied crops to extreme changes of weather. It is demonstrated by a combined field and simulation experiment in which the weather data came from observations at the corresponding experimental field. This way the reality of the simulation study was controlled by the field data. The main treatment applied was the amount of rain. Real soils (clay loam, loam, sandy loam) and weather scenarios were selected from the Hungarian region to compare the influences of the soil and weather on pea development and yields. The dry and the wet year treatments had 42% and 142% of the average rainfall respectively. The result showed 14–15 day difference in the maturity date and 2600–3000 kg·ha^{-1} yield difference caused by the weather. The effect of soil led to 800 and 1200 kg·ha^{-1} yield differences in dry and wet years respectively 6 to 1 days differences in emergence date and 7 to 8 days differences in maturity date (*Table 1*).

Table 1. *Simulated pea development and yield in dry and wet years on different soils.*

Soil types	Emergence after sowing		Maturity day after sowing		Yield (kg/ha)	
	dry year	wet year	dry year	wet year	dry year	wet year
clay loam	22	11	75	90	2072	5014
sandy loam	16	10	72	87	1224	3836
loam	16	10	68	82	1679	4831

Difference of emergence date showed correlation with initial soil water content (ISWC). The initial soil water content linearly decreased the required time for emergence. See the rate of ISWC/DUL at *Fig 1.*

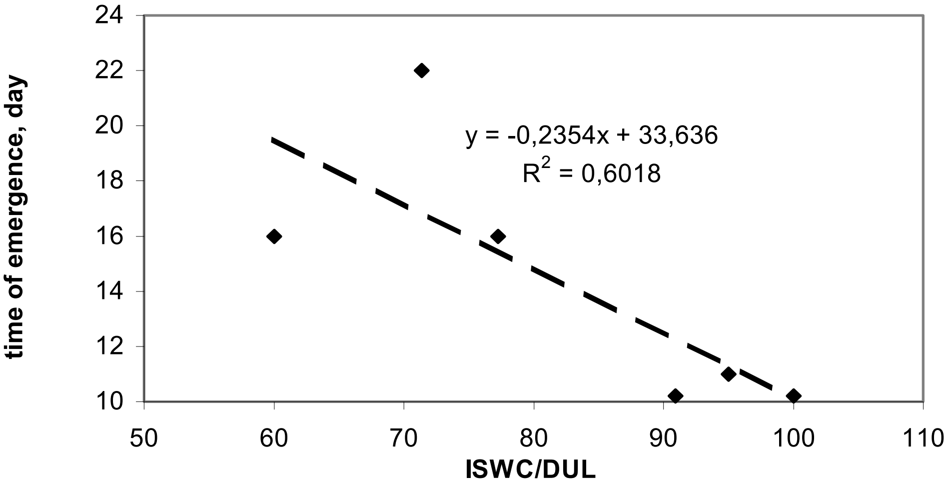

Figure 1. *Time of emergence vs. ISWC/DUL.*

Simulation experiments under controlled environment

Yields of three crops were simulated using modified weather. The decreased night and daily temperature from 22–34 °C to 16–25 °C respectively and caused different changes of yield of pea and maize (*Table 2*). The yield of maize decreased and in the contrary the yield of pea increased by lowering the temperature. This shows the difference in optimum temperatures of the two crops. This is the way in which the effect can be singled out by simulation not only for the final yield but also for the dynamic of growth and development. Even the transpiration and nutrient uptake can be studied day by day. Since the operation of the system is very complex human brain cannot follow all the mutual effects of factors and processes on a daily time step. Using simulation a lot of hypothesis can be tested.

Table 2. *Temperature effect on yields of maize and pea.*

Temperature (°C)	Crop yield (kg/ha) maize	pea
16/25	11042	7520
22/34	12230	4000

Water demands of maize and pea crops and radiation were compared in the next simulation experiment. The interdependency of the photosynthesis and transpiration is demonstrated by this simulation. Higher radiation increases the water demand and decreases the soil moisture content (*Fig. 2*).

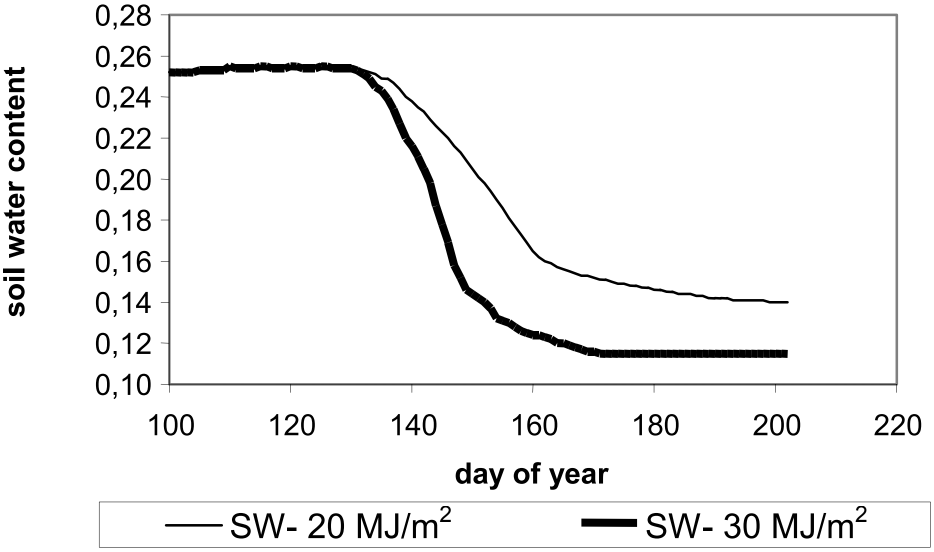

Figure 2. *Influence of radiation on the soil water content.*

Practical application of simulation

Irrigation technology can be developed for any soil and weather combination by optimisation via model application (*Table 3*). Then economic analysis can be added to help the farmers to choose the irrigation amounts and timing and other agronomic treatments according to the risk acceptability level of the given farmers.

Table 3. *Simulated pea yields with different plant densities and irrigations in dry and wet year.*

Plant density effect			Irrigation effect		
Plant/m^2	Grain yield (kg/ha)		Irrigation dose (mm)	Grain yield (kg/ha)	
	dry year	wet year		dry year	wet year
50	2270	4141	0	2072	5014
60	2203	4567	20	2520	5207
70	2180	4842	40	3594	5207
80	2129	5014	60	4053	5207
90	2072	5053	80	4823	5207
100	2031	5115	100	4946	5207
110	1985	5165	120	5040	5207
120	1978	5207	140	5200	5000

Important question of production technology is the sequencing of crops. A lot of field experiments were done to investigate the best combinations of crops according to their vegetation periods, water and nutrient demands, etc. Long term, more than 30 years, Hungarian National Experimental Network (OTK) has proven that pea is a better pre-crop of maize than wheat. We used simulation to figure out the reasons of this experience. We applied the local soils and weather data, as well as the genetic parameters of the original plant materials to regenerate the water status of the soils at each year of the experiment (*Table 4*). It has become obvious that the reason of the favourable effect of pea was that more water had remained in the soil after the harvest.

Table 4. *Simulated soil water content after pea and wheat.*

Soil layer (cm)	Soil water content (v%)	
	After pea	After wheat
0-5	27.1	17.4
5-15	27.1	25.3
15-30	29.7	26.7
30-45	30.5	26.9
45-60	31.2	26.6
60-90	31.0	25.2
90-120	29.0	24.1
120-150	27.1	23.3
150-170	26.2	22.5

Acknowledgements. This study was supported partly by grants of OTKA T032768 and T042778.

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THE SPECIES COMPOSITION OF TRUE BUG ASSEMBLAGES EXTRACTED WITH BERLESE FUNNELS

(DATA TO THE KNOWLEDGE ON THE GROUND-LIVING HETEROPTERA OF HUNGARY, № 1)

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(Received 21th March 2003; accepted 15th May 2003)

Abstract. A rich collection of Heteroptera extracted with Berlese funnel by Dr. I. Loksa between 1953–1974 in Hungary, has been examined. Altogether 157 true bug species have been identified. The great majority of them have been found in very low number, there are only 27 species of which more than 10 adult individuals have been found. Some species considered to be rare or very rare in Hungary have been collected in relatively great number (*Ceratocombus coleoptratus*, *Cryptostemma pusillimum*, *C. waltli*, *Acalypta carinata*, *A. platycheila*, *Loricula ruficeps*, *Myrmedobia exilis*). The three families, which are more or less rich in species and have the highest ratio of extracted species, were Rhyparochromidae, Tingidae and Nabidae. Out of them, the family Rhyparochromidae has been found to be most diverse and most characteristic at the ground-level. Individuals of the families Tingidae, Hebridae and Rhyparochromidae have been found in greatest number. The occurrence of the lace bug *Campylosteira orientalis* Horváth, 1881 in Hungary has been verified by a voucher specimen. In respect to the environmental changes through the country, parallel changes have been observed in the zoogeographical distribution of the ground-living bugs.

Keywords: *Heteroptera, ground-level, Berlese funnel, species composition, zoogeography*

Introduction

The majority of the terrestrial heteropterans can be collected from plants in great number by the usual methods for Heteroptera collecting (sweep-netting, beating etc.). Collecting bugs from the ground-level needs great effort and generally has trifling result compared with collecting from the vegetation. Therefore, the species occurring mostly or exclusively on the ground usually escape the zoologists' attention. The methods for collecting ground-living invertebrates (pitfall trap, sifting, Berlese funnels etc.) are only occasionally used by heteropterologists. Consequently, our knowledge on the faunistical, ecological, cenological data of species occurring mostly or exclusively on the ground is far poorer than that of species collected regularly in great number from the vegetation.

On this account, the authors examined numerous materials and identified a great number of true bugs collected in Hungary with Berlese funnels and pitfall traps. The present work – which is the first part of a series of publications – deals with the true bugs collected with Berles e funnel over 20 years in Hungary. Because of the identical way of collecting, the samples can be well compared on the basis of the true bugs found in them. In present paper the faunistic data and general observations on the species compositions as well as the zoogeographical analysis of Loksa's material are given.

Review of literature

The Heteroptera fauna of Hungary was investigated only sporadically before 1870. The first researcher was G. Horváth, who published numerous taxonomical, faunistical, ethological etc. data to the knowledge of the true bugs of Hungary from 1870 until his death in the year of 1937.

The results of the early exploration of the Hungarian fauna was summarized in a great and unique work, *Fauna Regni Hungariae*, which listed all of the animals known from the country at the time. The part „Hemiptera" was compiled by Horváth [39], who later published also additional data [41].

The organized research of the fauna of Hungary, especially in the protected areas, started after the Second World War. One of the first results was the volume *Bátorliget élővilága* [The Natural Life of Bátorliget] in 1953, which presented data on the flora and fauna of the Bátorliget Nature Reserves and listed 107 heteropteran species from the area [29]. Later some works dealing with the true bugs of certain Hungarian areas [10, 28] and the species of some groups of Heteroptera [11, 12, 13, 16, 30, 31] were also published. Some of them provide data on some ground-inhabiting species, too.

The monumental work, *Fauna Hungariae* has a goal to provide keys for the identification of all the animals occurring in Hungary. Five booklets of the series dealing with parts of the order Heteroptera have been published up to now [14, 32, 60, 62, 64], and a further booklet [45] is under publication.

In the 1970s, after the establishment of the first Hungarian national parks, the investigations of the fauna of these areas started with renewed effort. The results of the research are published in the series *Natural History of the National Parks of Hungary*, in which numerous studies dealing with true bugs have appeared up to now [6, 7, 8, 9, 26, 50, 63]. In addition to this series there are also many works providing data on the heteropteran fauna of certain areas of Hungary [1, 17, 22, 23, 24, 25, 42, 43, 47, 48, 49, 51, 52, 65, 67, 68]. The true bugs occurring in Bakony and Mátra mountains were investigated and the data were published mainly by the researchers of the Natural History Museum of Bakony (Zirc) and the Mátra Museum (Gyöngyös) [18, 19, 20, 21, 33, 34, 35, 36].

Recently Kondorosy [46] has compiled the most complete checklist of the Hungarian bug fauna.

As a summary, each of the above-mentioned works elaborates a taxonomical group of the true bugs occurring in a geographical area. If the subjects of the examination are the bugs inhabiting a certain habitat, so this is usually the water and/or the water surface. In the Hungarian literature, no publication discussing the Heteroptera inhabiting the ground-level is known. Also, in the international literature, data on the species living on the ground can be found only very sporadically, mostly as parts of great, comprehensive works discussing the soil-inhabiting animals, e.g. [27].

Materials and methods

The material examined

The investigations were carried out on the rich ground-living animal material collected by the staff of the Department of Systematic Zoology and Ecology of Eötvös Loránd University under the guidance of the late Dr. I. Loksa between 1953–1974. The material preserved in vials of 70% methyl alcohol was extracted from different substrata with Berlese funnels. All of the heteropteran specimens of Loksa's collection have been sorted and identified.

Altogether 3657 samples taken in all regions of Hungary have been examined. *Table 1* contains the list of the localities where heteropteran specimens have been collected, and their UTM codes. The localities are also shown in *Fig. 1*.

Species identification and nomenclature

The species have been identified by D. Rédei. For the identification of adults, the following works were used: Dipsocoromorpha, Aradidae: [62]; Nepomorpha: [60]; Gerromorpha, Leptopodomorpha, Nabidae, Reduviidae: [14]; Tingidae: [54]; Miridae: [69, 70, 71, 72, 73, 74]; Microphysidae: [53]; Lygaeidae sensu lato: [55, 56, 57]; Coreidae, Alydidae, Rhopalidae, Stenocephalidae, Pyrrhocoridae, Berytidae, Piesmatidae: [64]; Pentatomoidea: [44].

The larvae, apart from some exceptions, have been identified only at family level using Vásárhelyi's key [66]. Some elder larvae have been identified at subfamily, genus or species level using the works mentioned above as well as Benedek's key [15].

The classification and name of species are given according to the Catalogue of Aukema and Rieger [2, 3, 4, 5]. In case of taxa, which are not treated in this series, the nomenclature of the works used for identification are followed. To classify the Lygaeidae sensu lato taxa Henry's work [37] was followed.

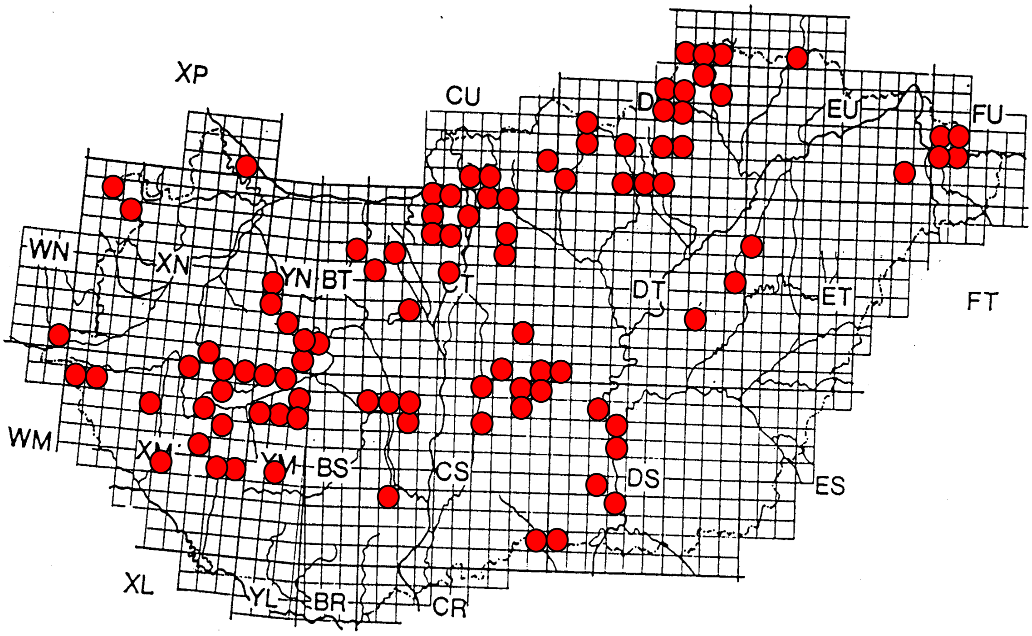


Figure 1. *The localities where heteropteran specimens have been collected.*

***Table 1**. List of the localities where heteropteran specimens have been collected, and their UTM codes.*

	Town / village	UTM
1	Alsópetény	CU60
2	Alsószentiván	CS28
3	Alsószuha	DU65
4	Andocs	YM27
5	Ábrahámhegy	XM98
6	Ágasegyháza	CS88
7	Ásotthalom	DS01
8	Ásványráró	XP80
9	Bajánsenye	XM08
10	Bak	XM47
11	Bakonybél	YN03
12	Baktalórántháza	EU81
13	Balatonalmádi	BT71
14	Balatonberény	XM77
15	Balástya	DS24
16	Bánd	YN12
17	Beregdaróc	FU13
18	Bélapátfalva	DU52
19	Bódvarákó	DU87
20	Böhönye	XM84
21	Budaörs	CT45
22	Bükkszenterzsébet	DU32
23	Cece	CS18
24	Csanytelek	DS36
25	Csaroda	FU03
26	Csákvár	CT05
27	Csongrád	DS37
28	Csöde	XM18
29	Csővár	CT79
30	Dömös	CT39
31	Eger	DU50
32	Egerbakta	DU40
33	Esztergom	CT39
34	Felsőörs	YN21
35	Fenyőfő	YN04
36	Fülöpháza	CS89
37	Gödöllő	CT77
38	Gulács	FU02
39	Harka	XN27
40	Jákfalva	DU65
41	Jánd	FU03
42	Jósvafő	DU67
43	Kakasd	CS13
44	Káptalantóti	XM99
45	Kecskemét	CS99
46	Kelebia	CS91
47	Kelemér	DU55
48	Kenderes	DT73
49	Kékkút	XM99
50	Kosd	CT69
51	Kővágóörs	XM99
52	Kunbaracs	CT70
53	Lajosmizse	CT90
54	Lengyeltóti	YM07
55	Lesenceistvánd (Uzsabánya)	XN70
56	Lovas	YN20
57	Marcali	XM86
58	Mátraszőlős	CU91
59	Mesztegnyő	XM85
60	Mezőszilas	CS08
61	Monoszló	YM09
62	Nagybajom	XM94
63	Nagyiván	DT95
64	Nagykanizsa	XM43
65	Nagykovácsi	CT47
66	Nagykőrös	DT00
67	Nagymaros	CT49
68	Nemesgulács	XM89
69	Nemesvid	XM75
70	Nemesvita	XM88
71	Nikla	XM96
72	Ohat	ET07
73	Oroszlány	BT96
74	Pásztó	DU00
75	Pécel	CT76
76	Piliscsaba	CT37
77	Piliscsév	CT38
78	Pilisszentkereszt	CT48
79	Pilisszentkereszt (Dobogókő)	CT48
80	Pilisszentlászló	CT48
81	Pócsmegyer	CT58
82	Pusztaszemes	YM28
83	Pusztavacs	CT82
84	Putnok	DU54
85	Répáshuta	DU62
86	Sándorfalva	DS33
87	Sajókaza	DU64
88	Salgótarján	DU12
89	Salgótarján (Somoskőújfalu)	DU13
90	Simontornya	CS18
91	Sirok	DU30
92	Solymár	CT47
93	Somogyaszaló	YM14
94	Somogytúr	YM17
95	Somogyzsitfa	XM75
96	Sopron	XN18

Table 1. *(continued).*

	Town / village	UTM
97	Szabadszállás	CS69
98	Szár	CT16
99	Szendrőlád	DU85
100	Szendehely	CU50
101	Szentbékkálla	XM99
102	Szentendre	CT58
103	Szentgotthárd	WN90
104	Szenyér	XM84
105	Szigetmonostor	CT58
106	Szögliget	DU77
107	Tarpa	FU12
108	Telkibánya	EU27
109	Tihany	YM19

	Town / village	UTM
110	Tiszaalpár	DS28
111	Tornakápolna	DU76
112	Vajta	CS27
113	Vámosatya	FU03
114	Velence	CT23
115	Vindornyaszőlős	XM69
116	Badacsony	*
117	Bakony	*
118	Cserhát	*
119	Karancs	*
120	Naszály	*
121	Putnoki-dombság (Hills)	*
122	Somló	*

*The exact collecting place is unknown because Loksa recorded only the name of the region or geographic area.

Results

Faunistical results: an annotated checklist

A total number of 5060 heteropteran specimens have been found in the examined material. The specimens represent 157 species belonging to 31 families. The majority (57.63%) of the extracted specimens are larvae (*Table 2*).

Table 2. *The distribution of specimens examined.*

Level of identification	Number of specimens
adults identified at species level	2096
larvae identified at species level	118
adults identified to family or genus level (mostly defected)	48
larvae identified to family or genus level	2708
unidentified larvae (1st and 2nd instars)	90
altogether	5060

In the list below, the order of families follows the Palaearctic catalogue of Aukema & Rieger [2, 3, 4, 5]. The name of species or subspecies is followed by the recorded collecting localities marked by Arabic numbers in italics (see *Table 1*), then by Roman numerals referring to the month in which specimens were collected, and finally the enumeration of the examined material. When giving the time of samplings, duration (V–VII. e.g.) is only indicated when we have data from each month of the period.

CERATOCOMBIDAE

Ceratocombus (Ceratocombus) coleoptratus (Zetterstedt, 1819). *7*, *12*, *15*, *23*, *24*, *25*, *27*, *32*, *33*, *46*, *47*, *57*, *59*, *62*, *63*, *69*, *74*, *83*, *86*, *95*, *105*, *113*, *120*. IV–XI. 24 ♂♂, 14 ♀♀, 43 larvae. — The only species of the family known from Hungary. A very limited number of specimens have been collected in the country before Loksa, who extracted large series of this species in some places. Based on this material, the species' distribution, coenology, wing polymorphism and phenology in Hungary were discussed by the authors [58].

DIPSOCORIDAE

The family is represented by 3 species in Hungary. A very limited number of specimens of each species have been collected in the country before. Only two of them have been captured by Loksa. The distribution, coenology, wing polymorphism and phenology of the species in Hungary based on Loksa's materials were discussed by the authors [58].

Cryptostemma (Pachycoleus) pusillimum (J. Sahlberg, 1870). *7*, *9*, *15*, *27*, *33*, *36*, *40*, *47*, *49*, *53*, *56*, *62*, *75*, *77*, *100*, *101*, *103*, *113*, *118*, *120*, *121*. III, V–VII, IX–XI. 24 ♂♂, 50 ♀♀, 56 larvae. — It is distributed all over the country. In some places a great number of it have been extracted with Berlese funnel.

Cryptostemma (Pachycoleus) waltli (Fieber, 1860). *59*. IX. 18 ♂♂, 15 ♀♀, 14 larvae. — It seems to be rare in Hungary. Several specimens have been extracted with Berlese funnel from the same locality.

PLEIDAE

Plea minutissima minutissima Leach, 1817. *46*. XI. 1 ♂. — A single, probably overwintering specimen has been extracted from wet debris collected at waterside.

HEBRIDAE

Hebrus (Hebrus) pusillus pusillus (Fallén, 1807). *8*, *40*, *50*, *51*. IV, VI, X, XI. 5 ♂♂, 5 ♀♀. — According to literature data, it occurs sporadically in Hungary, frequent at some places [14]. However, Loksa has captured only a few specimens. Most of the specimens have been collected around waters, and one specimen has been found also in moss far from waters.

Hebrus (Hebrusella) ruficeps Thomson, 1871. *9*, *15*, *25*, *26*, *27*, *28*, *32*, *33*, *35*, *36*, *40*, *47*, *49*, *50*, *51*, *62*, *75*, *76*, *79*, *91*, *94*, *101*, *110*, *115*, *121*. II, III, V–VII, IX–XII. 239 ♂♂, 168 ♀♀. — According to literature data, it occurs sporadically in Hungary, not frequent [14]. However, Loksa has extracted a great number of it. Specimens have been collected mainly at waterside places, and in other habitats, too.

HYDROMETRIDAE

Hydrometra gracilenta Horváth, 1899. *5*. X. 1 ♀. — Quite rare in Hungary. A single specimen has been extracted from wet debris collected at waterside.

VELIIDAE

Microvelia reticulata (Burmeister, 1835). *51*, *61*, *115*. X, XII. 14 ♂♂, 3 ♀♀, 2 larvae. — Each of the specimens has been collected at waterside places.

GERRIDAE

Gerris (Gerris) thoracicus Schummel, 1832. *1*. XI. 1 ♀. —A single, probably overwintering female has been extracted from a sample collected at shore.

Gerris (Gerris) argentatus Schummel, 1832. *8*, *59*. IV, IX. 1 ♂, 1 ♀. — Specimens have been extracted from a sample collected at waterside.

SALDIDAE

Chartoscirta cincta cincta (Herrich-Schäffer, 1841). *14*, *47*. VIII, XI. 2 ♂♂.

Chartoscirta elegantula (Fallén, 1807). *5*, *47*. III, X. 1 ♂, 1 ♀. — For a long time it was known in Hungary only from Bátorliget [14], but lately it has been recorded from several places (Bugac, Tabdi [8], Budapest [43]). It seems to be rare everywhere in the country.

Saldula saltatoria (Linnaeus, 1758). *14*, *51*, *61*, *113*. VIII, X, XI. 5 ♂♂.

TINGIDAE

Campylosteria verna (Fallén, 1826). *13*, *16*, *18*, *25*, *26*, *33*, *37*, *38*, *42*, *50*, *58*, *67*, *68*, *76*, *78*, *79*, *80*, *85*, *98*, *100*, *109*, *112*, *113*, *117*. II–VII, IX–XII. 60 ♂♂, 101 ♀♀. — Distributed everywhere in Hungary. It has been found mainly in mountainous regions.

Campylosteira orientalis Horváth, 1881. *24*. IX. 1 ♀. — Very rare, its life habits are practically unknown. It is mentioned in the literature as a species occurring in Hungary (f. n.: Tokaj [38], Budapest [62]; f. *suspecta* Horváth, 1892: Szentendre [40]). However, no voucher specimen is known [62]. Therefore, the only specimen (standing near to the form *suspecta*) collected by Loksa is regarded as the first specimen representing the species in Hungary. Data of collection: Csanytelek, 5. IX. 1972, 1 brachypterous ♀, *leg*. Loksa.

Acalypta carinata (Panzer, 1806). *59*, *64*, *85*, *100*, *108*, *113*. V–VII, IX. 26 ♂♂, 40 ♀♀. — For a long time it was recorded only from Zirc [39], but without voucher specimen. Later it was found at Bátorliget [61], and lately several specimens of it have been captured in this place with pitfall trap and by sifting [68]. Also the majority of the specimens collected by Loksa have been found in the territory to the east of the river Tisza (Vámosatya). It seems to be rare in Hungary, locally more frequent.

Acalypta platycheila (Fieber, 1844). *25*, *26*, *33*, *35*, *113*. V, VI, VIII, IX. 4 ♂♂, 7 ♀♀. — Only a few specimens have been found in Hungary hitherto [7, 61, 62, 68]. Probably it occurs sporadically all over the country but it seems to be rare everywhere.

Acalypta nigrina (Fallén, 1807). *18*. V, VII. 5 ♀♀. — Only a single specimen has been recorded from Hungary hitherto (Hegyalja [61, 62]). Loksa has also extracted some specimens from moss. One of the rarest *Acalypta* species in Hungary.

Acalypta marginata (Wolff, 1804). *18*, *19*, *23*, *35*, *60*, *75*, *78*, *81*, *85*, *88*, *89*, *107*, *108*, *109*, *113*, *119*. IV–VII. 18 ♂♂, 36 ♀♀. — Not frequent in Hungary but occurs sporadically all over the country. Several specimens have been extracted by Loksa.

Acalypta parvula (Fallén, 1807). *10*, *13*, *30*, *33*, *39*, *44*, *50*, *58*, *67*, *68*, *70*, *76*, *78*, *79*, *80*, *85*, *92*, *96*, *100*, *103*, *109*, *119*, *122*. III–V, VII, IX–XII. 75 ♂♂, 70 ♀♀. — According to Vásárhelyi [61, 62] it is rare in Hungary and known only from a few localities. However, Loksa has extracted numerous specimens of this species. It seems to occur everywhere in the country and to be frequent.

Acalypta gracilis (Fieber, 1844). *19*, *52*, *81*, *83*, *109*. V–VII, X. 3 ♂♂, 8 ♀♀. — Several localities are known from Hungary, mainly on the Great Hungarian Plain (Alföld) [7, 8, 62]. It seems to be quite rare in the country.

Acalypta musci (Schrank, 1781). *3*, *11*, *18*, *19*, *30*, *31*, *33*, *42*, *47*, *50*, *65*, *70*, *74*, *78*, *79*, *80*, *84*, *85*, *96*, *99*, *100*, *102*, *106*, *110*, *111*, *117*. II–XII. 201 ♂♂, 155 ♀♀, 1 adult (damaged specimen). — Frequent in Hungary. Most of the specimens captured by Loksa have been collected in the mountains Bükk. In some places, large series of this species have been extracted.

Derephysia (Derephysia) foliacea (Fallén, 1807). *32*, *80*, *85*. VII, VIII. 2 ♂♂, 1 ♀.

Stephanitis pyri (Fabricius, 1822). *113*. XI. 1 ♀.

Lasiacantha capucina capucina (Germar, 1836). *9*, *21*, *62*, *65*, *77*, *112*. III, X–XII. 3 ♂♂, 5 ♀♀.

Tingis (Tingis) cardui (Linnaeus, 1758). *117*. ?. 1 ♂, 1 ♀.

Tingis (Tropidocheila) geniculata (Fieber, 1844). *70*. ?. 1 ♀.

Tingis (Tropidocheila) reticulata Herrich-Schäffer, 1835. *79*. X. 1 ♀.

Catoplatus carthusianus (Goeze, 1788). *21*, *68*. III. 2 ♀♀.

Copium teucrii teucrii (Host, 1788). *?*. ?. 1 ♀. — This Mediterranean species is quite rare in Hungary, and known only from the environs of Budapest, the mountains Mátra [61, 62] and the area of the Aggtelek National Park [26]. The data on the single species collected by Loksa are lost.

Physatocheila costata (Fabricius, 1784). *20*, *94*. XI. 2 ♂♂, 1 ♀. — Hitherto known in Hungary only from few places (Göd, Kapuvár, Mosonmagyaróvár, Parád) [61, 62].

Oncochila scapularis (Fabricius, 1794). *53*. XI. 1 ♀.

Dictyla humuli (Fabricius, 1794). *25*. IX. 1 ♂.

Dictyla rotundata (Herrich-Schäffer, 1835). *42*. IX. 1 ♂.

Dictyla echii (Schrank, 1781). *7*, *44*, *122*. III, XI. 2 ♂♂, 2 ♀♀.

Agramma (Agramma) confusum (Puton, 1879). *7*, *36*, *53*, *60*, *62*, *90*. V, IX, XI. 5 ♂♂, 6 ♀♀.

Agramma (Agramma) minutum Horváth, 1874. *39*, *52*, *53*. X, XI. 3 ♀♀.

MICROPHYSIDAE

The family is represented by 5 species in Hungary [46]. A very limited number of specimens of each species have been collected in the country before because of their minute size and cryptic life habits.

Loricula pselaphiformis Curtis, 1833. *78*. VI. 1 ♂. — Recorded only from Eger [62], Bazsi [34] and Bátorliget [68] so far.

Loricula ruficeps (Reuter, 1844). *26*, *37*, *85*, *113*. V–VIII. 4 ♂♂, 16 ♀♀. — Very rare in Hungary, only one place of occurrence has been recorded in the country up to now (Tahi [62]). However, in one occasion Loksa extracted 11 female specimens from the same sample.

Loricula elegantula (Bärensprung, 1858). *50*. VI. 1 ♂, 5 ♀♀. — Rare in Hungary, only some specimens have been collected so far, mainly in the highlands [62].

Myrmedobia exilis (Fallén, 1807). *12*, *42*, *55*, *62*, *69*, *104*, *115*. VI, VIII, IX. 11 ♀♀. — Recorded only from Budapest [62], Bátorliget [68] and Darány [48] so far.

MIRIDAE

Monalocoris (Monalocoris) filicis (Linnaeus, 1758). *47*. IX. 1 ♀. —Boreo-montaneous species, rare in Hungary.

Deraeocoris (Knightocapsus) lutescens (Schilling, 1837). *3*, *109*. XI. 1 ♂, 1 ♀.

Lygus rugulipennis Poppius, 1911. *5*, *87*, *113*. X, XI. 3 ♂♂, 2 ♀♀.

Lygus pratensis (Linnaeus, 1758). *44*, *80*. III, XII. 2 ♀♀.

Lygus gemellatus gemellatus (Herrich-Schäffer, 1835). *47*, *52*. XI. 2 ♀♀.

Orthops (Orthops) campestris (Linnaeus, 1758). *58*. XI. 1 ♂.

Orthops (Orthops) kalmii (Linnaeus, 1758). *58*. XI. 1 ♂.

Stenodema (Brachystira) calcarata (Fallén, 1807). *8*. IV. 1 ♀.

Halticus apterus apterus (Linnaeus, 1758). *74*. VI. 1 ♂.

Tytthus pygmaeus (Zetterstedt, 1838). *61*. X. 1 ♀. — Can be found in humid meadows, bogs, etc., probably mainly at the ground-level. Although its occurrence in Hungary has only been proved recently [68], the species does not seem to be rare in suitable places.

NABIDAE

Alloeorhynchus (Alloeorhynchus) flavipes (Fieber, 1836). *37*, *100*. IV, VII. 1 ♀, 1 larva. — Rare in Hungary, known mainly from lowlands.

Himacerus (Aptus) mirmicoides (O. Costa, 1834). *5*, *18*, *44*. II, III, X. 2 ♂♂, 2 ♀♀.

Nabis (Nabis) rugosus (Linnaeus, 1758). *55*, *58*. VIII, XI. 1 ♂, 1 ♀.

Nabis (Nabis) ferus (Linnaeus, 1758). *13*, *83*, *112*, *113*. III, XI, XII. 1 ♂, 5 ♀♀.

Nabis (Nabis) pseudoferus pseudoferus Remane, 1949 ♂♂. *18*, *20*, *58*, *79*, *117*. III, X, XI. 5 ♂♂.

Nabis (Nabis) pseudoferus pseudoferus Remane, 1949 and **N. (N.) punctatus punctatus** A. Costa, 1847 ♀♀. *5*, *43*, *47*, *61*, *113*. IX–XI. 5 ♀♀. — Because of the very difficult distinguishing, the females of this two species have not been identified.

REDUVIIDAE

Phymata crassipes (Fabricius, 1775). *81*. VI. 1 larva. — Not rare in Hungary, distributed mainly in the mountainous regions.

ARADIDAE

Aradus cinnamomeus Panzer, 1806. *112*. XII. 1 ♀, 1 larva. — According to the literature [62], the species overwinters as adult. However, a 5th instar larva has also been extracted from a sample taken in December (03. XII). This suggests that occasionally elder larvae can also overwinter.

Aradus distinctus Fieber, 1860. *37*, *68*. XII. 2 ♂♂.

Aneurus (Aneurodes) avenius (Dufour, 1833). *113*. XI. 1 ♂.

Aneurus (Aneurus) laevis (Fabricius, 1775). *?*. X. 1 ♂.

PIESMATIDAE

Piesma capitatum (Wolff, 1804). *7*, *19*, *112*. XI, XII. 4 ♂♂.

Piesma maculatum (Laporte, 1833). *25*, *29*, *38*, *43*, *48*, *63*, *72*, *74*, *93*, *104*, *113*. IV, VI, IX, XI. 19 ♂♂, 18 ♀♀.

Parapiesma quadratum (Fieber, 1844). *45*, *53*. X, XI. 3 ♀♀.

Parapiesma silenes (Horváth, 1888). *45*, *122*. X, XI. 1 ♂, 1 ♀. — Far more rare than the species before, known mainly from the Great Hungarian Plain.

Parapiesma salsolae (Becker, 1867). *7*, *45*, *83*, *112*. X–XII. 5 ♂♂, 3 ♀♀.

Parapiesma kochiae (Becker, 1867). *7*, *112*. XI, XII. 4 ♂♂, 3 ♀♀. — Relatively rare in Hungary, known mostly from the territory between the rivers Danube and the Tisza.

BERYTIDAE

Berytinus (Berytinus) minor minor (Herrich-Schäffer, 1835). *74*. VI. 1 ♀.

Berytinus (Lizinus) signoreti (Fieber, 1859). *58*. XI. 1 ♀. — Rare in Hungary, known only from the environs of Budapest, the Bakony Mountains and Velem [64]. Its life habits and phenology are unknown but its occurrence in late autumn suggests that it overwinters as adult.

Berytinus (Lizinus) montivagus (Meyer-Dür, 1841). *58*, *68*, *78*, *86*, *117*. VII, IX, XI. 3 ♂♂, 3 ♀♀.

Berytinus (Lizinus) geniculatus (Horváth, 1885). *109*. ?. 1 ♀. — Relatively rare in Hungary, known mostly from the lowlands.

LYGAEIDAE

Horvathiolus superbus (Pollich, 1781). *18*. V. 1 ♂. — Rare in Hungary, only a few places of occurrence are known.

Lygaeosoma sardeum sardeum Spinola, 1837. *70*. ?. 1 ♀.

Nysius senecionis senecionis (Schilling, 1829). *29*, *83*. XI. 1 ♂, 1 ♀.

CYMIDAE

Cymus glandicolor Hahn, 1832. *46*. XI. 1 ♂.

Cymus aurescens Distant, 1833. *3*, *62*. XI. 3 ♀♀. — The rarest species of the genus in Hungary, known mainly from the highlands.

BLISSIDAE

Dimorphopterus spinolae (Signoret, 1857). *7*, *48*, *52*, *97*. IV, XI. 6 ♂♂, 2 ♀♀.

Dimorphopterus doriae (Ferrari, 1874). *23*, *52*, *90*, *112*. V, X, XII. 16 ♂♂, 6 ♀♀.

GEOCORIDAE

Geocoris (Geocoris) ater (Fabricius, 1787). *112*. XII. 1 ♂, 1 ♀.

HETEROGASTRIDAE

Platyplax salviae (Schilling, 1829). *44*. ?. 1 ♂.

OXYCARENIDAE

Oxycarenus (Oxycarenus) modestus (Fallén, 1829). *94*. XI. 1 ♂.

Macroplax preyssleri (Fieber, 1837). *6*, *45*, *112*. X, XII. 8 ♂♂, 2 ♀♀.

Macroplax fasciata fasciata (Herrich-Schäffer, 1835). *50*. X. 1 ♂.

Metopoplax origani (Kolenati, 1845). *45*, *48*, *76*, *112*. IV, X–XII. 5 ♂♂, 1 ♀.

Camptotelus lineolatus lineolatus (Schilling, 1829). *109*. ?. 1 ♂.

Tropidophlebia costalis (Herrich-Schäffer, 1850). *114*. V. 1 ♂, 1 ♀. — Rare in Hungary, has been found at Barcs, Bugac, Fülöpháza, Nagyszénás and the environs of Budapest up to now [45].

RHYPAROCHROMIDAE

Plinthisus (Plinthisus) brevipennis (Latreille, 1807). *37*, *47*, *50*, *55*, *83*, *85*, *109*. III–VIII, X–XII. 14 ♂♂, 13 ♀♀.

Plinthisus (Plinthisus) longicollis Fieber, 1861. *68*, *70*, *112*. IX, XII. 1 ♂, 5 ♀♀. — It occurs sporadically throughout the country but is quite rare.

Plinthisus (Plinthisomus) pusillus (Scholtz, 1847). *2*, *23*, *44*, *54*, *55*, *58*, *65*, *66*, *69*, *83*, *85*, *95*, *97*, *109*, *112*. V, VII–IX, XI, XII. 12 ♂♂, 17 ♀♀.

Stygnocoris sabulosus (Schilling, 1829). *33*, *55*, *78*, *83*, *117*. VI–VIII, X. 2 ♂♂, 4 ♀♀.

Stygnocoris pygmaeus (R. F. Sahlberg, 1848). *19*, *26*, *50*, *55, 83*. VII, VIII, XI. 5 ♂♂, 3 ♀♀. — According to the literature [56], the species overwinters in the egg stage. However, an adult has also been collected in late November (29. XI).

Acompus pallipes (Herrich-Schäffer, 1834). *86*. IX. 1 ♀.

Drymus (Sylvadrymus) sylvaticus (Fabricius, 1775). *9*, *25*, *68*, *82*. VII, IX, X. 2 ♂♂, 2 ♀♀.

Drymus (Sylvadrymus) ryeii Douglas & Scott, 1865. *26*, *44*, *61*, *64*, *77*, *115*. V, VI, VIII, X–XII. 6 ♂♂, 4 ♀♀.

Drymus (Sylvadrymus) brunneus brunneus (R. F. Sahlberg, 1848). *25*, *59*, *62*, *64*, *88*. VI, IX, XI. 10 ♂♂, 6 ♀♀.

Eremocoris podagricus (Fabricius, 1775). *1*, *13*, *34*, *43*, *44*, *49*, *83*, *96*. III, V, X, XI. 7 ♂♂, 5 ♀♀.

Eremocoris plebejus (Fallén, 1807). *9*. X. 1 ♂. — Rare in Hungary, distributed mainly in the mountainous regions.

Scolopostethus thomsoni Reuter, 1875. *47*, *96*, *113*. V, IX, XI. 1 ♂, 4 ♀♀.

Scolopostethus affinis (Schilling, 1829). *17*, *50*, *67*, *114*. IV, V, X. 3 ♂♂, 2 ♀♀.

Scolopostethus puberulus Horváth, 1887. *33*, *37*. X. 1 ♂, 1 ♀. — According to literature data [45], it is very rare in Hungary.

Scolopostethus pilosus pilosus Reuter, 1874. *12*, *47*, *85*. V, IX, XI. 2 ♂♂, 4 ♀♀.

Ischnocoris punctulatus Fieber, 1861. *44*, *63*, *76*. III, IV, IX. 1 ♂, 2 ♀♀. — Very rare in Hungary, it has been collected only at two localities (Budapest, Sátoraljaújhely) so far [45].

Ischnocoris hemipterus (Schilling, 1829). *44*, *70*, *92*. X. 4 ♂♂, 1 ♀.

Tropistethus holosericus (Scholtz, 1846). *18*, *37*, *43*, *44*, *63*, *68*, *69*, *70*, *87*, *109*, *113*. III, IV, VIII, IX, XI. 13 ♂♂, 6 ♀♀.

Pionosomus opacellus Horváth, 1895. *112*. XII. 1 ♂, 2 ♀♀. — A lowland species, known exclusively from the Great Hungarian Plain (Alföld).

Emblethis verbasci (Fabricius, 1803). *97*, *117*. XI. 1 ♂, 1 ♀.

Emblethis griseus (Wolff, 1802). *37*. XII. 1 ♂, 1 ♀.

Emblethis denticollis Horváth, 1878. *45*. X. 1 ♂, 1 ♀.

Emblethis ciliatus Horváth, 1875. *112*. XII. 3 ♂♂.

Trapezonotus (Trapezonotus) arenarius arenarius (Linnaeus, 1758). *5*, *44*, *45*, *50*, *51*, *112*. X, XII. 5 ♂♂, 1 ♀.

Trapezonotus (Trapezonotus) dispar Stål, 1872. *85*. X. 1 ♂.

Aphanus rolandri (Linnaeus, 1758). *46*. XI. 1 ♂.

Megalonotus chiragra (Fabricius, 1794). *41*, *85*, *122*. II, VIII, IX. 1 ♂, 3 ♀♀.

Megalonotus sabulicola (Thomson, 1870). *1*, *5*, *37*, *50*, *62*, *68*, *100*, *109*, *117*. III, IX–XI. 4 ♂♂, 9 ♀♀.

Megalonotus antennatus (Schilling, 1829). *78*, *100*. III, X. 1 ♂, 1 ♀. — Quite rare in Hungary, more frequent in the highlands.

Megalonotus praetextatus (Herrich-Schäffer, 1835). *83*, *112*. XI, XII. 2 ♀♀.

Peritrechus geniculatus (Hahn, 1832). *19*. XII. 1 ♂.

Peritrechus gracilicornis Puton, 1877. *7*, *15*, *25*, *45*. IX–XI. 4 ♀♀.

Peritrechus nubilus (Fallén, 1807). *44*, *83*. V, XI. 2 ♂♂.

Beosus maritimus (Scopoli, 1763). *33*, *94*. X, XI. 1 ♂, 1 ♀.

Graptopeltus lynceus (Fabricius, 1775). *19*, *117*. VIII, X. 4 ♀♀.

Raglius alboacuminatus (Goeze, 1778). *37*. X. 1 ♂.

Rhyparochromus pini (Linnaeus, 1758). *122*. XI. 1 ♀.

Rhyparochromus vulgaris (Schilling, 1829). *47*, *106*. III, VI, IX, XI. 3 ♂♂, 14 ♀♀.

Pachybrachius fracticollis (Schilling, 1829). *9*, *12*, *28*, *95*, *103*. VIII–X. 1 ♂, 4 ♀♀.

PYRRHOCORIDAE

Pyrrhocoris apterus (Linnaeus, 1758). *16*. V. 1 ♀.

Pyrrhocoris marginatus (Kolenati, 1845). *50*. X. 1 ♀.

COREIDAE

Coreus marginatus (Linnaeus, 1758). *94*. XI. 1 ♀.

Spathocera obscura (Germar, 1842). *52*, *112*. X, XII. 1 ♂, 1 ♀. — Rare in Hungary, known only from the Great Hungarian Plain.

Bathysolen nubilus (Fallén, 1807). *68*, *117*. V. 1 ♂, 1 ♀. — Quite rare in Hungary.

Coriomeris denticulatus (Scopoli, 1763). *70*. IV. 2 ♀♀.

Ceraleptus gracilicornis (Herrich-Schäffer, 1835). *37*, *68*. X. 3 ♂♂, 2 ♀♀.

RHOPALIDAE

Rhopalus (Rhopalus) subrufus (Gmelin, 1788). *62*. XI. 1 ♂.

Brachycarenus tigrinus (Schilling, 1817). *50*, *58*, *109*. III, XI. 2 ♂♂, 2 ♀♀.

CYDNIDAE

Microporus nigritus (Fabricius, 1794). *37*, *68*. V, XII. 1 ♂, 1 ♀.

Cydnus aterrimus (Forster, 1771). *44*. III. 1 ♂.

Legnotus limbosus (Geoffroy, 1785). *18*, *19*, *29*, *37*, *44*, *57*, *59*, *62*, *68*, *70*, *73*, *79*, *80*, *83*, *95*, *106*, *109*, *122*. III–XII. 35 ♂♂, 40 ♀♀.

Tritomegas bicolor (Linnaeus, 1758). *57*, *71*. VII. 1 ♂, 1 ♀.

Adomerus biguttatus (Linnaeus, 1758). *103*. X. 1 ♂.

THYREOCORIDAE

Thyreocoris scarabaeoides (Linnaeus, 1758). *4*, *22*, *43*, *54*, *59*, *62*, *68*, *79*. VI, VII, IX–XI. 5 ♂♂, 3 ♀♀. — Occurs sporadically in Hungary, nowhere frequent.

SCUTELLERIDAE

Eurygaster austriaca (Schrank, 1776). *29*, *37*, *68*, *112*, *113*, *122*. VII, XI, XII. 3 ♂♂, 3 ♀♀.

Eurygaster maura (Linnaeus, 1758). *47*, *68*, *70*, *76*, *122*. IV, IX–XI. 3 ♂♂, 3 ♀♀.

Eurygaster testudinaria (Geoffroy, 1758). *47*, *50*, *68*, *93*, *116*, *122*. III, XI. 2 ♂♂, 8 ♀♀.

PENTATOMIDAE

Podops inuncta (Fabricius, 1775). *1*. XI. 1 ♂.

Sciocoris (Sciocoris) cursitans (Linnaeus, 1758). *44*, *117*. III, V. 2 ♂♂, 2 ♀♀.

Sciocoris (Aposciocoris) homalonotus Fieber, 1851. *44*, *50*, *68*, *70*, *78*, *79*, *80*, *109*, *116*. III, V, VI, X. 16 ♂♂, 22 ♀♀. — According to literature data [32], it is rare in Hungary, occurs only sporadically. However, Loksa has extracted a great number of it.

Sciocoris (Aposciocoris) microphthalmus Flor, 1860. *50*. VI. 1 ♂.

Dyroderes umbraculatus (Fabricius, 1775). *44*. III. 1 ♀.

Aelia acuminata (Linnaeus, 1758). *16*, *44*, *47*, *50*. III, V, IX–XI. 7 ♂♂, 5 ♀♀.

Aelia rostrata Boheman, 1852. *44*. III. 1 ♀.

Neottiglossa leporina (Herrich-Schäffer, 1830). *52*. XI. 1 ♂.

Eusarcoris aeneus (Scopoli, 1763). *3*. XI. 1 ♀.

Dolycoris baccarum (Linnaeus, 1758). *117*. ?. 1 ♂.

Palomena prasina (Linnaeus, 1758). *70*. ?. 1 ♀.

Eurydema ventrale Kolenati, 1846. *122*. XI. 1 ♂.

Eurydema oleraceum (Linnaeus, 1758). *11*, *116*. III, X. 1 ♂, 1 ♀.

ACANTHOSOMATIDAE

Elasmucha grisea (Linnaeus, 1758). *96*. XI. 1 ♂. — Quite rare in Hungary.

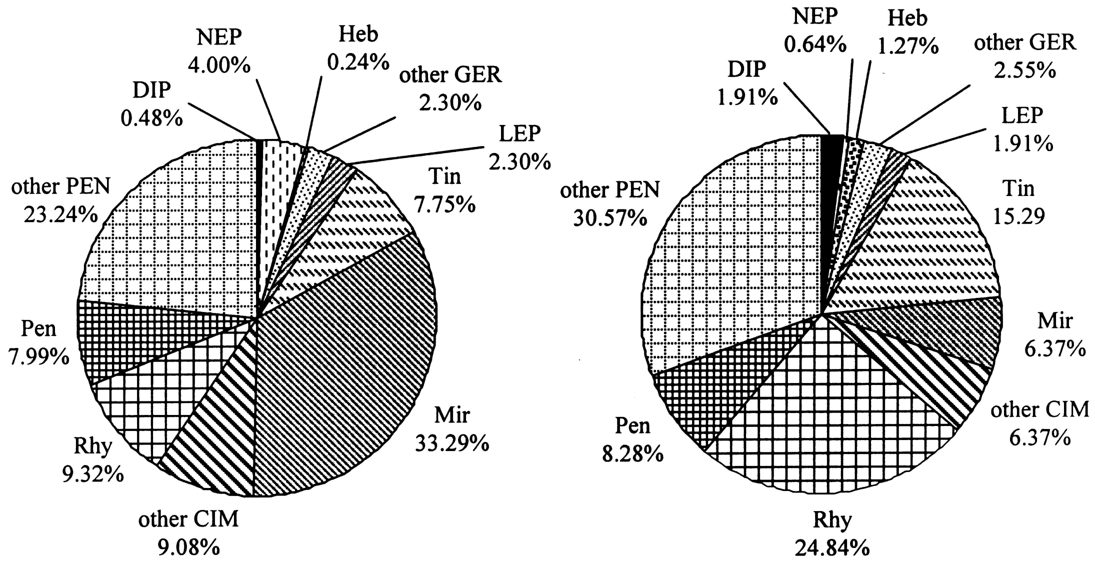
Species composition

The number of species and specimens belonging to different families are summarized in *Table 3*. The ratio of species and specimens belonging to some major groups of Heteroptera are shown in *Figs. 2–4*.

Table 3. *The number and ratio of the species known from Hungary and identified from Loksa's materials, and the ratio of the number of the collected specimens (N = number, % = percentage).*

Family	Species known from Hungary*		Identified species found in Loksa's materials		$\left(\frac{N(1)}{N(2)}\right)$	Adult specimens found in Loksa's materials	
	N(1)	%	*N*(2)	%	%	*N*	%
Ceratocombidae	1	0.12	1	0.64	**	38	1.81
Dipsocoridae	3	0.36	2	1.27	**	107	5.10
Nepidae	2	0.24	—	—	—	—	—
Corixidae	23	2.78	—	—	—	—	—
Naucoridae	1	0.12	—	—	—	—	—
Aphelocheiridae	1	0.12	—	—	—	—	—
Notonectidae	5	0.61	—	—	—	—	—
Pleidae	1	0.12	1	0.64	**	1	0.05
Mesoveliidae	2	0.24	—	—	—	—	—
Hebridae	2	0.24	2	1.27	**	417	19.90
Hydrometridae	2	0.24	1	0.64	**	1	0.05
Veliidae	6	0.73	1	0.64	**	17	0.81
Gerridae	9	1.09	2	1.27	**	3	0.14
Saldidae	18	2.18	3	1.91	16.67	9	0.43
Leptopodidae	1	0.12	—	—	—	—	—
Tingidae	64	7.75	24	15.29	37.50	854	40.74
Microphysidae	5	0.61	4	2.55	**	38	1.81
Miridae	275	33.29	10	6.37	3.64	17	0.81
Nabidae	16	1.94	5	3.18	31.25	18	0.86
Anthocoridae	31	3.75	—	—	—	—	—
Cimicidae	3	0.36	—	—	—	—	—
Reduviidae	20	2.42	1	0.64	5.00	—	—
Aradidae	22	2.66	4	2.55	18.18	5	0.24
Piesmatidae	7	0.85	6	3.82	**	61	2.91
Berytidae	15	1.82	4	2.55	26.67	9	0.43
Lygaeidae	24	2.91	3	1.91	12.50	4	0.19
Cymidae	4	0.48	2	1.27	**	4	0.19
Blissidae	3	0.36	2	1.27	**	30	1.43
Geocoridae	6	0.73	1	0.64	**	2	0.10
Artheneidae	2	0.24	—	—	—	—	—
Heterogastridae	5	0.61	1	0.64	**	1	0.05
Oxycarenidae	10	1.21	6	3.82	**	21	1.00
Rhyparochromidae	77	9.32	39	24.84	50.65	243	11.59
Pyrrhocoridae	2	0.24	2	1.27	**	2	0.10
Stenocephalidae	3	0.36	—	—	—	—	—
Coreidae	23	2.78	5	3.18	21.74	12	0.57
Alydidae	3	0.36	—	—	—	—	—
Rhopalidae	17	2.06	2	1.27	11.76	5	0.24
Plataspidae	2	0.24	—	—	—	—	—
Cydnidae	20	2.42	5	3.18	25.00	81	3.86
Thyreocoridae	2	0.24	1	0.64	**	8	0.38
Scutelleridae	15	1.82	3	1.91	20.00	22	1.05
Pentatomidae	66	7.99	13	8.28	19.70	65	3.10
Acanthosomatidae	7	0.85	1	0.64	**	1	0.05
Altogether	826	100.00	157	100.00	19.01	2096	100.00

*According to Kondorosy [46]. The occurrences of some other species in Hungary have been proved since Kondorosy's checklist. However, for the sake of simplicity we took no notice of these species.
**Percentage is given, for practical reasons, in the case of larger numbers only.



2 **3**

Figures 2–3. *2. The ratio of the species known from Hungary belonging to major groups of Heteroptera. 3. The ratio of the species identified from Loksa's materials belonging to major groups of Heteroptera.* CIM = *Cimicomorpha,* DIP = *Dipsocoromorpha,* GER = *Gerromorpha,* LEP = *Leptopodomorpha,* NEP = *Nepomorpha,* PEN = *Pentatomomorpha,* Heb = *Hebridae,* Mir = *Miridae,* Pen = *Pentatomidae,* Rhy = *Rhyparochromidae,* Tin = *Tingidae.*

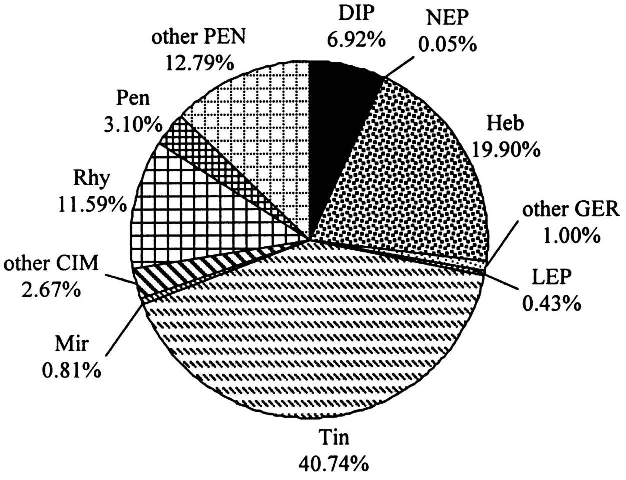


Figure 4. *The ratio of the adult specimens identified from Loksa's materials belonging to major groups of Heteroptera. Abbreviations as on Fig. 2 and 3.*

Zoogeographical distribution

Loksa collected samples in all of the great phytogeographical provinces of Hungary (*Fig. 5*). The numbers of samples taken in the provinces Praeillyricum, Praenoricum and in the Arrabonicum district of province Eupannonicum are considerable lower than that of the other provinces. Therefore, only the samples collected in provinces Eupannonicum (except Arrabonicum), Bakonyicum and Matricum have been compared.

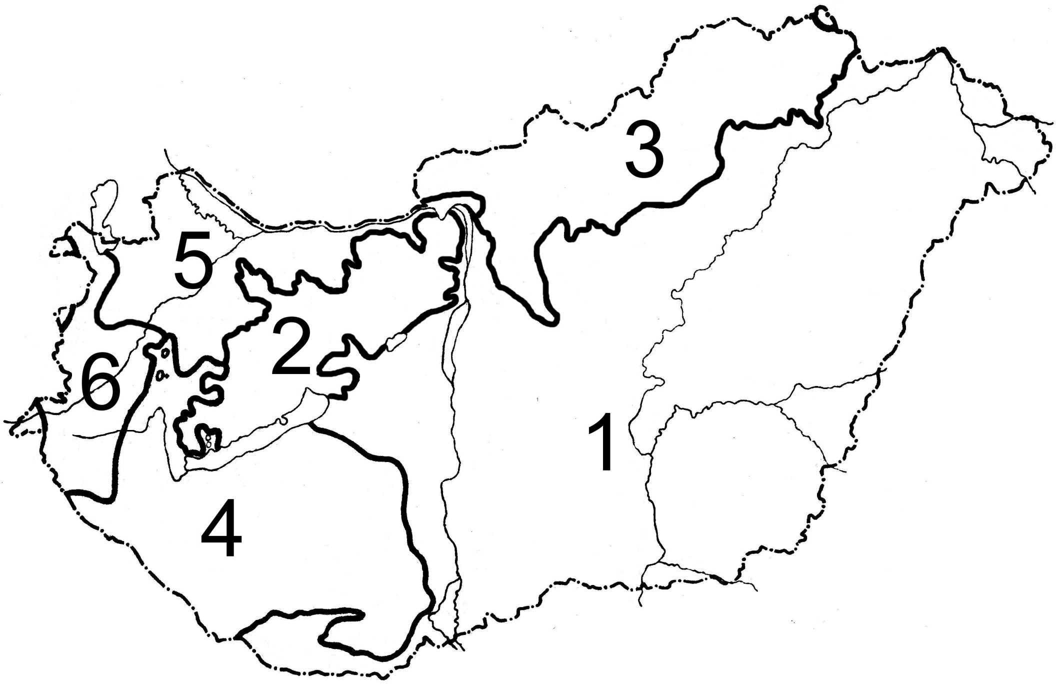


***Figure 5**. The great phytogeographical provinces of Hungary (after Soó* [59]*, modified).* 1 = *Eupannonicum (except Arrabonicum),* 2 = *Bakonyicum,* 3 = *Matricum,* 4 = *Praeillyricum,* 5 =*Eupannonicum (Arrabonicum),* 6 = *Praenoricum.*

The zoogeographical distribution of heteropteran species and specimens collected in the three most exhaustively investigated provinces in Hungary are shown in *Table 4* and *5*.

***Table 4**. The zoogeographical distribution of heteropteran species collected in the three most exhaustively investigated provinces in Hungary (N = number of species, % = percentage).*

Zoogeographical distribution	Eupannonicum		Bakonyicum		Matricum		altogether	
	N	%	*N*	%	*N*	%	*N*	%
Cosmopolite	—	—	1	1.20	—	—	2	1.26
Holarctic	3	4.17	5	6.02	4	5.26	6	3.77
Palaearctic (+ Ethiopian)	12	16.67	12	14.46	13	17.11	30	18.87
Eurosiberian (+ Nearctic)	21	29.17	17	20.48	16	21.05	34	21.38
South-Eurosiberian	5	6.94	3	3.61	1	1.32	7	4.40
West-Eurosiberian	3	4.17	2	2.41	3	3.95	5	3.14
West-Palaearctic	3	4.17	9	10.84	10	13.16	14	8.81
European	7	9.72	12	14.46	11	14.47	18	11.32
Euro-Mediterranean (+ Middle-Asian)	8	11.11	14	16.87	10	13.16	22	13.84
Mediterranean (+ Middle-Asian)	1	1.39	3	3.61	3	3.95	6	3.77
Ponto-Mediterranean (+ Middle-Asian)	5	6.94	1	1.20	1	1.32	7	4.40
North-Mediterranean-European (+ Middle-Asian)	4	5.56	2	2.41	2	2.63	5	3.14
Boreo-montaneous	—	—	2	2.41	2	2.63	3	1.89
altogether	72	100	83	100	76	100	159	100

Table 5. *The zoogeographical distribution of heteropteran specimens collected in the three most exhaustively investigated provinces in Hungary (N = number of specimens, % = percentage).*

Zoogeographical distribution	Eupannonicum		Bakonyicum		Matricum	
	N	%	*N*	%	*N*	%
Cosmopolite	—	—	1	0.14	—	—
Holarctic	7	1.43	11	1.59	10	1.31
Palaearctic (+ Ethiopian)	49	10.00	35	5.04	19	2.48
Eurosiberian (+ Nearctic)	166	33.88	83	11.96	93	12.16
South-Eurosiberian	7	1.43	5	0.72	1	0.13
West-Eurosiberian	126	25.71	112	16.14	148	19.35
West-Palaearctic	3	0.61	88	12.68	99	12.94
European	73	14.90	243	35.01	360	47.06
Euro-Mediterranean (+ Middle-Asian)	10	2.04	66	9.51	26	3.40
Mediterranean (+ Middle-Asian)	3	0.61	41	5.91	3	0.39
Ponto-Mediterranean (+ Middle-Asian)	37	7.55	1	0.14	1	0.13
North-Mediterranean-European (+ Middle-Asian)	9	1.84	6	0.86	3	0.39
Boreo-montaneous	—	—	2	0.29	2	0.26
altogether	490	100	694	100	765	100

Discussion

As compared to the great effort of collecting, it can be said that the number of heteropteran specimens collected is low. There are only 27 species of which more than 10 adult individuals have been found. Out of these, *Ceratocombus coleoptratus*, *Cryptostemma pusillimum*, *C. waltli*, *Acalypta carinata*, *A. platycheila*, *Loricula ruficeps*, *Myrmedobia exilis* have been considered to be rare or very rare in Hungary. However, these species have been collected with Berlese funnel in relatively great numbers. Most of them must live mostly at ground-level of suitable plant communities, therefore can not or only accidentally be collected by the usual methods for Heteroptera collecting.

The majority of the species have been collected in very low numbers. Some of these have been also regarded as rare species in Hungary. Such species are *Acalypta nigrina*, *Physatocheila costata*, *Loricula pselaphiformis*, *L. elegantula, Tytthus pygmaeus*, *Acompus pallipes*, *Bathysolen nubilus*, *Spathocera obscura* and *Sciocoris homalonotus*. Many of them might to be far more frequent in Hungary as expected. However, they usually escape the heteroperists' attention because they live mostly at ground-level or in related substrata.

No adult individuals belonging to the following families have been collected: Nepidae, Corixidae, Naucoridae, Aphelocheiridae, Notonectidae (aquatic life habits); Mesoveliidae (semi-aquatic life habits); Leptopodidae (usually under stones); Cimicidae (parasitic life habits); Artheneidae, Stenocephalidae, Alydidae, Plataspidae (only few, not characteristic ground-living species in Hungary, it is only accidental that none of them have been collected). The following taxa, more or less rich in species, are represented by only a few species in the material collected: Nepomorpha (aquatic life habits); Gerromorpha (mostly semi-aquatic life habits); Saldidae (the relatively rare species have a relatively big ratio); Miridae (usually on plants), Reduviidae (the relatively rare species and those on plants, in buildings etc. have a relatively big ratio); Aradidae (usually under bark), Rhopalidae (usually on plants).

The three families, which are more or less rich in species and have the highest ratio of extracted species, are Rhyparochromidae (50.65%), Tingidae (37.50%) and Nabidae (31.25%). Out of them, the family Rhyparochromidae is the most diverse and most characteristic at the ground-level. Most tingid species have been collected in very low numbers, only some members of the genera *Campylosteira* and *Acalypta* have been extracted in great numbers. The number of the nabid specimens has also been low.

The three families having the highest ratio of extracted individuals are Tingidae (40.74% of the total specimens), Hebridae (19.90%) and Rhyparochromidae (11.59%). Out of the family Tingidae, the *Campylosteira* and *Acalypta* species – first of all *A. musci* – are the most characteristic, often occurring in great numbers in ground substrata. Specimens of the 2 *Campylosteira* and the 7 *Acalypta* species represent 94.96% of the total tingid specimens extracted. Out of the species of these two genera, *A. musci* was the most dominant, having a relative dominance of 41.80%. 97.60% of the total hebrid specimens belong to the species *Hebrus ruficeps*. This species seems to be characteristic at the ground-level of suitable (mostly riparian or other humid) plant communities. The family Rhyparochromidae, containing mainly seed-feeder species, occurs widely at the ground-level.

By exploring the zoogeographic distribution of the heteropteran species collected in the Hungarian provinces, the followings have been concluded. In case of the province Eupannonicum (except district Arrabonicum) is the percentage of the species with Mediterranean and Ponto-Mediterranean distribution especially high (8.33% of the species, 8.16% of the specimens). No boreo-montaneous species have been found in this area. The total ratio of the West-Palaearctic, European and Euro-Mediterranean species is the lowest (25.00% of the species, 17.55% of the specimens), whereas that of the Eurosiberian, South-Eurosiberian and West-Eurosiberian species is the highest (40.28% of the species, 61.02% of the specimens) in this area out of the three examined phytogeographical provinces. Consequently, the ground-living bug assemblage of the province Eupannonicum has a relation to the considerable continental and a far less important subatlantic climatic influence of this area.

In the province Bakonyicum, the ratio of the Mediterranean and Ponto-Mediterranean elements is lower than in the province Eupannonicum (4.81% of the species, 6.05% of the specimens). Two species with boreo-montaneous distribution have also been found (*Megalonotus antennatus*, *Tytthus pygmaeus*; 2.41% of the species, 0.29% of the specimens). The total percentage of the West-Palaearctic, European and Euro-Mediterranean species is relatively low (42.17% of the species, 63.40% of the specimens), whereas that of the Eurosiberian, South-Eurosiberian and West-Eurosiberian species is high (26.50% of the species, 28.82% of the specimens) in this province.

Also in the phytogeographic province Matricum, the percentage of the Mediterranean and Ponto-Mediterranean species is far less than in the province Eupannonicum (5.27% of the species, 0.52% of the specimens). Two boreo-montaneous elements have been found in this area (*Megalonotus antennatus*, *Monalocoris filicis*; 2.63% of the species, 0.26% of the specimens). The total percentage of the West-Palaearctic, European and Euro-Mediterranean species is relatively low (40.79% of the species, 50.93% of the specimens), whereas that of the Eurosiberian, South-

Eurosiberian and West-Eurosiberian species is high (26.32% of the species, 31.64% of the specimens) in this area.

As a summary, in respect to the environmental changes through the country, different parallel changes can be observed in the zoogeographical distribution of the ground-living heteropteran communities of the different provinces. The percentage of the fauna elements indicating continentality (Eurosiberian, South-Eurosiberian and West-Eurosiberian) is the highest in the province Eupannonicum. Their ratio is far lower in the two hilly provinces. The percentage values of the species preferring humid subatlantic climate (West-Palaearctic, European and Euro-Mediterranean) show an increase in the direction Eupannonicum → Matricum → Bakonyicum, consequently are the highest in the western part of the country. The Mediterranean and Ponto-Mediterranean fauna elements have been collected in the lowlands (province Eupannonicum) in greatest number. Boreo-montaneous elements have been found only in the two hilly provinces (Bakonyicum and Matricum).

Acknowledgements. We are very grateful to Prof. Dr. K. Dózsa-Farkas for providing Dr I. Loksa's collection, thereby making our investigations possible; to Dr. E. Kondorosy for providing his unpublished zoogeographical data; to Ms. M. Rédei-Szerencsi and Ms. T. Tölgyesi-Nell for technical help at various phases of the project. At last, but in the first place of course, we would like to express our special thanks to the late Dr. I. Loksa (1923–1992), eminent Hungarian zoologist, former head of the Department of Systematic Zoology and Ecology of the Eötvös Loránd University, researcher of many soil-inhabiting invertebrate groups, especially Arachnoidea and Myriapoda. Without his pioneering and assiduous activity on the research of the soil fauna of Hungary it would have been impossible to implement our work.

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SPATIAL AND TEMPORAL PATTERNS OF TRUE BUG ASSEMBLAGES EXTRACTED WITH BERLESE FUNNELS

(DATA TO THE KNOWLEDGE ON THE GROUND-LIVING HETEROPTERA OF HUNGARY, №. 2)

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(Received 21th March 2003; accepted 15th May 2003)

Abstract. A rich material of Heteroptera extracted with Berlese funnels by Dr. I. Loksa between 1953–1974 in Hungary, has been examined. Altogether 157 true bug species have been identified. The ground-living heteropteran assemblages collected in different plant communities, substrata, phytogeographical provinces and seasons have been compared with multivariate methods. Because of the unequal number of samples, the objects have been standardized with stochastic simulation. There are several true bug species, which have been collected in almost all of the plant communities. However, characteristic ground-living heteropteran assemblages have been found in numerous Hungarian plant community types. Leaf litter and debris seem to have characteristic bug assemblages. Some differences have also been recognised between the bug fauna of mosses growing on different surfaces. Most of the species have been found in all of the great phytogeographical provinces of Hungary. Most high-dominance species, which have been collected, can be found at the ground-level almost throughout the year. Specimens of many other species have been collected with Berlese funnels in spring, autumn and/or winter. The diversities of the ground-living heteropteran assemblages of the examined objects have also been compared.

Keywords: *Heteroptera, ground-level, Berlese funnel, plant community, substratum*

Introduction

The majority of terrestrial heteropterans can be collected from plants in great numbers by the usual methods for Heteroptera collecting (sweep-netting, beating etc.). Collecting bugs from ground-level needs great effort and generally has trifling result compared with collecting from the vegetation. Therefore, the species occurring mostly or exclusively on the ground usually escape the zoologists' attention. The methods for collecting ground-living invertebrates (pitfall trap, sifting, Berlese funnel etc.) are only occasionally used by heteropterologists. Consequently, our knowledge on the faunistical, ecological, cenological data of species occurring mostly or exclusively on the ground is far poorer than that of species collected regularly in great numbers from the vegetation.

On this account, the authors have examined numerous materials and identified a great number of true bugs collected in Hungary with Berlese funnels and pitfall traps. The present work – which is the second part of a series of publications – deals with the true bugs collected with Berlese funnels over 20 years in Hungary. Because of the identical way of collecting, the samples can be well compared on the basis of the true bugs found in them. In present paper the ground-living bug assemblages inhabiting different substrata and plant communities, occurring in different parts of Hungary and in different seasons are compared.

Review of literature

The literature on the subject has been surveyed in the first part of this series of publications [5].

Materials and methods

The material examined and identification of species

The investigations have been carried out on the rich ground-living animal material collected by the staff of the Department of Systematic Zoology and Ecology of Eötvös Loránd University under the guidance of the late Dr. I. Loksa between 1953–1974. The material preserved in vials of 70% methyl alcohol was extracted from different substrata with Berlese funnels. All of the heteropteran specimens of Loksa's collection have been sorted and identified. Further data on the material examined as well as the works used for the identification has been presented in the first part of this series of publications [5].

Statistical methods

The relative dominance of most of the species studied is very low. Therefore, by the statistical analysis, the species (including the nymphs unidentified at species level as groups) with a relative dominance less than 0.20% have been grouped on the basis of their taxonomical position and body size. It can be presumed that the result of this grouping approaches that of a grouping by the life habits of the species. The species groups created are shown in *Table 2*.

The following sample parameters (object categories), each being comparable with multivariate methods, have been examined: (1) the plant communities where the samples were taken; (2) the extracted substrata; (3) the great phytogeographical provinces of Hungary where the samples were taken; (4) the seasons in which the samples were taken.

The statistical analyses started from a cenological database in which the rows represented the taxa, the columns the objects, and the cells contained the numbers of the individuals. These tables have to be suitable for the comparison of the objects and for the significance analysis of the differences. Accordingly we used the following methods:

(1) The original Berlese samples were sorted by the parameter examined.
(2) Only thus samples were considered, which have data from all the four parameters (primary data filter).
(3) For every group of the given parameter we examined the combinations with the other three parameters. Only thus combinations were considered, which were present in all of the groups to be compared (secondary data filter).
(4) The numbers of samples have been also standardized: the number of the specimens of each species collected in a given combination has been divided by the number of samples taken in that combination. These standardized values were summed for every group.

(5) As a result of the previous steps, every group was described by only one column, which contained the numbers of the individuals of the different taxa with the same sampling method.
(6) From every column random samples, with the same number of individuals, were taken with an own-developed Excel macro. With the aim of this stochastic simulation (bootstrapping) we can generate arbitrary number of pseudo-replicates. In this case 10 new objects, each containing 100 (70 in case of the plant communities) heteropteran specimens, have been randomly generated.
(7) The variables have also been standardized with their standard deviation.

To explore the similarity relations of the new objects obtained by stochastic simulation, principal coordinates analysis (metrical multidimensional scaling) has been used based on Euclidean distance:

$$EU_{jk} = \sqrt{\sum_{i=1}^{n}\left(x_{ij} - x_{ik}\right)^2} \ .$$

There are many samples, where not each of the sample parameters (object categories) examined were recorded by Loksa. Therefore, the method described above has been carried out on two sorts of data: (1) on the data matrix containing all samples (unfiltered data matrix, with looser criteria of comparability, without the steps 2–4); (2) on the data matrix containing only the samples, of which all of the four examined sample parameters (objects) are known (filtered data matrix, with stronger criteria of comparability, steps 1–7). The similarity patterns obtained by the two different methods have been compared in every case.

With two-sided *t*-test carried out on the coordinates obtained by PCoA of the randomly generated new objects, it can be examined whether the differences between the groups of objects are significant. If two groups of objects differ significantly along whether the horizontal or the vertical axis, their difference is significant. If no difference can be observed along either the horizontal or the vertical axis, their difference along another axis can be significant. This axis generally goes through the averages of the coordinates of the one and the other group of objects.

It is to be noted that data have been processed using numerous multivariate methods, other standardizations, similarity functions, etc., out of which only a few are published in this paper, but all of them have been used to draw the conclusions.

To compare diversity relations, Rényi's diversity ordering method has been applied.

For the multivariate data analysis the program package SYN-TAX 5.1 [2, 3] has been used. The diversity ordering has been carried out with the program package NuCoSA 1.05 [6, 7, 8].

Results and discussion

5060 specimens of Heteroptera have been found in the 3657 samples examined. The relative dominance of only 30 species is greater than 0.20% (*Table 1*).

Table 1. *The heteropteran species (at species level unidentified larvae included) with a relative dominance greater than 0.20%.*

Family	Included species	Relative dominance (%)
Ceratocombidae	*Ceratocombus (s. str.) coleoptratus* (Zetterstedt, 1819)	1.80
Dipsocoridae	*Cryptostemma (Pachycoleus) pusillimum* (J. Sahlberg, 1870)	2.37
	Cryptostemma (Pachycoleus) waltli (Fieber, 1860)	0.93
Hebridae	*Hebrus (Hebrus) pusillus pusillus* (Fallén, 1807)	0.20
	Hebrus (Hebrusella) ruficeps Thomson, 1871	8.08
	Hebrus spp. larvae	0.69
Veliidae	*Microvelia reticulata* (Burmeister, 1835)	0.38
Tingidae	*Campylosteira verna* (Fallén, 1826)	3.18
	Acalypta carinata (Panzer, 1806)	1.30
	Acalypta platycheila (Fieber, 1844)	0.22
	Acalypta marginata (Wolff, 1804)	1.07
	Acalypta parvula (Fallén, 1807)	2.87
	Acalypta gracilis (Fieber, 1844)	0.26
	Acalypta musci (Schrank, 1781)	7.08
	Acalypta spp. larvae	37.89
	Agramma (Agramma) confusum (Puton, 1879)	0.22
	tingid larvae	1.17
Microphysidae	*Loricula ruficeps* (Reuter, 1884)	0.40
	Myrmedobia exilis (Fallén, 1807)	0.22
	microphysid larvae	1.94
Miridae	mirid larvae	0.85
Anthocoridae	Anthocoridae (indet.)	0.47
Blissidae	*Dimorphopterus doriae* (Ferrari, 1874)	0.43
Piesmatidae	*Piesma maculatum* (Laporte, 1833)	0.73
Berytidae	berytid larvae	0.22
Rhyparochromidae	*Plinthisus (Plinthisus) brevipennis* (Latreille, 1807)	0.53
	Plinthisus (Plinthisomus) pusillus (Scholtz, 1847)	0.57
	Stygnocorini larvae	0.32
	Drymus (Sylvadrymus) ryeii Douglas & Scott, 1865	0.22
	Drymus (Sylvadrymus) b. brunneus (R. F. Sahlberg, 1848)	0.32
	Eremocoris podagricus (Fabricius, 1775)	0.24
	Tropistethus holosericus (Scholtz, 1846)	0.38
	Megalonotus sabulicola (Thomson, 1870)	0.26
	Rhyparochromus vulgaris (Schilling, 1829)	0.34
Lygaeidae s. lato families	Lygaeidae sensu lato larvae	9.09
Cydnidae	*Legnotus limbosus* (Geoffroy, 1785)	1.48
	cydnid larvae	0.42
Scutelleridae	*Eurygaster testudinaria* (Geoffroy, 1785)	0.20
Pentatomidae	*Sciocoris (Aposciocoris) homalonotus* Fieber, 1851	0.75
	Aelia acuminata (Linnaeus, 1758)	0.24
—	heteropteran larvae (indet.)	1.78

The majority of the species were collected in a very low number (with a relative dominance less than 0.20%). These species have been grouped for the statistical analysis (*Table 2*).

Table 2. *The species groups created by grouping the species (or at species level unidentified larvae) having a low (less than 0.20%) relative dominance based on their taxonomical position and body size.*

Species group	Included species	Relative dominance (%)
Nepomorpha + Gerromorpha	*Plea minutissima minutissima* Leach, 1817	0.02
	Hydrometra gracilenta Horváth, 1899	0.02
	Gerris (Gerris) thoracicus Schummel, 1832	0.02
	Gerris (Gerris) argentatus Schummel, 1832	0.04
	Gerris spp. larvae	0.02
	veliid larvae	0.02
Saldidae	*Chartoscirta cincta cincta* (Herrich-Schäffer, 1841)	0.04
	Chartoscirta elegantula (Fallén, 1807)	0.04
	Saldula saltatoria (Linnaeus, 1758)	0.10
	saldid larvae	0.20
Tingidae	*Campylosteira orientalis* Horváth, 1881	0.02
	Acalypta nigrina (Fallén, 1807)	0.10
	Derephysia (Derephysia) foliacea (Fallén, 1807)	0.06
	Stephanitis pyri (Fabricius, 1822)	0.02
	Lasiacantha capucina capucina (Germar, 1836)	0.16
	Tingis (Tingis) cardui (Linnaeus, 1758)	0.04
	Tingis (Tropidocheila) geniculata (Fieber, 1844)	0.02
	Tingis (Tropidocheila) reticulata Herrich-Schäffer, 1835	0.02
	Catoplatus carthusianus (Goeze, 1788)	0.04
	Copium teucrii teucrii (Host, 1788)	0.02
	Physatocheila costata (Fabricius, 1784)	0.06
	Oncochila scapularis (Fabricius, 1794)	0.02
	Dictyla humuli (Fabricius, 1794)	0.02
	Dictyla rotundata (Herrich-Schäffer, 1835)	0.02
	Dictyla echii (Schrank, 1781)	0.08
	Agramma (Agramma) minutum Horváth, 1874	0.06
	Agramma sp. larvae	0.04
Microphysidae	*Loricula pselaphiformis* Curtis, 1833	0.02
	Loricula elegantula (Bärensprung, 1858)	0.12
Miridae (< 5 mm)	*Monalocoris (Monalocoris) filicis* (Linnaeus, 1758)	0.02
	Deraeocoris (Knightocapsus) lutescens (Schilling, 1837)	0.04
	Orthops (Orthops) campestris (Linnaeus, 1758)	0.02
	Orthops (Orthops) kalmii (Linnaeus, 1758)	0.02
	Halticus apterus apterus (Linnaeus, 1758)	0.02
	Tytthus pygmaeus (Zetterstedt, 1838)	0.02
Miridae (5–10 mm)	*Lygus rugulipennis* Poppius, 1911	0.10
	Lygus pratensis (Linnaeus, 1758)	0.04
	Lygus gemellatus gemellatus (Herrich-Schäffer, 1835)	0.04
	Lygus sp.	0.04
	Stenodema (Brachystira) calcarata (Fallén, 1807)	0.02
	Miridae (indet.)	0.10
Nabidae (< 5 mm)	*Alloeorhynchus (Alloeorhynchus) flavipes* (Fieber, 1836)	0.04
Nabidae (5–10 mm)	*Himacerus (Aptus) mirmicoides* (O. Costa, 1834)	0.08
	Nabis (Nabis) rugosus (Linnaeus, 1758)	0.04
	Nabis (Nabis) ferus (Linnaeus, 1758)	0.12
	Nabis (Nabis) pseudoferus pseudoferus Remane, 1949 ♂♂	0.10
	Nabis (Nabis) pseudoferus pseudoferus Remane, 1949 ♀♀	0.10
	Nabis (Nabis) punctatus punctatus A. Costa, 1847 ♀♀	

ISSN 1589 1623

***Table 2** (continued).*

Species group	Included species	Relative dominance (%)
Reduviidae	*Phymata crassipes* (Fabricius, 1775)	0.02
	reduviid larvae	0.08
Aradidae	*Aradus cinnamomeus* Panzer, 1806	0.04
	Aradus distinctus Fieber, 1860	0.04
	Aneurus (Aneurodes) avenius (Dufour, 1833)	0.02
	Aneurus (Aneurus) laevis (Fabricius, 1775)	0.02
	aradid larvae	0.06
Piesmatidae	*Piesma capitatum* (Wolff, 1804)	0.08
	Parapiesma quadratum (Fieber, 1844)	0.06
	Parapiesma silenes (Horváth, 1888)	0.04
	Parapiesma salsolae (Becker, 1867)	0.16
	Parapiesma kochiae (Becker, 1867)	0.14
	Parapiesma sp.	0.02
Berytidae	*Berytinus (Berytinus) minor minor* (Herrich-Schäffer, 1835)	0.02
	Berytinus (Lizinus) signoreti (Fieber, 1859)	0.02
	Berytinus (Lizinus) montivagus (Meyer-Dür, 1841)	0.12
	Berytinus (Lizinus) geniculatus (Horváth, 1885)	0.02
	Berytinus (Lizinus) sp.	0.02
Lygaeidae s. str.	*Horvathiolus superbus* (Pollich, 1781)	0.02
	Lygaeosoma sardeum sardeum Spinola, 1837	0.02
	Nysius senecionis senecionis (Schilling, 1829)	0.04
Cymidae	*Cymus glandicolor* Hahn, 1832	0.02
	Cymus aurescens Distant, 1883	0.06
	Cymus sp.	0.16
Blissidae	*Dimorphopterus spinolae* (Signoret, 1857)	0.16
Geocoridae	*Geocoris (Geocoris) ater* (Fabricius, 1787)	0.04
Heterogastridae	*Platyplax salviae* (Schilling, 1829)	0.02
Oxycarenidae	*Oxycarenus (Oxycarenus) modestus* (Fallén, 1829)	0.02
	Macroplax preyssleri (Fieber, 1837)	0.20
	Macroplax fasciata fasciata (Herrich-Schäffer, 1835)	0.02
	Metopoplax origani (Kolenati, 1845)	0.12
	Camptotelus lineolatus lineolatus (Schilling, 1829)	0.02
	Tropidophlebia costalis (Herrich-Schäffer, 1850)	0.04
Rhyparochromidae (< 5 mm)	*Plinthisus (Plinthisus) longicollis* Fieber, 1861	0.12
	Plinthisus sp.	0.02
	Plinthisus spp. larvae	0.14
	Stygnocoris sabulosus (Schilling, 1829)	0.12
	Stygnocoris pygmaeus (R. F. Sahlberg, 1848)	0.16
	Acompus pallipes (Herrich-Schäffer, 1834)	0.02
	Drymus (Sylvadrymus) sylvaticus (Fabricius, 1775)	0.08
	Scolopostethus thomsoni Reuter, 1875	0.10
	Scolopostethus affinis (Schilling, 1829)	0.10
	Scolopostethus puberulus Horváth, 1887	0.04
	Scolopostethus pilosus pilosus Reuter, 1875	0.12
	Ischnocoris punctulatus Fieber, 1861	0.06
	Ischnocoris hemipterus (Schilling, 1829)	0.10
	Pionosomus opacellus Horváth, 1895	0.06
	Trapezonotus (Trapezonotus) a. arenarius (Linnaeus, 1758)	0.12
	Trapezonotus (Trapezonotus) dispar Stål, 1872	0.02
	Megalonotus chiragra (Fabricius, 1794)	0.08
	Megalonotus antennatus (Schilling, 1829)	0.04
	Megalonotus praetextatus (Herrich-Schäffer, 1835)	0.04

***Table 2** (continued).*

Species group	Included species	Relative dominance (%)
Rhyparochromidae (5–10 mm)	*Eremocoris plebejus* (Fallén, 1807)	0.02
	Emblethis verbasci (Fabricius, 1803)	0.04
	Emblethis griseus (Wolff, 1802)	0.04
	Emblethis denticollis Horváth, 1878	0.04
	Emblethis ciliatus Horváth, 1875	0.06
	Aphanus rolandri (Linnaeus, 1758)	0.02
	Peritrechus geniculatus (Hahn, 1832)	0.02
	Peritrechus gracilicornis Puton, 1877	0.08
	Peritrechus nubilus (Fallén, 1807)	0.04
	Beosus maritimus (Scopoli, 1763)	0.04
	Graptopeltus lynceus (Fabricius, 1775)	0.08
	Raglius alboacuminatus (Goeze, 1778)	0.02
	Rhyparochromus pini (Linnaeus, 1758)	0.02
	Pachybrachius fracticollis (Schilling, 1829)	0.10
Pyrrhocoridae	*Pyrrhocoris apterus* (Linnaeus, 1758)	0.04
	Pyrrhocoris marginatus (Kolenati, 1845)	0.02
Stenocephalidae	*Dicranocephalus* spp. larvae	0.02
Coreidae (5–10 mm)	*Spathocera obscura* (Germar, 1842)	0.04
	Bathysolen nubilus (Fallén, 1807)	0.04
	Coriomeris denticulatus (Scopoli, 1763)	0.04
	coreid larvae	0.04
Coreidae (> 10 mm)	*Coreus marginatus* (Linnaeus, 1758)	0.10
	Ceraleptus gracilicornis (Herrich-Schäffer, 1835)	0.02
Rhopalidae	*Rhopalus (Rhopalus) subrufus* (Gmelin, 1788)	0.02
	Brachycarenus tigrinus (Schilling, 1817)	0.08
Cydnidae (< 5 mm) + Thyreocoridae	*Microporus nigritus* (Fabricius, 1794)	0.04
	Thyreocoris scarabaeoides (Linnaeus, 1758)	0.16
Cydnidae (5–10 mm)	*Cydnus aterrimus* (Forster, 1771)	0.02
	Tritomegas bicolor (Linnaeus, 1758)	0.04
	Adomerus biguttatus (Linnaeus, 1758)	0.02
Scutelleridae (5–10 mm)	*Odontoscelis* spp. larvae	0.04
	scutellerid larvae	0.02
Scutelleridae (> 10 mm)	*Eurygaster austriaca* (Schrank, 1776)	0.12
	Eurygaster maura (Linnaeus, 1758)	0.12
Pentatomidae (< 10 mm)	*Podops inuncta* (Fabricius, 1775)	0.02
	Sciocoris (Sciocoris) cursitans (Fabricius, 1794)	0.08
	Sciocoris (Aposciocoris) microphthalmus Flor, 1860	0.02
	Dyroderes umbraculatus (Fabricius, 1775)	0.02
	Neottiglossa leporina (Herrich-Schäffer, 1830)	0.02
	Eusarcoris aeneus (Scopoli, 1763)	0.02
	Eurydema ventrale Kolenati, 1846	0.02
	Eurydema oleraceum (Linnaeus, 1758)	0.04
	pentatomid larvae	0.16
Pentatomidae (> 10 mm)	*Aelia rostrata* Boheman, 1852	0.02
	Dolycoris baccarum (Linnaeus, 1758)	0.02
	Palomena prasina (Linnaeus, 1758)	0.02
Acanthosomatidae	*Elasmucha grisea* (Linnaeus, 1758)	0.02

The ground-living heteropteran assemblages of different plant communities

The material

Loksa collected samples in numerous plant communities in Hungary (*Table 3*). To examine their similarity, the cenoses have to be pooled into cenosis groups because of the limited number of samples. The groups created are shown in *Table 4*.

Table 3. *The number of the samples taken in the different plant communities and community groups and the number of heteropteran specimens found in the samples.*

	Cenosis	Number of samples	Number of specimens
1	*Phragmitetum*	42	139
2	*Bolboschoenetum*	8	47
3	*Caricetum elatae*	18	41
4	*Caricetum acutiformis*	5	26
5	*Caricetum vulpinae*	5	26
6	*Carici-Sphagnetum*	7	9
7	*Eriophoro-Sphagnetum*	57	52
8	*Phragmiti-Sphagnetum*	32	46
9	other *Ledetalia*	2	13
10	*Callunetum*	4	3
11	*Juncetum subnodulosi*	1	13
12	*Molinietum*	2	8
13	*Agrostetum albae*	4	10
14	*Festucetum pratensis*	8	17
15	other *Molinio-Juncetea*	8	26
16	*Puccinellio-Salicornietea*	15	13
17	*Festucetum vaginatae*	7	25
18	*Brometum*	6	17
19	*Seslerietum* (*heuflerianae*)	20	16
20	*Festucetum dalmaticae*	2	—
21	*Festucetum sulcatae*	32	110
22	*Festucetum valesiacae*	11	22
23	*Festucetum pseudovinae*	7	10
24	*Stipetum*	6	9
25	*Dryopteridi-Alnetum*	24	22
26	*Calamagrosti-Salicetum*	18	83
27	*Betulo-Sphagnetum*	45	9
28	*Salicetea*	64	74
29	*Querco-Ulmetum*	96	239
30	*Salicion albae*	32	24
31	*Alnetum glutinosae-incanae*	40	188
32	*Carici-Alnetum*	30	98
33	*Aconito-Fagetum*	5	6
34	*Luzulo-Fagetum*	51	15
35	other *Fagetum*	117	108
36	*Mercuriali-Tilietum*	4	—
37	*Querco-Carpinetum*	311	332
38	other *Carpinetum*	14	5
39	*Luzulo-Quercetum*	64	26
40	*Cotino-Quercetum*	10	5
41	*Orno-Quercetum*	75	22

***Table 3** (continued).*

	Cenosis	Number of samples	Number of specimens
42	*Quercetum petraeae-cerris*	246	151
43	*Ceraso-Quercetum*	40	426
44	*Festuco-Quercetum*	31	18
45	*Spiraeetum mediae*	30	72
46	*Tilio-Fraxinetum*	91	125
47	*Aceri (tatarico)-Quercetum*	3	—
48	*Corno-Quercetum*	36	18
49	*Convallario-Quercetum*	5	3
50	*Robinietea*	58	52
51	*Pinetea + Piceetea*	96	83

***Table 4.** The groups of cenoses created from the associations investigated by Loksa.*

	Cenosis group	Included cenoses (see *Table 3*)
1	reed beds and large sedge communities (*Phragmitetea*)	1–5
2	bogs and acidic fens (*Caricetalia fuscae + Ledetalia*)	6–9
3	humid grassland communities (*Molinio-Juncetea*)	11–15
4	steppe and dry calcareous grasslands (*Festuco-Brometea*)	18–24
5	alder swamp woods (*Alnetea glutinosae*)	25–27
6	riparian willow formations, stream ash-alder woods and other riverine forests (*Alno-Padion + Alnenion glutinosae-incanae + Salicetea*)	28–32
7	Medio-European beech forests and oak-hornbeam forests (*Fagion medio-europaeum*)	33–38
8	dry and mesophile oak woods, mixed forests and deciduous thickets (*Quercion pubescenti-petraeae*)	42–50
9	coniferous forests (*Pinetea + Piceetea*)	51

If we examine the data matrix containing only the samples, of which all the four sample parameters (object categories) examined are known, not all of the plant community groups mentioned before can be compared because of the limited number of samples. Therefore, other groups of cenoses have to be created (*Table 5*).

***Table 5.** The number of the samples taken in different groups of cenoses obtained from filtered data matrix (see in text) and the number of heteropteran specimens found in this samples.*

	Cenosis group	Included cenoses (see *Table 3*)	Number of samples	Number of specimens
1	humid treeless communities	1–9, 11–15	137	190
2	humid wooded communities	25–32	286	675
3	Medio-European beech forests and oak-hornbeam forests	33–38	341	425
4	dry and mesophile oak woods, mixed forests and deciduous thickets	42–50	399	516

The patterns observed

The similarity pattern of the objects obtained from different groups of plant communities of the unfiltered data matrix by stochastic simulation is shown in *Fig. 1.*

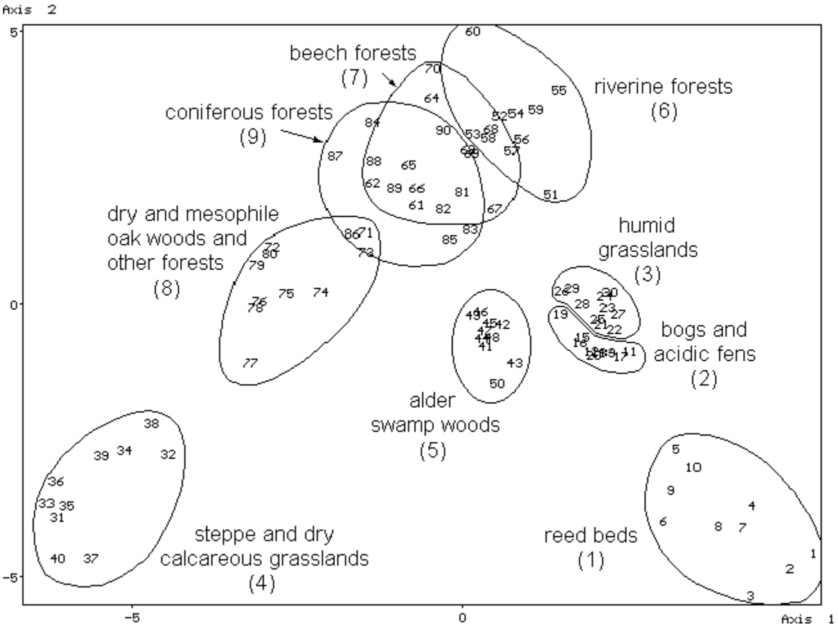

Figure 1. *The similarity pattern of the objects obtained from cenosis groups 1–9 (unfiltered data matrix; see Table 4) by stochastic simulation.*

With *t*-test carried out on the coordinates obtained by PCoA of the new objects generated, it can be established that differences between any two cenoses – except that between beech and oak-hornbeam forests (cenosis group 7) and coniferous forests (cenosis group 9) – are significant at least at 0.05 level (*Table 6*).

Table 6. *Comparison of the coordinates obtained by PCoA of the objects obtained by stochastic simulation from cenosis groups 1–9 (unfiltered data matrix; see Table 4) by t-test. In the cells, the upper value means the significance along Axis 1 and the lower value the significance along Axis 2. Significant differences are marked by shaded cells. (*$p < 0.05$, **$p < 0.01$)*

	1	2	3	4	5	6	7	8	9
1	1.00 1.00	$4.70\cdot10^{-6}$ ** $1.12\cdot10^{-7}$ **	$1.02\cdot10^{-5}$ ** $1.95\cdot10^{-8}$ **	$1.91\cdot10^{-16}$ ** $1.63\cdot10^{-1}$	$6.18\cdot10^{-8}$ ** $2.79\cdot10^{-14}$ **	$1.34\cdot10^{-8}$ ** $7.09\cdot10^{-14}$ **	$1.09\cdot10^{-10}$ ** $5.73\cdot10^{-13}$ **	$1.16\cdot10^{-13}$ ** $2.41\cdot10^{-10}$ **	$3.97\cdot10^{-11}$ ** $1.46\cdot10^{-12}$ **
2		1.00 1.00	$9.73\cdot10^{-1}$ $4.94\cdot10^{-6}$ **	$8.50\cdot10^{-14}$ ** $1.86\cdot10^{-6}$ **	$4.75\cdot10^{-10}$ ** $2.71\cdot10^{-1}$	$1.89\cdot10^{-6}$ ** $7.97\cdot10^{-9}$ **	$3.74\cdot10^{-8}$ ** $1.04\cdot10^{-7}$ **	$8.74\cdot10^{-1}$ ** $3.46\cdot10^{-4}$ **	$1.24\cdot10^{-7}$ ** $2.46\cdot10^{-7}$ **
3			1.00 1.00	$1.94\cdot10^{-13}$ ** $1.30\cdot10^{-7}$ **	$9.98\cdot10^{-11}$ ** $2.27\cdot10^{-3}$ **	$1.97\cdot10^{-6}$ ** $4.23\cdot10^{-8}$ **	$5.06\cdot10^{-5}$ ** $8.37\cdot10^{-7}$ **	$1.48\cdot10^{-10}$ ** $7.48\cdot10^{-2}$	$1.60\cdot10^{-7}$ ** $3.38\cdot10^{-6}$ **
4				1.00 1.00	$3.87\cdot10^{-11}$ ** $3.83\cdot10^{-7}$ **	$2.38\cdot10^{-14}$ ** $3.70\cdot10^{-13}$ **	$3.29\cdot10^{-13}$ ** $3.03\cdot10^{-12}$ **	$8.69\cdot10^{-9}$ ** $2.71\cdot10^{-9}$ **	$1.29\cdot10^{-11}$ ** $9.47\cdot10^{-12}$ **
5					1.00 1.00	$4.66\cdot10^{-2}$ * $1.39\cdot10^{-9}$ **	$3.12\cdot10^{-3}$ ** $3.88\cdot10^{-8}$ **	$6.50\cdot10^{-8}$ ** $1.26\cdot10^{-3}$ **	$5.19\cdot10^{-4}$ ** $1.20\cdot10^{-7}$ **
6						1.00 1.00	$2.56\cdot10^{-4}$ ** $1.08\cdot10^{-1}$	$7.70\cdot10^{-10}$ ** $7.16\cdot10^{-8}$ **	$4.79\cdot10^{-5}$ ** $3.25\cdot10^{-3}$ **
7							1.00 1.00	$2.99\cdot10^{-7}$ ** $3.68\cdot10^{-6}$ **	$1.39\cdot10^{-1}$ $1.34\cdot10^{-1}$
8								1.00 1.00	$2.99\cdot10^{-7}$ ** $3.68\cdot10^{-6}$ **
9									1.00 1.00

The similarity pattern of the objects obtained from the cenosis groups of the filtered data matrix by stochastic simulation is shown in *Fig. 2.* The segregation of the humid treeless (cenosis group 1), the humid wooded (cenosis group 2) communities from each other and from the beech and oak woods (cenosis groups 3 and 4) can be observed. With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that only the difference between beech and oak woods is not significant at 0.05 level (*Table 7*).

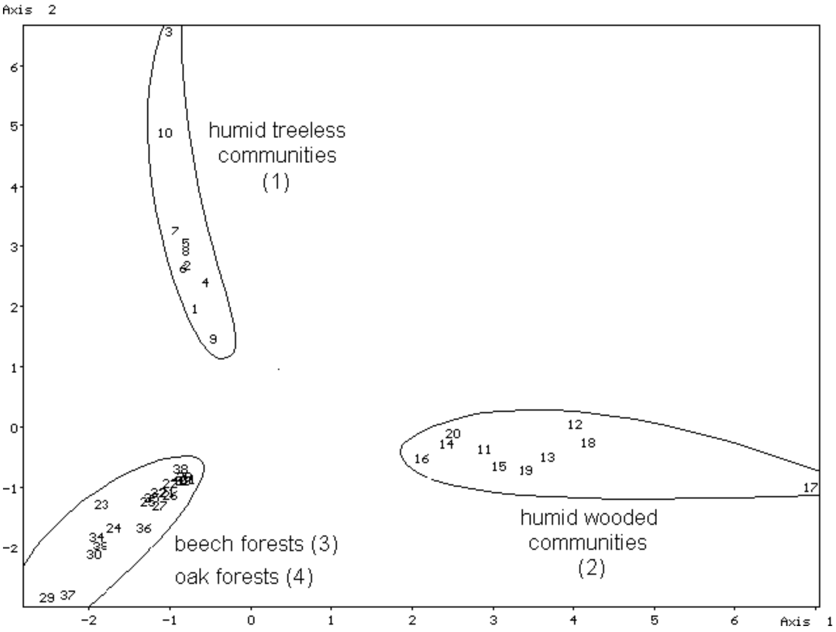

***Figure 2**. The similarity pattern of the objects obtained from cenosis groups 1–4 (filtered data matrix; see Table 5) by stochastic simulation.*

***Table 7.** Comparison of the coordinates obtained by PCoA of the objects obtained by stochastic simulation from cenosis groups 1–4 (filtered data matrix; see Table 5) by t-test (probabilities). In the cells, the upper value means the difference along Axis 1 and the lower value the difference along Axis 2. Significant differences are marked by shaded cells.(*p < 0.05,**p < 0.01)*

	1	2	3	4
1	1.00 1.00	$3.40\cdot10^{-6}$ ** $2.36\cdot10^{-5}$ **	$5.62\cdot10^{-3}$ ** $1.06\cdot10^{-6}$ **	$1.45\cdot10^{-2}$ * $1.03\cdot10^{-6}$ **
2		1.00 1.00	$2.55\cdot10^{-7}$ ** $4.59\cdot10^{-4}$ **	$3.59\cdot10^{-7}$ ** $1.29\cdot10^{-3}$ **
3			1.00 1.00	$6.36\cdot10^{-1}$ $8.54\cdot10^{-1}$
4				1.00 1.00

By studying the diversity conditions of samples collected in the six most exhaustively investigated plant communities by Rényi's method, the diversity profiles shown in *Fig. 3* have been obtained. It can be established that at the begin of scale parameter, in the section sensitive to rare species, the diversities of samples extracted from reed beds and large sedge communities, riverine forests and beech forests are considerably higher than that of bogs and acidic fens, dry grassy communities and dry and mesophile woods. The ground-living true bug assemblages of the three latter community groups have a very low diversity at the great values of scale parameter, in the section sensitive to frequent species, because there is one species in each having a very high dominance. These are the sphagnum bug *Hebrus ruficeps* (with a relative dominance of 90.08%) in bogs and acidic fens, the Lygaeidae sensu lato larvae (40.32%) in dry grasslands and the larvae of *Acalypta* spp. (43.40%) in dry and mesophile oak woods, mixed forest and deciduous thickets.

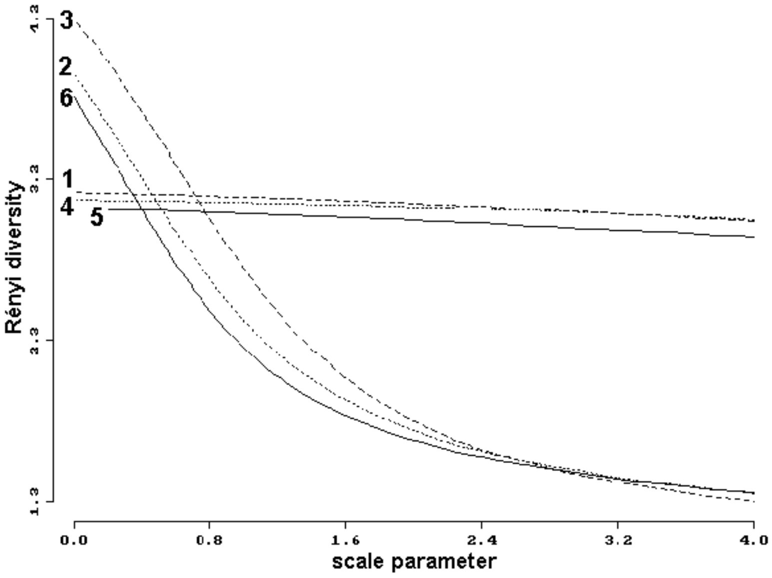

Figure 3. *The diversity profiles of the samples taken from different groups of plant communities (Rényi-diversity). The numbers mean the groups of coenoses:* **1** *= reed beds and large sedge communities,* **2** *= bogs and acidic fens,* **3** *= steppe and dry calcareous grasslands,* **4** *= riparian willow formations, stream ash-alder woods and other riverine forests,* **5** *= Medio-European beech forests and oak-hornbeam forests,* **6** *= dry and mesophile oak woods, mixed forests and deciduous thickets.*

Discussion of the patterns

The similarity pattern (*Fig. 1*) obtained from the unfiltered data matrix shows that in some plant communities characteristic ground-living bug assemblages can be found. Regarding the pattern, it seems to be clear that the variability of the objects through Axis 1 have relation to the humidity and that of through Axis 2 to the wooded or treeless character of the plant communities. By examining the unfiltered data matrix, it can be observed that the pattern obtained is determined mostly by the relations of the three species and species groups having the highest relative dominance: *Hebrus ruficeps*, larvae of *Acalypta* spp. and Lygaeidae sensu lato larvae. Each of them can be found in almost all communities, but the relative dominance of *Hebrus ruficeps* shows increase, that of Lygaeidae sensu lato larvae shows decrease parallel with the increase of the value of Axis 1. On the other hand, the relative dominance of *Acalypta* spp. larvae shows increase parallel with the increase of the value of Axis 2. Accordingly, *Hebrus ruficeps*, a semiaquatic bug species, can be found with highest dominance at the ground-level of humid treeless plant communities, Lygaeidae sensu lato larvae in dry treeless and wooded communities and so in the alder swamp woods, and the larvae of *Acalypta* spp. in wooded cenoses (except the alder swamp woods). Consequently, this three species and species groups determine the triangular shape of the similarity pattern (*Fig. 4*).

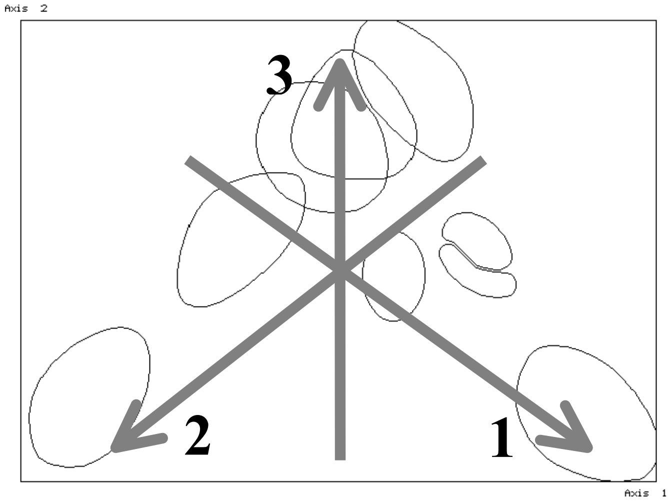

Figure 4. *The direction of the increase of relative dominance of the three species and species group with highest dominance on the similarity pattern (Fig. 1).* **1** *= Hebrus ruficeps,* **2** *= Lygaeidae sensu lato larvae,* **3** *= Acalypta spp. larvae.*

Regarding the individual plant communities and heteropteran species, it can be established that, in addition to the species and species groups before, in most of the cenoses the species *Ceratocombus coleoptratus*, *Rhyparochromus vulgaris*, *Aelia acuminata* and so the species groups Tingidae, Miridae, Oxycarenidae, Rhyparochromidae and pentatomid adults with a body size of 5–10 mm can be found. The species belonging to the species groups mentioned before have by all means more or less well-defined habitat preference, but the groups united from various species with diverse preferences can be found in most of the plant communities. Furthermore, the species pooled into groups cannot be examined one by one because of their very low relative dominance.

No frequent species or species group were found to be characteristic of all treeless communities (cenosis groups 1–4). *Acalypta carinata* and all microphysid species (*Loricula ruficeps*, *Myrmedobia exilis* and the group united from the low-dominance species of the family) seem to occur characteristically at the ground-level of dry and humid wooded cenoses (cenosis groups 5–9).

At the ground-level of most of the humid communities regardless of their wooded or treeless character (cenosis groups 1–3, 5, 6), the saldids and cymids occur. The species *Acalypta parvula*, *A. gracilis*, *Dimorphopterus doriae* and *Megalonotus sabulicola* were found to be characteristic of all dry communities (cenosis groups 4, 7–9).

The following species and species groups seem to occur characteristic in hygrophilous treeless associations (cenosis groups 1–3): *Cryptostemma pusillimum*, *Hebrus pusillus* and *H. ruficeps*, *Microvelia reticulata*, *Agramma confusum* and the group Nepomorpha + Gerromorpha. Out of these, *Hebrus ruficeps* can be found in most of the plant communities. Nevertheless, it can be extracted in these groups of cenoses usually in large numbers, but occurs only sporadically in the others. The segregation of the ground-living bug assemblages of the reed beds and large sedge communities (cenosis group 1) from that of the other two hygrophilous treeless associations (cenosis groups 2–3) is caused mostly by the occurrence of the aquatic and semiaquatic bugs. The relative dominance of *Hebrus ruficeps* was strikingly higher in the former cenosis group than in the latter two groups of cenoses. Furthermore, the species *Hebrus pusillus*, *Microvelia reticulata* and the species group Nepomorpha + Gerromorpha were collected only in the former cenosis group.

Usually none or a very limited number of the above-mentioned species occur in dry grasslands (cenosis group 4). The ground-living heteropteran assemblages of this group of plant communities consist of mostly the frequent species occurring in most of the communities and the species, which are characteristic of dry forests. The relative dominance of the Lygaeidae sensu lato larvae is high, too. The species *Campylosteira verna*, *Acalypta musci*, *Piesma maculatum* and the species groups of Nabidae with a size of 5–10 mm and Piesmatidae occur in dry grassy communities as well as in most of the (humid and dry) wooded cenoses, but are to be found in any of the humid treeless communities.

The single species collected mostly in wet forests (cenosis groups 5 and 6) is the seed bug *Drymus brunneus*. The ground-living heteropteran assemblages of these forests consist of frequent species occurring in most cenoses and species characteristic of all humid plant communities.

The segregation of the ground-living bug communities of the different mesophile, xero-mesophile or xerophile forests (cenosis groups 7–9) seems to have relation with the humidity. The difference between the community of beech and oak-hornbeam forests (cenosis group 7) and that of coniferous forests (cenosis group 9) are not significant at 0.05 level. The seed bug *Drymus ryeii* occurs in all of these groups of communities. This species seems to be more xerophilous than the other high-dominance species of the genus, *D. brunneus*.

Comparison of the ground-living heteropteran assemblages of different substrata

The material

The most important substrata examined are shown in *Table 8*. Another 1198 samples of other or unrecorded substrata were also extracted.

Table 8. *The number of the samples of different substratum categories extracted by Loksa and the number of heteropteran specimens found in these samples.*

	Substratum	Number of samples	Number of specimens
1	mosses on tree trunks	225	725
2	mosses on stones and rocks	292	1240
3	mosses on ground	259	520
4	other mosses (growing on unrecorded surface)	117	221
5	*Sphagnum*	94	107
6	soil	390	159
7	leaf litter, debris	795	586
8	tussocks, tufts of sedges	287	209

If we examine the data matrix containing only the samples, of which all of the four sample parameters (object categories) examined are known, not all of the substratum categories mentioned before can be compared because of the limited number of samples. Therefore, new substratum categories have to be created (*Table 9*).

Table 9. *The number of the samples of different substratum categories obtained from filtered data matrix (see in text) and the number of heteropteran specimens found in these samples.*

	Substratum	Number of samples	Number of specimens
1	tussocks, tufts of sedges	132	133
2	mosses	448	978
3	*Sphagnum*	66	64
4	soil, leaf litter, debris	539	335

The patterns observed

The similarity pattern of the objects obtained from different substrata of the unfiltered data matrix by stochastic simulation is shown in *Fig. 5.* The different mosses appear very close to each other, therefore their analysis have been performed separately, too (*Fig. 6*).

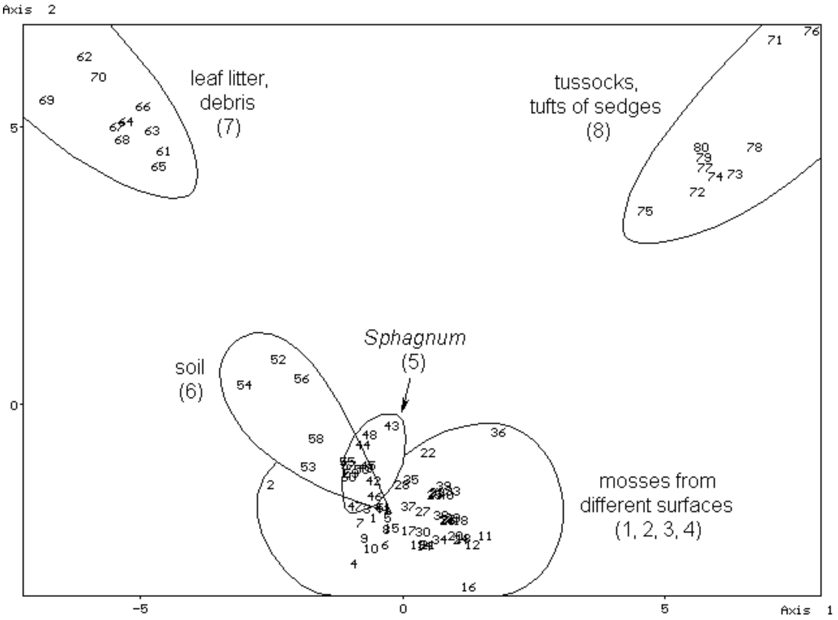

Figure 5. *The similarity pattern of the objects obtained from substrata 1–8 (unfiltered data matrix; see Table 8) by stochastic simulation.*

By studying the similarity relations, it has been established that characteristic ground-living heteropteran communities were segregated in some substrata. The similarity pattern shows that the assemblages extracted from soil and from different mosses including *Sphagnum* species are highly similar. On the other hand, the assemblages of debris and that of tussocks differ from the assemblages of preceding substrata and from each other, too.

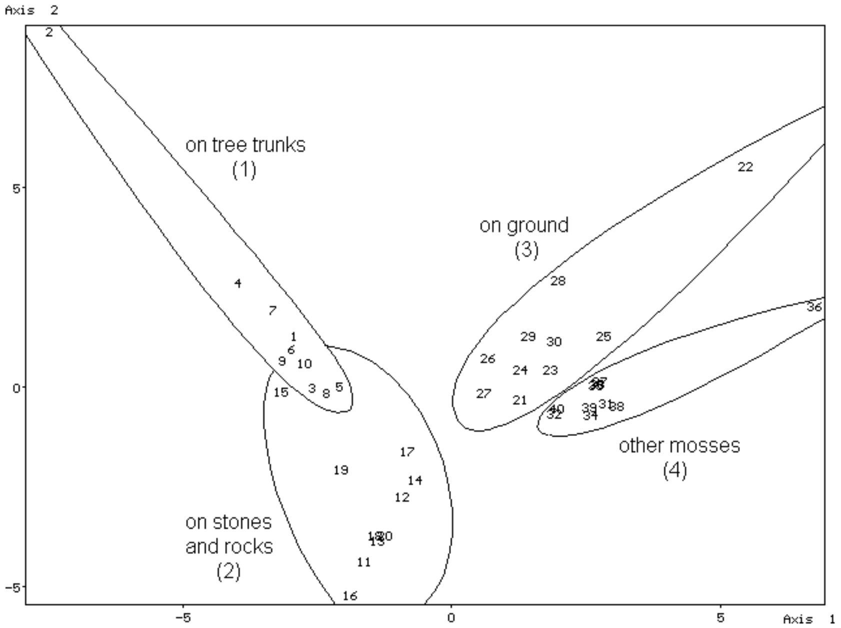

__Figure 6.__ The similarity pattern of the objects obtained from different mosses (unfiltered data matrix; see Table 8) by stochastic simulation.

With *t*-test carried out on the obtained coordinates of the generated new objects, it can be proved that differences between any two substrata – except from the group of the mosses growing on the ground and that of the „other” (on unrecorded surface growing) mosses – are significant at least at 0.05 level. The above-mentioned two groups of mosses do not differ significantly along either the horizontal or the vertical axis, but their difference is significant along the axis going through the averages of the coordinates of the one and the other group of objects.

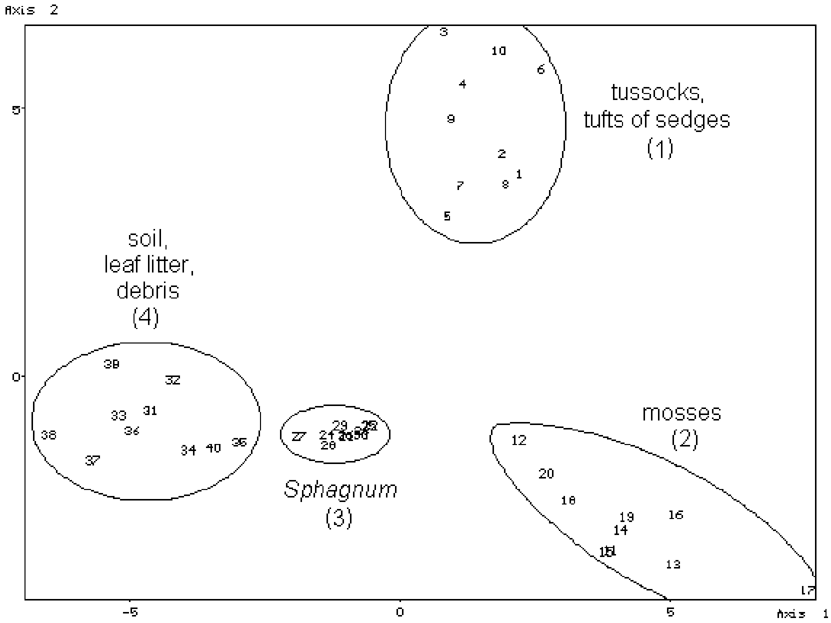

__Figure 7.__ The similarity pattern of the objects obtained from substrata 1–4 (filtered data matrix; see Table 9) by stochastic simulation.

The similarity pattern of the objects obtained from different substratum categories of the filtered data matrix by stochastic simulation is shown in *Fig. 7.* It can be observed that this pattern is substantially identical to that obtained from the unfiltered data matrix (*Fig. 5*). By examining the data matrix, it can be established that the similarity pattern obtained is determined mostly by the dominance relations of the same species and species groups as the similarity pattern obtained from the unfiltered data matrix. With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that differences between the assemblages living in any substrata are significant at least at 0.05 level.

By studying the diversity conditions of heteropteran communities by Rényi's method the diversity profiles shown in *Fig. 8* have been obtained. It can be established that the diversity of samples extracted from different mosses and from leaf litter are lower than that extracted from soil and from *Sphagnum*.

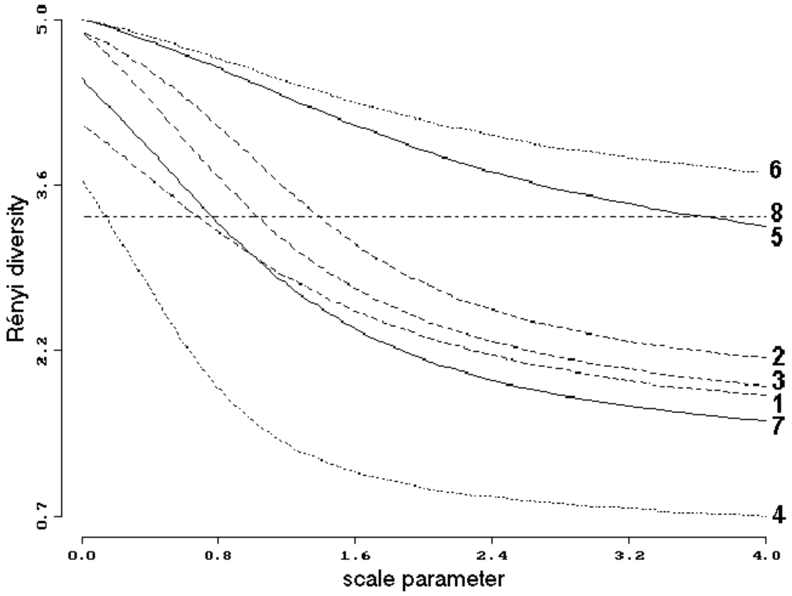

Figure 8. *The diversity profiles of the samples extracted from different substrata (Rényi-diversity). The numbers mean the substratum types (see in Table 8).*

Discussion of the patterns

By examining the unfiltered data matrix, it can be established that the obtained similarity pattern is determined mostly by the dominance relations of the three most dominant species and species groups: *Acalypta musci*, larvae of *Acalypta* spp. and Lygaeidae sensu lato larvae. Each of them can be found in almost all of the substrata, but the relative dominance of *Acalypta musci* is considerably high in coats of different mosses. Also, that of the larvae of *Acalypta* spp. in the mosses and in/on the soil, and that of Lygaeidae sensu lato larvae in the leaf litter is high. The relative dominance of each of them is low in tussocks.

Regarding the individual heteropteran species, it can be observed that the number of species, which can be found in most of the substrata including soil, is considerably high. Such species are *Hebrus ruficeps*, *Campylosteira verna*, *Acalypta carinata*, *A. parvula*, *Loricula ruficeps*, *Piesma maculatum*, *Plinthisus brevipennis* (the relative dominance of

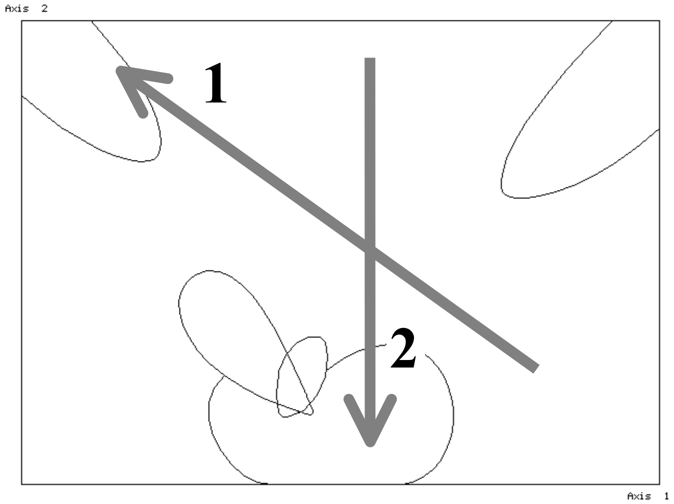

Figure 9. *The direction of the increase of relative dominance of the three most dominant species and species group on the similarity pattern (Fig. 5).* **1** *= Lygaeidae sensu lato larvae,* **2** *= Acalypta musci and Acalypta spp. larvae.*

P. brevipennis is especially high in leaf litter). In most of the substrata the following species groups can be found: Nabidae with a size of 5–10 mm, Rhyparochromidae with a size of 5–10 mm. A great number of the preceding species and species groups are zoophagous (*Hebrus ruficeps*, *Loricula ruficeps*, nabids), whereas another great number feed on mature seeds (most of rhyparochromid adults, maybe *Plinthisus brevipennis* too, whose life habits are insufficiently known). According to literature data [1], the species of the lace bug genera *Campylosteira* and *Acalypta* are phytophagous, living mostly in coats of mosses or on stems of different herbaceous plants. However, many of them were found in leaf litter, or even in/on the soil.

The number of ground-living bug species, which can be found in most of the living or died vegetal substrata but not in soil, is high, too. Such species are: *Ceratocombus coleoptratus*, *Cryptostemma pusillimum*, *Acalypta platycheila*, *A. marginata*, *A. musci*, *Myrmedobia exilis*, *Rhyparochromus vulgaris*, and the following species groups: Saldidae, Tingidae (adults and larvae), Miridae with a size of 5–10 mm, mirid larvae, Oxycarenidae. The zoophagous and seed feeder species of the previous taxa (*Ceratocombus coleoptratus*, Saldidae, *Myrmedobia exilis*, *Rhyparochromus vulgaris*) may occur directly on the ground, too. The species of the genus *Acalypta* are phytophagous, therefore they live mostly on their host plants and occur in different vegetal substrata. Our knowledge on the life habits of *Cryptostemma pusillimum* is insufficient, but according to our recent data, it is associated with humid vegetal substrata [4].

Most of the dominant species typical in leaf litter and debris belong to the family Rhyparochromidae (*Drymus ryeii*, *D. brunneus*, *Eremocoris podagricus*, *Megalonotus sabulicola*). In this type of substrata, the relative dominance of the Lygaeidae sensu lato larvae is the highest, whereas that of *Acalypta musci* and the *Acalypta* spp. larvae is low.

No species was found to be characteristic of tussocks or tufts of sedges. The relative dominances of the most dominant three species and species groups (*Acalypta musci*, *Acalypta* spp. larvae, Lygaeidae sensu lato larvae) are very low in these substrata.

No species was found to be characteristic of *Sphagnum*, either. *Ceratocombus coleoptratus* and *Hebrus ruficeps* have the highest relative dominance in this type of substrata; *Cryptostemma pusillimum*, the groups Saldidae and Miridae occurs here, too. The similarity between the ground-living bug assemblage of this type of substratum and that of the other mosses is due to the low relative dominance of the Lygaeidae sensu lato larvae.

Furthermore, any high-dominance species have been proved to be characteristic of coats of different mosses. According to literature data [1], the species of lace bug genera *Campylosteira* and *Acalypta* are mostly muscicolous. However, most species of them were collected in a great number from many other substrata, too. More specimens of the *Acalypta* species were found in mosses than in any other substrata. On the other hand, only 16.2% of the adults of *Campylosteira verna* were collected from mosses; 61.6% of them were extracted from leaf litter. The following species and species groups can be collected in a great number from coats of different mosses: *Campylosteira verna*, *Acalypta marginata*, *A. parvula*, *Loricula ruficeps*, *Plinthisus pusillus*, *Rhyparochromus vulgaris*, mirids with a size of 5–10 mm, nabids with a size of 5–10 mm, Anthocoridae, pentatomids with a size of 5–10 mm.

Some species prefer a certain moss type. The moss coats growing on stones and rocks are preferred by *Acalypta musci*, the *Acalypta* spp. larvae and the Stygnocorini larvae. The mosses growing on tree trunks, on the ground and on other surfaces are preferred by *Ceratocombus coleoptratus*, both *Cryptostemma* as well as both *Hebrus* species and their larvae, the species *Acalypta carinata*, *A. platycheila*, *Myrmedobia exilis*. Furthermore the group obtained from the low-dominance species of Microphysidae, *Piesma maculatum* and the group obtained from the low-dominance species of Piesmatidae, the Lygaeidae sensu lato larvae and both species groups of rhyparochromid adults are characteristic in this type of substratum.

Differences between the heteropteran communities of the different moss types can be explained by the different circumstances in the coats of mosses. For example, the mosses growing on the ground are usually more humid than on tree trunks, and the mosses growing on stones and rocks are, as a rule, drier than the above mentioned two types. Consequently, a great number of the species preferring humid conditions can be generally found in mosses growing on the ground, on tree trunks, etc., but never in mosses growing on stones and rocks. The seed feeder rhyparochromid species, which move mostly on the ground, can be found usually in the mosses growing on the ground.

Comparison of ground-living heteropteran assemblages collected in different phytogeographical provinces of Hungary

The material

Loksa collected samples in all of the great phytogeographical provinces of Hungary (*Table 10*). The numbers of samples taken in the provinces Praeillyricum, Praenoricum and in the Arrabonicum district of province Eupannonicum are considerably lower than that of the other provinces. Therefore, only the samples collected in provinces Eupannonicum (except Arrabonicum), Bakonyicum and Matricum have been compared.

Table 10. *The number of the samples taken by Loksa in different provinces or districts of Hungary and the number of heteropteran specimens found in this samples.*

	Provinces (districts)	Number of samples	Number of specimens
1	Eupannonicum (except Arrabonicum)	731	1283
2	Bakonyicum	964	1225
3	Matricum	1444	1844
4	Praeillyricum	182	277
5	Eupannonicum (Arrabonicum)	20	12
6	Praenoricum	139	323

The patterns observed

The similarity pattern of the objects obtained from samples of the unfiltered data matrix by stochastic simulation is shown in *Fig. 10.*

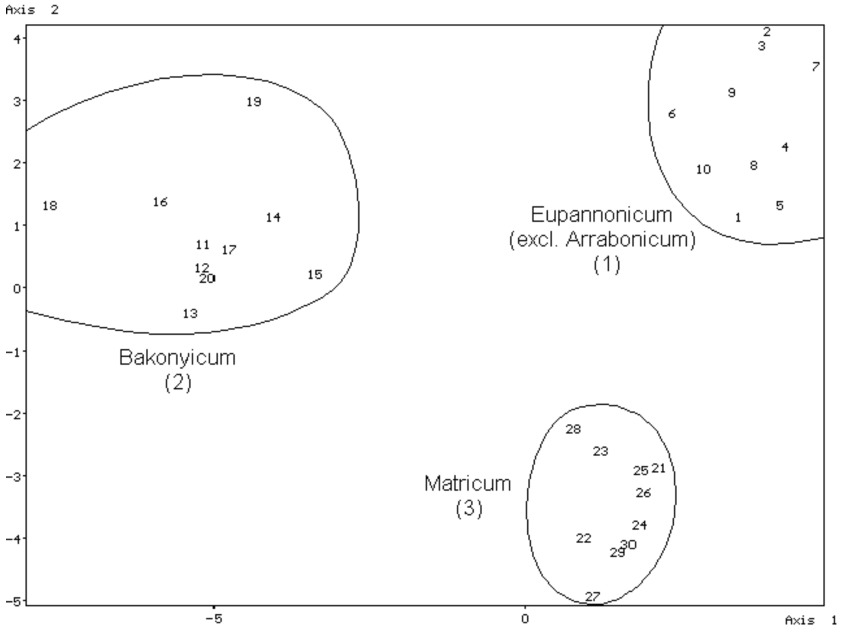

Figure 10. *The similarity pattern of the objects obtained by stochastic simulation from samples taken in the phytogeographical provinces 1–3 (unfiltered data matrix; see Table 10).*

With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that differences between any two provinces are significant at 0.01 level.

The similarity pattern of the objects obtained from different phytogeographical provinces of the filtered data matrix by stochastic simulation is shown in *Fig. 11.* It can be observed that this pattern is substantially identical to that obtained from the unfiltered data matrix (*Fig. 10*). By examining the data matrix, it can be established that the similarity pattern obtained is determined mostly by the dominance relations of the same species and species groups as the similarity pattern obtained from the unfiltered data matrix. With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that the differences between any two provinces are significant at 0.01 level.

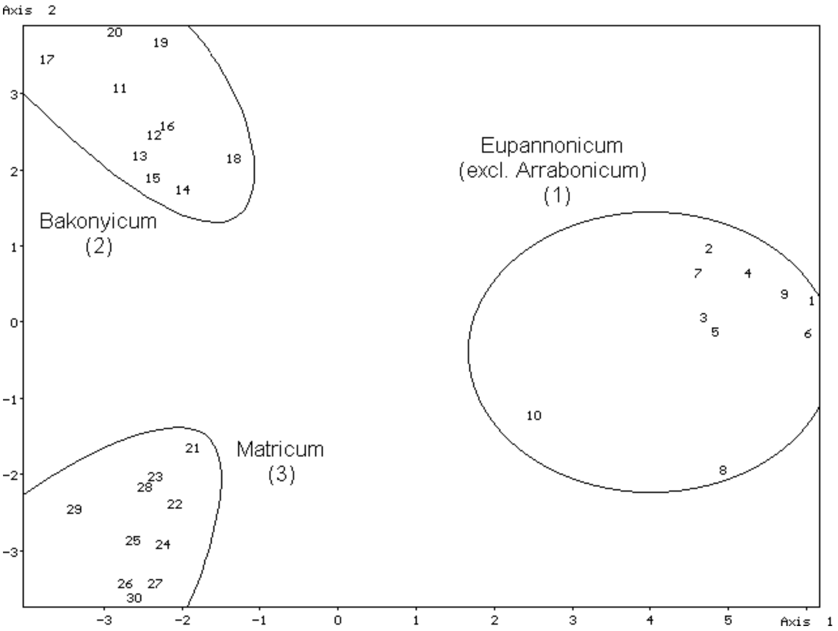

Figure 11. *The similarity pattern of the objects obtained by stochastic simulation from samples taken in the phytogeographical provinces 1–3 (see Table 10).*

By studying the diversity conditions of ground-living heteropteran assemblages by Rényi's method, the diversity profiles shown in *Fig. 12* have been obtained. It can be established that the diversity of the samples collected in the Bakonyicum is higher than that of the samples collected in the Matricum. Furthermore, at the begin of scale

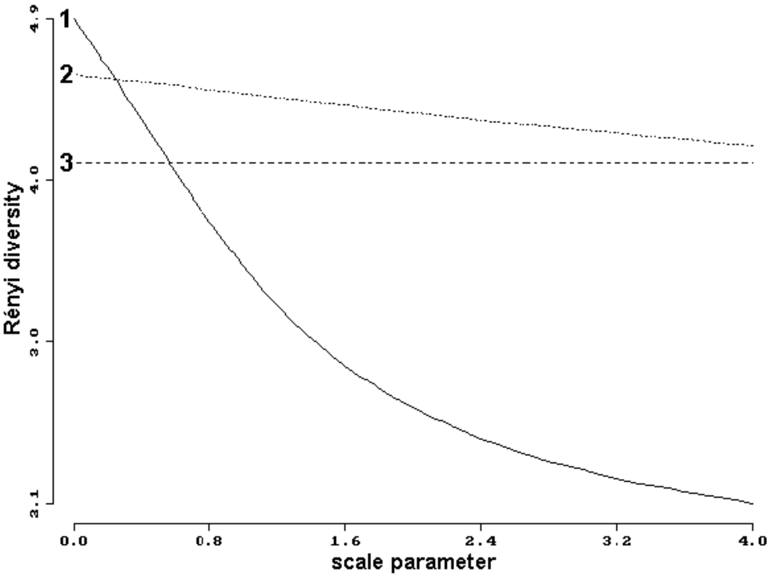

Figure 12. *The diversity profiles of the samples taken in different phytogeographical provinces in Hungary (Rényi-diversity).* **1** *= Eupannonicum (except Arrabonicum),* **2** *= Bakonyicum,* **3** *= Matricum.*

parameter, in the section sensitive to rare species, the samples collected in the former two provinces are less diverse than the ones collected in the province Eupannonicum. At the great values of scale parameter, in the section sensitive to frequent species, this relation is just the opposite.

Discussion of the patterns

By examining the unfiltered data matrix, it can be established that the similarity pattern obtained is determined mostly by the dominance relations of the four most dominant species and species groups: *Hebrus ruficeps*, *Acalypta musci*, larvae of *Acalypta* spp. and Lygaeidae sensu lato larvae. The relative dominance of the former three species and species group shows decrease parallel with the increase of the value of Axis 2. The relative dominance of Lygaeidae sensu lato larvae increases parallel with the increase of the value of Axis 1.

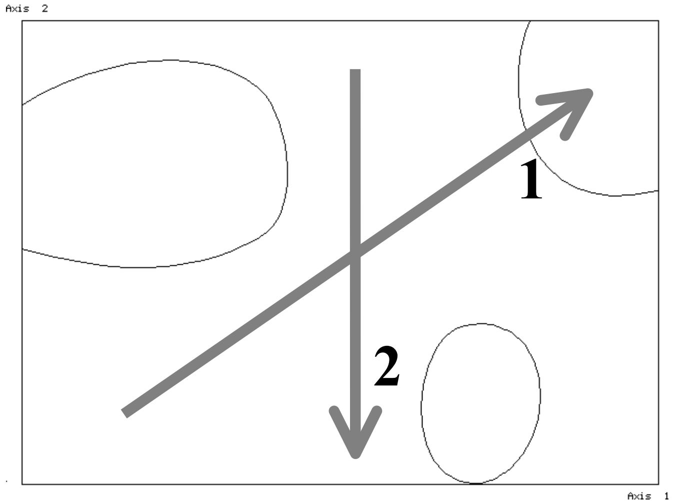

***Figure 13**. The direction of the increase of relative dominance of the most dominant four species and species group on the similarity pattern (Fig. 10).* **1** *= Lygaeidae sensu lato larvae,* **2** *= Hebrus ruficeps, Acalypta musci and Acalypta spp. larvae.*

Regarding the individual heteropteran species, it can be observed that the majority of the species were collected in all of the three examined provinces of Hungary. The species *Agramma confusum*, *Dimorphopterus spinolae* and the families Piesmatidae, Cymidae and Geocoridae were found mostly in lowlands (province Eupannonicum). The following ones were collected mostly in the hilly provinces (Bakonyicum and Matricum): *Microvelia reticulata*, *Acalypta parvula*, *Megalonotus sabulicola*, *Rhyparochromus vulgaris*, *Eurygaster testudinaria*, *Sciocoris homalonotus*.

Comparison of ground-living heteropteran assemblages collected in different seasons

The material

For the sake of simplicity, we mean „spring” by the period between the 1st of March and 31st of May, „summer” between 1st of June and 31st of August, „autumn” between 1st of September and 30th of November, „winter” between 1st of December and 28/29th of February further on. Accordingly, the number of samples taken in these seasons and the number of heteropteran specimens found in them are shown in *Table 11.*

Table 11. *The number of the samples taken by Loksa in different seasons and the number of heteropteran specimens found in these samples.*

	Seasons	Number of samples	Number of specimens
1	spring (1. III–31. V)	848	866
2	summer (1. VI–31. VIII)	824	1133
3	autumn (1. IX–30. XI)	1420	2304
4	winter (1. XII–28/29. II)	236	440

The patterns observed

The similarity pattern of the objects obtained from samples of the unfiltered data matrix by stochastic simulation is shown in *Fig. 14.* With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that differences between any two seasons are significant at 0.01 level.

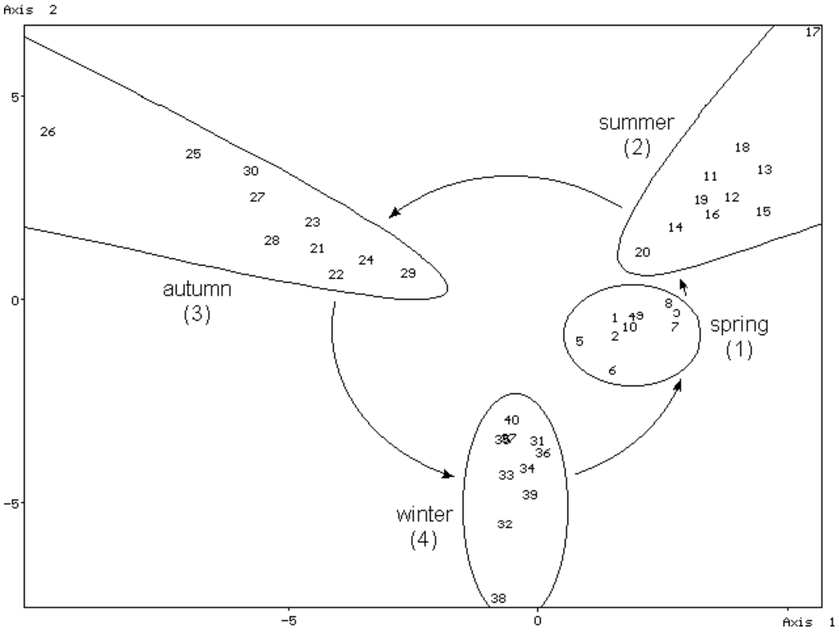

Figure 14. *The similarity pattern of the objects obtained by stochastic simulation from samples taken in the four seasons (unfiltered data matrix; see* Table 11*).*

The similarity pattern of the objects obtained from seasons of the filtered data matrix by stochastic simulation is shown in *Fig. 15.* It can be observed that this pattern is substantially identical to that obtained from the unfiltered data matrix (*Fig. 14*). By examining the data matrix, it can be established that the similarity pattern obtained is determined mostly by the dominance relations of the same species and species groups as the similarity pattern obtained from the unfiltered data matrix. With *t*-test carried out on the obtained coordinates of the new objects generated, it can be proved that differences between any two seasons are significant at 0.01 level.

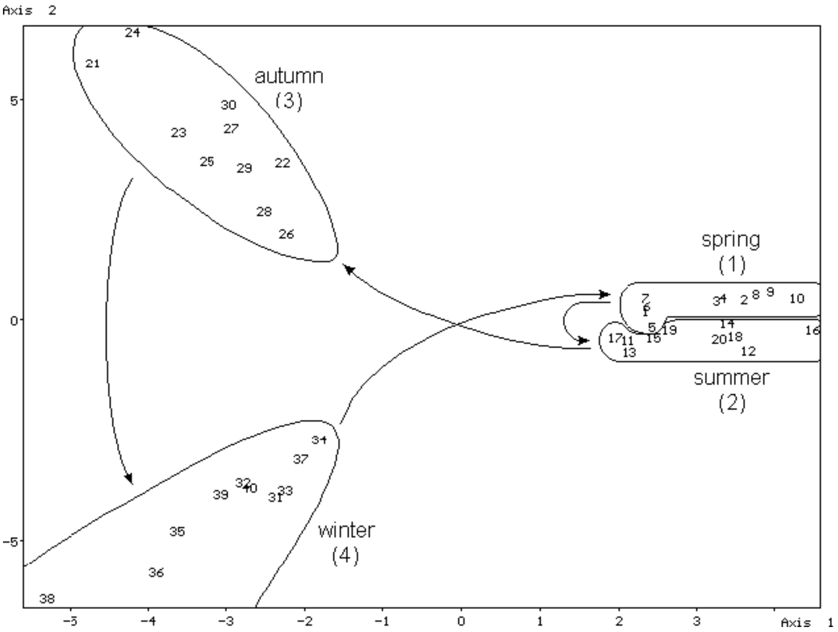

Figure 15. The similarity pattern of the objects obtained by stochastic simulation from samples taken in the four seasons (filtered data matrix; see Table 11).

By studying the diversity conditions of ground-living heteropteran assemblages by Rényi's method, the diversity profiles shown in *Fig. 16* have been obtained. It can be established that the diversity of the samples collected in summer, autumn and winter decreases in this order. At the begin of scale parameter, in the section sensitive to rare species, the samples collected in spring are more diverse than the ones collected in the other seasons.

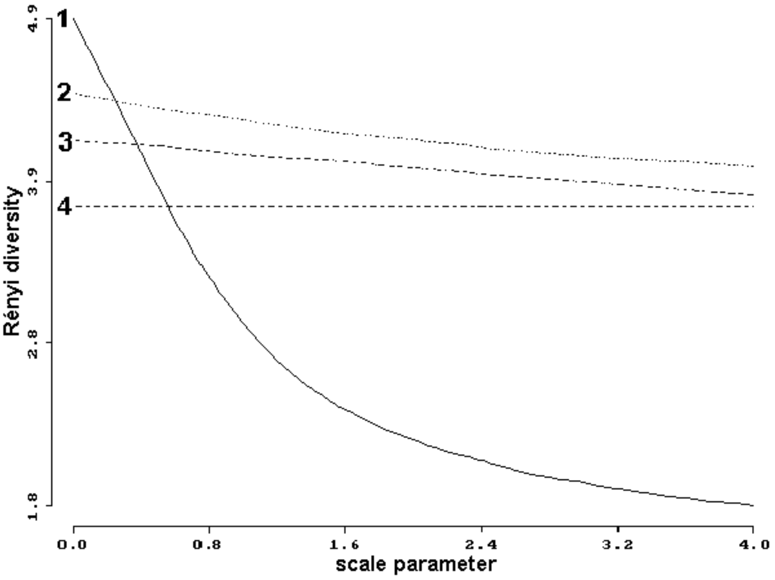

Figure 16. The diversity profiles of the samples taken in different seasons (Rényi-diversity). The meanings of the numbers see in Table 11.

Discussion of the patterns

By examining the unfiltered data matrix, it can be established that the similarity pattern obtained is determined mostly by the dominance relations of the four most dominant species and species groups: *Hebrus ruficeps*, *Acalypta musci*, larvae of *Acalypta* spp. and Lygaeidae sensu lato larvae. Each of them can be found in almost throughout the year, but the relative dominances of the former three species and species group are highest in autumn, while that of the Lygaeidae sensu lato larvae reaches its maximum in summer. In winter, the relative dominance of each is low. Accordingly, the relative dominances of the former three species and species group show increase parallel with the increase of the value of Axis 2 and show decrease parallel with the increase of the value of Axis 2. The relative dominance of the Lygaeidae sensu lato larvae shows increase parallel with the increase of the value both of Axis 1 and 2. Consequently, this four species and species groups determine the triangular shape of the similarity pattern (*Fig. 17*).

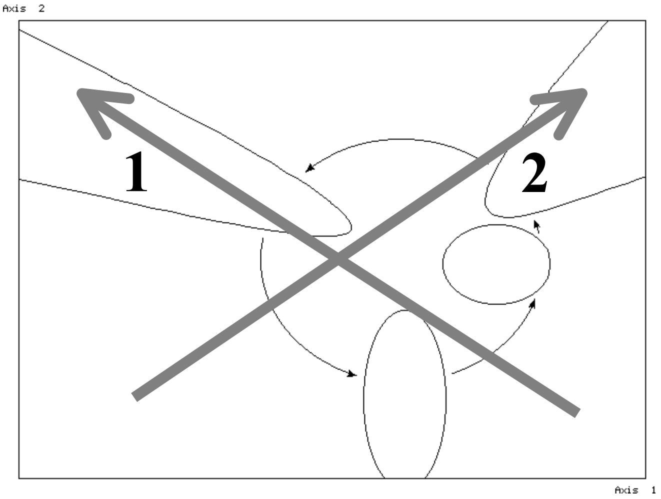

Figure 17. *The direction of the increase of relative dominance of the most dominant four species and species group on the similarity pattern (Fig. 14).* **1** *= Hebrus ruficeps, Acalypta musci and Acalypta spp. larvae,* **2** *= Lygaeidae sensu lato larvae.*

Numerous species and species groups can be collected at the ground-level throughout the year. Such species are *Hebrus ruficeps*, *Campylosteira verna*, *Acalypta parvula*, *A. musci* and the larvae of *Acalypta* spp., *Plinthisus brevipennis* and *P. pusillus*, *Drymus ryeii*, *Legnotus limbosus*, the *Eurygaster* spp. Such species groups are the following: Tingidae, Miridae with a size of 5–10 mm, Nabidae with a size of 5–10 mm, Anthocoridae, both size groups of Rhyparochromidae, Coreidae with a size of 5–10 mm, Thyreocoridae and Cydnidae with a size less than 5 mm. The former high-dominance species without exceptions as well as most species of the families Tingidae, Nabidae, Anthocoridae, Rhyparochromidae, Coreidae, Cydnidae and Thyreocoridae and some mirids, overwinter as adults. This explains the occurrence of these species at the ground-level in winter, too.

Rhyparochromid adults can be collected throughout the year, but their relative dominance is the highest in summer. Most species of the family overwinter as adults. In case of these species the mating and oviposition occur usually in spring, the larvae can be found throughout summer and the new adults appear in mid-summer or early autumn. Some species of the family overwinter in larval stage (usually in addition to adult stage). Therefore, larvae can be found at the ground-level in winter, too.

Many species and species groups occur at the ground-level in all seasons except winter. Such species are *Ceratocombus coleoptratus*, *Cryptostemma pusillimum*, *Hebrus pusillus*, *Acalypta carinata*, *A. platycheila*, *A. gracilis*, *Piesma maculatum*, *Tropistethus holosericus*, *Rhyparochromus vulgaris*, *Sciocoris homalonotus*, as well as the species groups Pyrrhocoridae, Cydnidae with a size of 5–10 mm, Pentatomidae with a size of 5–10 mm. Out of these, *Ceratocombus coleoptratus* overwinters in Hungary probably in egg stage [4], whereas the others as adults. The absence of these species and species groups in samples taken in winter can be explained by the low number of these samples.

The following species were collected only throughout summer and early autumn: *Myrmedobia exilis*, the species group containing the low-dominance mirid species with a body size less than 5 mm, furthermore the larvae of the families Hebridae, Microphysidae, Berytidae, Stenocephalidae and tribe Stygnocorini of the family Rhyparochromidae. *Myrmedobia exilis* overwinters in the egg stage, its adults can be found only in summer. Like the species before, the majority of the minute mirid species overwinter as egg. Most species of the families listed before overwinter as imagos, therefore their larvae can be found only from the early summer until mid-summer or early autumn. Numerous species and species groups were found at the ground-level in spring, autumn and/or in winter, however, they were not found at all or only in low number in the summer. Such are the group of Nepomorpha + Gerromorpha, the species *Microvelia reticulata*, *Agramma confusum*, the groups containing the low-dominance imagines of Aradidae, Lygaeidae, Cymidae, Blissidae, Oxycarenidae, Rhopalidae, Pentatomidae with a body size greater than 10 mm, Acanthosomatidae, the species *Eurygaster testudinaria* and *Aelia acuminata*. In the breeding-season, these species and species groups occur at the ground-level only accidentally, because they follow one of the following life habits:

- to live on plants and are phytophagous or seed feeder (*Agramma confusum*, Lygaeidae, Cymidae, Blissidae, Oxycarenidae, Rhopalidae, Acanthosomatidae, *Eurygaster testudinaria*, *Aelia acuminata*, Pentatomidae with a size greater than 10 mm);
- to hide on stems or trunks, or even under bark (Aradidae);
- to occur in different waters or on their surfaces, or even on the waterside vegetation (*Microvelia reticulata*, Nepomorpha, Gerromorpha).

Overwintering specimens of the former species and species groups can be collected at the ground-level regularly.

Theses

(1) Numerous Hungarian plant community types have characteristic ground-living heteropteran assemblage. The composition of these is related to the treeless or wooded character and the humidity of the community. The humid treeless cenoses, dry grasslands and dry or mesophilous forests have specific ground-living bug assemblages. In the riverine forests the species, which occur in all wet communities, are most frequent. Several species can be found in almost all of the plant communities, whereas others are characteristic of hygrophilous communities

regardless of their wooded or treeless character, or of woodland habitats regardless of their humidity.

(2) The number of bug species, which can be found in almost all of the substrata, is considerably high. The leaf litter and debris has characteristic heteropteran assemblage. The community living in tussocks and in coats of *Sphagnum* spp. and other mosses consist mostly of species occurring in most of the substrata. According to the microclimatic circumstances, some differences can be recognised between the bug fauna of mosses growing on different surfaces.

(3) The lace bugs *Campylosteira verna* and the *Acalypta* spp., which occur in Hungary, are regarded as typical muscicolous species. Indeed, they can be extracted in great number from different mosses. However, numerous specimens have been collected from other substrata, especially from leaf litter.

(4) Most of the high-dominance species collected at the ground-level occur in all of the great Hungarian phytogeographical provinces examined. Some species have been found mostly in the highlands or in the lowlands.

(5) Most ground-living heteropteran species, which overwinter as adults, can be found at the ground-level almost throughout the year. Many of these species have not been collected in winter but this is caused probably by the limited number of samples taken in this season. The adults of species, which overwinter in the egg stage, and the larvae of species, which overwinter as adults can be found at the ground-level only in summer and in autumn. Overwintering specimens of numerous species, which are not characteristic members of the ground-living fauna, can be collected with Berlese funnels in spring, autumn and/or winter, usually with low relative dominance.

(6) By examining the different objects, similar conclusions could have been drawn when analysing the data matrix containing all samples (unfiltered data matrix) or the data matrix containing only the samples, of which all the examined objects are known (filtered data matrix). By examining the filtered data matrix, the loss of information is far significant, because of the limited number of samples. Consequently, it is expedient to analyse the unfiltered data matrix.

Acknowledgements. We are very grateful to Prof. Dr. K. Dózsa-Farkas for providing Dr. I. Loksa's collection, thereby making our investigations possible; to Ms. M. Rédei-Szerencsi and Ms. T. Tölgyesi-Nell for technical help at various phases of the project. At last, but in the first place of course, we would like to express our special thanks to the late Dr. I. Loksa (1923–1992), eminent Hungarian zoologist, former head of the Department of Systematic Zoology and Ecology of the Eötvös Loránd University, researcher of many soil-inhabiting invertebrate groups, especially Arachnoidea and Myriapoda. Without his pioneering and assiduous activity on the research of the soil fauna of Hungary it would have been impossible to implement our work.

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PROBLEMS AND SOLUTIONS OF FIELD SCALE AGRO-ECOLOGICAL DATA ACQUISITION AND DATA INTERPRETATIONS IN AGROINFORMATICAL DOMAIN

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(Received 3rd Nov 2002; accepted 26th June 2003)

Role of agro-ecological data sources for sustainable development

Agricultural production is an activity of high economic and environmental risk, nowadays especially. Handling of widening scientific knowledge and up-to-date technological appliances needs rethinking of foregoing theory and practice; according to some researchers, total paradigm change is needed. The “sustainable development” theory of Agenda 21 made up by the Rio Summit (1992) means long-term tasks for all branches of economy, so as for agriculture. As a result, the change of land use planned from economic and environmental points of view would realign the overall view of the Carpathian Basin for centuries in a territory where the ratio of agricultural regions is one of the highest (72%) in Europe. Risks of decisions refer to any period or area can be decreased by having more and more data and analysed information. Agricultural activity, as an open ecological system, has a hardly elaborative data requirement even by the present information technological devices [12] About half of the input data interfering the results are changed during a fragment of the phenological cycle, that can not be described exactly by such widely used ecological models as CERES [25] or CROPWAT [44] during particularly extreme changes validated for Central-European model border conditions. These results in more data need in space and time, which has properly been satisfied so far by the development of digital sensors, but the practice is not able to keep up with the manipulation integration and interpretation of the collected data. Similar process occurs on the field of data mining technology performed on Internet, where effective solution of information production still has to be waited for. Seemingly, this causes contradiction, the decision maker uses smaller and smaller part of the information available, but this data amount – in absolute sense – grows at a highly increased rate in time. During many decisions the incomplete interpretation assumes the reliability of data or their interval and value of uncertainty are not known. As a result, decision makers have no numerical risk values actualised according to the information built up from the data, thus the farmer dares to undertake lower and lower risk level in the smaller decision space.

How one can escape from the trap of this lack of data and data dumping that sometimes comes up at the same time in destructive cases? The key element of the decision-making process is improvement of the interpretation techniques that must be optimised during the whole data flow.

Optimisation of data mass, data quality and set of information effectively support the sustainable development at the given decision level, where the decision maker knows the levels of uncertainty of the data, the error spreading processes and the undertaken decision risk in space and time.

In decisions, the economic market information was dominant up to the mid 1990's in the Hungarian industrialised agriculture. The structure of ecological-environmental information data was determined by this dominantly agrochemical point of view in Hungary. From amongst the ecological and economic environments in spite of the renewing economic crisis the European Common Agricultural Policy is calculably stable, in which the agro-ecological and rural development elements have been upgraded. The ecological environment keeps on changing capriciously, in fact the rapid urbanization and the conversion of the environment causes more often natural hazards (draught, floods, exceeds waters etc.) with significant damages. In the agro-decision space the economic and classical crop production and animal husbandry questions mean smaller, while the ecological tasks bigger role [36]. Determination of potential of natural resources, monitoring of the changes is an agro-information task even nowadays in the ideal several-meter spatial resolution as well as in the several-hour temporal resolution, whose mass distribution is a big challenge and high-tech task for establishment of an information society.

Therefore amongst the interpretation techniques the possibilities and limitations of the agro-ecological digital data acquisition modelling that is prevailing for sustainable development will be overseen.

Evaluation of Hungarian natural resources

In the document Agenda 21 a proposal was born to establish the conditions of Sustainable Agriculture and Rural Development (SARD) that aims the establishment of food production and food safety as well as protection of the resources at the same time. Previously, in Hungary after the world energy-crisis of the 1970's several research and governmental programmes were started to evaluate the volume and utilization of natural resources used by agriculture [9, 30]. Results of the project called "Agro-ecological Potential of Agriculture on Millennium" led by Láng et al. (1983) [28] were systematised into a professional system by the *Agro-Ecological Integrated Information System (AIIR)*. AIIR is a professional system that manages and builds on settlement, soil, meteorological, land use and crop production data.

Its main advantage was that resources were evaluated by up-to-date, model methods. During the that time of "industrial-like" production purposes, where the goal was the hospitalisation of productivity (y), the limited possibility of sustainability of resources was pointed out and the questions of yield safety – risk as well as production site conditions were discussed.

According to the model factors of the methodological researches led by Harnos [15] the stationary state of the soil characteristics (x) in time (t) were assumed, where t is only one phenological cycle in evaluation of sustainability, while x can change depending on time [$x(t)$]. A group of climatic factors can change rapidly and randomly (ξ), while the other group applied in agricultural technology (u) containing all elements of production (seeds, nutrients, plant protection, soil cultivation, irrigation and crop rotation etc.), can change in every phenological cycle. The effect of the production site to the yield (η) was described by the following equation:

$$\eta = \eta(x, \xi, u).$$

In the sustainability model it was interpreted that productivity of a given x production site is not decreased by the u-type agricultural technology at t+1 time. That is, quantity of yield under the actual agro-technological solution will not decrease in a further production cycle.

$$y_{\text{act}}(t) \geq y(t+1)$$

Productivity is expressed by $E(\eta(x(t), \xi, u))$, where E is the deviation caused by the weather, whose value can be characterised by the $F(y) = P(\eta(x, \xi))$ distribution function, where $F(y) = P(\eta(x, \xi)) \leq y$ means that yield of the reference plant (y) will not be higher than the average yield expressed in t/ha. In the relation the P random variable is $0 \leq P \leq 1$. The approach above gave a possibility for the probability establishment of yield loss (p_v) as well. Hindrance of introduction of the theoretical model was that the analytical form of the $\eta(x, y, u)$ function describing the connection amongst yield–production site–agricultural engineering and the $x(t+1) = g(x(t), u(t))$ function describing the state change of the production site were not exactly known.

In practice the studies were focused on:

- genetic and agricultural engineering development and
- stochastic change of weather,

where the county units were used as spatial references, under the actual technical conditions.

Agricultural technology is expressed by the change in time of η. Accordingly the change of average yields in time (y_1, η_2) can be expressed by the $\eta(t, \xi) = y_1(t) + \eta_2(t, \xi)$ potential function, where $y_1(t)$ describes the stochasticity of genetics and applied technology, while η_2 is that of the weather. During the almost two decades passed since these studies the role and function of agriculture and its methods of research have been changed. The need of data and the methodology of evaluation of the regional and local ecological information systems build on large-scale field information systems are upgraded. Unfortunately, its introduction to practice delays because of lack of intellectual and financial capitals supports.

Soils and land use

Evolution of soils is affected by geological, climatic, topographical and biological features as well as by the age of soils. Analysing soil evolution factors, effects of human activity on soil cannot be neglected. This effect has been particularly intensive during the last several hundred years. On the one hand, this human activity resulted in the improvement of productivity of soils, while on the other hand, in certain regions, it accelerated soil degradation processes. All of the above-mentioned soil factors exerted their effects together in the Carpathian Basin and their interactions determined the form of appearance, the physical, chemical and biological features of the certain soils [41]. Processes in the soil represent opposite impact pairs that are in dynamic balance in space and time [1]. These balance processes can shift to one or the other direction, strengthen, change periodically in time or may have shorter periodic effects that can be temporary or permanent.

On the AGROTOPO 1 : 100 000-scale digital soil map of Hungary, Várallyay [50, 51] distinguished 3310 polygons based on 10 soil parameters. In case of 1 : 10 000 – 1 : 25 000 field-scale levels the characteristic values of the heterogeneity of spatial patterns grow at a highly increased rate. With increase of the spatial resolution the standard deviation of attributive data increased as well. In this dimension the digital topographical data was partly processed, which is the main data source for survey of soil resources and for performing an agro-ecological model. At determination of soil characteristics on field, the representativity of parameters got for a general purpose soil survey are interpreted by Webster [52] as how much it can explain from all the variances of the data. He asserts that in case of soil-physical characteristics about half of them, while in case of some soil-chemical characteristics less than one-tenth of all variances are revealed by the survey. It must be overcome by the soil-characteristics estimation based on environmental correlation.

From amongst the soil characteristics the biological, chemical and physical parameters can be measured in growing uncertainty order, respectively. Among the soil-physical characteristics, the water- and heat management values of the same sample can be differentiated at several thousand-fold measured either in situ on the field or in the laboratory.

Uncertainties of soil-chemical measurements are grown in order of magnitudes by preparation and extraction procedures prior to measurement, in comparison to the interval of value of analytical device measurements. The up-to-date field sensors and remote sensing data significantly lessen the volume and deviation of sample preparation and of laboratory errors. While ten years ago several weeks were needed from soil sample taking to the evaluation of the result, nowadays this can be lessened only to some hours. The measurement limits for example in agro-chemistry in case of field devices decreased to ppm, while in case of measurements in a laboratory to ppb level value.

Digital technology defined numerically the experimental fact that in the Great Plain regions of Hungary the pedological changes are significant even in vertically in sub-meter level and due to the intensive land use they take place much faster than it was estimated previously. This fosters new research directions. Applying simulation models can help in determination of direction and volume of the processes. A group of wide-spread used models contains such regional, for example erosion models like USLE and WEPP, while their other group deals with the nutrient management of the given site, e.g. SOIL-SOIL-N or with water movement at point scale [24, 35]. Some of these models are for research, need a big volume of input data and provide a very detailed process description, while the others are practice-orientated, robust models.

Water sources

After the Netherlands, the second largest area being threatened by floods and exceed waters can be found in Hungary. Frequency of extreme values in the statistics of hydrology has grown trend-like during the past decades [34]. The extreme changes in the water source together with the permanent contamination burden increase the variability of the quality of waters as well [38, 39].

Runoff of exceed waters closed out from flood areas, the volume, period and frequency of inundation are consequences of series of accidental hydrological events and phenomena [40]. Probability of floods in space and time can be basically determined by two ways: on the one hand, as volume of frequency values of inundations, on the other hand, as size of factor maps of exceed waters. Besides, combination of these two can occur, which means the subjective correction of the first method by using the second one.

With re-classification of the digital maps of such characteristics that take part in formation of exceed waters and show relative spatial stability (for example aquifer hydraulic conductivity and maximum storage capacity of the aquitard, convexity of the micro relief, critical possible depth of the underground water, land use), thematic maps can be prepared. From their subsequent overlaying an exceed water risk map can be prepared [4].

There are several possibilities for spatial distribution and interpretation of the infiltration factor. The simplest way would be making an isometric map if the co-ordinates of the sample taking sites were known. But this solution might come up only if we would like to interpret a soil-genetically or soil-physically homogeneous area. Then by choosing the proper interpolation technique a continuous surface can be modelled, that is suitable for interpretation to “all points”. But the heterogeneous regions have several anisotropy, that are anisotropies having such impacts that significantly change the regularities of spatial development of the infiltration factor. These are mainly the factors that play role in formation of the soils (for example the topography – i.e. the deep areas have low water conductivity).

Therefore, if a map that pictures a detailed physical kind of soil is available whose profile analysis data (for example the mechanical structure) are known – that are base of preparation of the map –, then through the revealed relations thematic maps displaying the hydraulic conductivity of the bigger regions can be prepared. These maps are true with the given input structure and boundary conditions. The spatial pattern of the change of the accumulation conditions overpasses the speed of change of soil characteristics in time [45]. Mathematical survey of time series analyses is indicated a fast developing field.

Climate

Material of knowledge of Hungary's climate potential is as revealed as that of soil sources. Climate potential for country size and meso-regions were determined to study the maximum yield [2, 42, 48], which provides spatial modelling possibilities. Based on their study, a part of the total radiation energy that reaches the plants (Q_0) is photosynthetically active energy (Q_p), whose certain part (ε) is used by the plants for biomass production (Y_b)

$$Y_b = \frac{Q_p}{Q_0} \cdot \varepsilon \, .$$

Burgos [5] concludes the value of the maximum possible utilisation of radiation from the estimated value of the energy reaches the Earth. Based on it, Varga-Haszonits et al. [49] calculated the value of ε to 22–23% for Hungarian conditions. Relying upon the Campbell method [7] performed also by him, he compares the energy of photons relate to the medium wave of the photosynthetically active radiation with the amount of energy bound chemically in 1 mol material. Its value is about the same: 22%.

Climate exerts its effect – besides the energy conditions – through the fluctuation of water resources. During modelling the Aridity Index that expresses the rate of potential evapotranspiration and precipitation during the vegetation season, has an average value of 1.6–2.8 in case of winter wheat in the 1951–1991 period of time.

According to the time series analyses calculated by Harnos et al. [16], for the period of 1951–1983 there are 3–5 draughty years in every 15 years, that cause yield loss of higher than 5%. From amongst the three cases the yield loss once is 10–15%, once is over 15%.

Eight research stations were included in the above-mentioned survey. But the field scale forecasts are very uncertain. The present destiny of field measuring stations of meteorological service is not able for supervised teaching of satellite multispectral images. They cannot supply continuous real-time data for field-scale water- and heat management analyses but at the same time both the spatial and spectral resolutions improved in order of size. The highest improvement is to be waited in the field of practical data supply of radar technology. In 2002 in research-level the hyperspectral measuring technology also appeared in Hungary [23].

Biological resources

Bio-diversity and homogenous monoculture of an agricultural crop seems to be an irresolvable contradiction. The strongly fragmentised ecological islands poor in species increase the energy need of the whole agricultural region. In Hungary the spatial mosaic-like structure of soils is confirmed by the land use databases originated from the CORINE 1 : 50 000 and 1 : 10 000-scale air photos. But complete interpretation of data source will be the future task of the agro-ecological modelling. According to Horváth [17], by a spatial extension of the soil–plant–weather–pest system that can be considered homogeneous within a small plot a space specific complex ecological model can be obtained [18, 25, 26]. The models of the ecological system are strongly connected to and dependent from each other, however, each of them works by itself.

The ecological examination of spatial processes is very important in life-systems of most species. Population ecology is a branch of ecology that studies the structure and dynamics of populations. Populations can be defined at various spatial scales. Local populations can occupy very small habitat patches like a puddle. A set of local populations connected by dispersing individuals is called a metapopulation. Populations can be considered at a scale of regions, islands, continents or seas. Even the entire species can be viewed as a population [3]. Populations differ in their stability. Some of them are stable for thousands of years. Other populations persist only because of continuous immigration from other areas [10].

Sharov [37] introduced the definition of physiological time via population ecological research to describe biological maturity and time relationships. Spatial processes of ecological analysis are very important in life-systems of most of the species. They may so significantly modify system behaviour that local models would be unable to predict population changes. Several methods are used for description of the spatial processes such as random walk, diffusion model, dispersal mechanism, metapopulation analysis etc.

Random walk is simulated after several time steps until the distribution of organisms becomes close to the 1 or 2 dimensional normal distribution. The diffusion models can be applied to any initial distribution of organisms. The combination of long- and short-distance dispersal mechanisms is known as stratified dispersal. Metapopulation is a set of local populations connected by migrating individuals.

One of the main strengths of the geo-statistical analyses is the investigation of spatial variance and correlation.

Sampling and classification

With geo-statistics, the GIS analyst gains a wide range of tools to detect and describe expressions of spatial dependency in a study area through sample data sets. (Very simply, spatial dependency refers to the extent to which neighbouring points have similar attributes.) These tools contribute to an exploratory analysis of data by helping to describe the nature of spatial dependency in the study area. These descriptions may then be used to build predictive models for full surfaces. Any geo-statistical project begins, prior to sampling, with obtaining as much knowledge as possible about the distribution characteristics of the phenomenon under study. In cases where one does not have direct control over the production of sample data, the project begins by gathering ancillary information about the study area, the sampling methods, and the sampling scheme. Next, if a geo-statistical analysis is to be fruitful, it is necessary to examine the spatial arrangement of data samples visually and produce summary statistics that reveal characteristics of the sample data distribution. Detecting and interpreting special features, characteristics, or abnormalities of the data set are the first steps of exploratory data analysis, the success of which will influence subsequent interpretations of geo-statistical measures of variability and continuity. In addition to displaying a map of the sample locations with different palettes, one can analyse histograms of the attributes and obtain a statistical summary of the data. With these results in hand, better interpretations of spatial structure are likely as one begins geo-statistical analysis [13].

An exploration of the modeller (as called Spatial Dependence – IDRISI, Exploratory Spatial Data Analysis – ArcMap) which provides tools for measuring spatial variability (or its complement, continuity) in sample data. Model fitting is to build models of spatial variability with the assistance of mathematical fitting techniques.

The variogram surface is a representation of statistical space based on the variogram cloud. The variogram cloud is the mapped outcome of a process that matches each sample data point with each and every other sample data point and produces a variogram value for each resulting pair. Typically, uncovering spatial continuity is a tedious process that entails significant manipulation of the sample data and the lag and distance parameters. With the Spatial Dependence Modeller, it is possible to interactively change lag widths, the number of lags, directions, and directional tolerances, use data transformations, and select among a large collection of modelling methods for the statistical estimator. If the degree of spatial dependence decreases equally at the same rates for all sample pair separation directions, the model design is isotropic. With model fitting, the continuity structures suggested by the semi-variograms produced can be interpreted as well as any additional information we have obtained. The parameters for the structure(s) will describe the mathematical curves that constitute a model variogram. These parameters include the sill, range, and anisotropy ratio for each structure. When there is no anisotropy, the anisotropy ratio is represented mathematically as a value of 1. The sill in model fitting is an estimated semi-variance that marks where a mathematical plateau begins. The plateau represents the semi-variance at which an increase in separation distance between pairs no longer has a corresponding increase in the variability between them. Theoretically, the plateau infinitely continues showing no evidence of spatial dependence between samples at this and subsequent distances. It is the semi-variance where the range is reached.

The goal is to decide on a pattern of spatial variability for the original surface. To carry out this goal successfully with limited information requires multiple views of the variability/continuity in the data set. This will significantly increase the understanding and knowledge of the data set and the surface the set measures. Finally, in the last section of the analysis, kriging, IDW and other spatial estimators can be used, to test models for the prediction and simulation of full surfaces. There are more types of kriging, which present different results.

Ordinary kriging is known to be a Best Linear Unbiased Estimator, because it assumes that constant mean (μ) unknown, simple kriging where μ is known and universal kriging where $\mu(s)$ is some deterministic (trend) function. The final result of kriging will be to produce two images, a surface of kriged estimates and a surface of estimated variances. Kriging estimates a new attribute for each location (pixel) on the basis of a local neighbourhood. Co-kriging is another useful geo-statistical tool that uses an additional sample data set to assist in the prediction process. Co-kriging assumes that the second data set is highly correlated with the primary data set to be interpolated. Co-kriging is useful, for example, when the cost of sampling is very high and other (cheaper or available) sample data can instead [20].

The interested reader should consult Cressie [11], Isaaks and Srivastava [19] for additional explanations of kriging and general geo-statistical questions.

Data conversion or comparability

In case of field-scale data collection and processing the agricultural application of machines having satellite-base GPS means technical breakthrough. The technological decision support system building around it is called precision agriculture (PA). It has an almost decade-long past concerning from the 1992 – the year of the first American conference. Standards for agro-environmental management systems have the same short past in practice. Both areas, from the view of methodology and applicable techniques, were efficiently inspired by the quite rapid and continuously traceable development in information technology. The more stringent quality assurance and increasing agro-environmental protection requirements made the need of elaboration of complex environmental indicators obvious for analysis of environmental management and for the loading capacity analysis of the environment as a living system.

Similarly to the large-scale and efficient control functions of industrial closed systems, in open agricultural environment system analysis of material and energy flow and life cycle assessment to be shown by us become possible. The conditions of maintenance and effective operation of the environmental management systems are the continuous and reproducible measuring, tracing, improvement and development that help to increase the environmental effectiveness of production. For this purpose proper knowledge of the site and environment of the agricultural production are essential.

For the common resolution of the above-mentioned topics, an alternative is offered by the simultaneous introduction of the precision production system and the environmental management system. The precision agriculture is about to increase the effectiveness of production with optimisation of raw materials’ (water, seeds, chemicals etc.) making plant growing more economic.

Determining elements of precision agriculture are: high-precision, continuous site determination, geographical information and remote sensing tools of analysis and the highly automated fieldwork [46].

This information system of precision agriculture can be the basis of establishment of the environmental management systems. Its first step is the survey and the evaluation of the environmentally active factors of the given production process and their effects. Knowing them the two most important fundamental principles, the continuous measuring–monitoring and the in parallel made continuous improvement–development can be realised.

For establishment of the environmental management systems the life cycle assessment provides help that determines the materials and energies used during the production as well as quantity and quality of the released potential toxic materials and wastes within the investigated production system. On the basis of these results the environmental effects of production can be estimated. The ISO 14040-49 family of standards contains the standards of life cycle assessment [8]. According to the examination standards, the life cycle (Hungarian Standard ISO 14040, 1997) is the subsequent, connecting stages of the influence system of a product, from purchasing the raw materials or from the formation of the natural resource to the reuse or waste disposal.

One of the problems of evaluation is the fact that effects of directly not measurable input materials must be calculated to directly not comparable effects.

In particular, this data integration process is often based on techniques for the management of uncertainty.

Bayesian probability theory has been proven to be sensitive to inaccuracies in the input probabilities. The Bayesian model often requires that events are independent of each other. This assumption is rarely true in real life. Neural networks and Fuzzy sets have an alternative approaches to handle spatial (mapped) and measured uncertainty. Keller [21] and Ultsch [47] give several examples of how to apply neural networks to environmental problems.

Uncertainty in any data layer will propagate through an analysis and combine with other spatial and attributive sources of error, including the uncertain relation of the data layer to the final decision set. In traditional GIS analysis, uncertainty is not taken into account in the database. As a result, hard decisions are made with very little concept of the risk involved in such decisions. Mays et. al. [31] demonstrate how simple it can be to work with measurement error and its propagation in the decision rule. The task of the decision maker is to evaluate a soft probability map and set an acceptable level of risk with which the decision maker is comfortable. By knowing the quality of the data, the decision maker can view the decision risk occurring across an entire surface, and make judgements and choices about that risk. Finally, any further analysis or simulation modelling of impacts with such data increases the precision of those decisions as well.

Results of the fuzzy analysis are the fuzzy layers, which are suitable for describing the decision on spatial uncertainties. Fuzzy set theory [22, 53, 54] is a mathematical method to characterise and quantify uncertainty and imprecision in data and functional relationships. Fuzziness represents situations where membership in sets cannot be defined on a yes/no basis since the boundaries of sets are vague. The fuzzy sets are classifications of data in which the boundary between classes is not distinct. The basics of fuzzy set theory have been presented and discussed in numerous articles [6, 32, 43]. Fuzzy set membership functions describe the degree to which data belongs to for each class (fuzzy set). These functions take on values between 0 and 1, and depict the grade of membership (also known as the possibility) that a certain entity has in that class. For the description of these continuous risk levels the fuzzy functions are more appropriate than the Boolean layers. Transient values correspond to risk levels in accordance with the applied functions.

Data management

Data management of environmental models comparing to the business applications contains some special problems.

The amount of data to be processed is extremely large particularly due to the exponential increase of spatial and spectral resolution values of air photos and space images.

The data managing hardware and software environments are heterogeneous and divided since data owners produce their data in different environments.

Standards of new generations of digital data collectors, for example mobile phones (MMS, GPRS) have not had always-compatible data form.

In case of precision agriculture, data formats of machine computers can only partially standardised.

Environmental data objects are often spatio-temporal and frequently uncertain. For natural resources no standard object library was made that could follow behaviour of complex logical connections, nested and joint objects.

In those situations, where one works with big volume or rapidly changing data, like in ecology, it seems favourable to establish a divided database, where each database is to be installed to those users, who use them most frequently. Successful application of divided database must meet the following requirements:

- Local autonomy, namely each user place has authority over the database and the operational system.
- Thus all user places are equal.
- Conditions of continuous operation are given, even if different user places make different interventions in the system at the same time.
- Physical and logical data independence must be assured.
- Physical fragmentation of the logical field must not be perceptible for the users.
- Combined application not to cause data duplication.
- Relation database should make the data distribution possible of those answers to the different places, but to give full value data as well.
- False changes are to be deleted.
- Divided DBMS should run on different type of computers as well, so not to be dependent on hardware.
- It must operate compatible with different operation systems since it may be supposed that in each place of the organisation different operational systems had been installed.
- Due to the heterogeneous network possibility mentioned in the introduction part, the network independence is a requirement as well.
- The divided relation database must be independent from the probably different relation databases used in the user places.
- It must be safe in data protection and loss of data points of view. In case of a divided relation database risk of deterioration of the database is smaller than of central databases.

The most common used relation database is a logically planned, traditionally two-dimensional data management system. Its disadvantage is that it describes the real world in tables. Records of these tables atomise the connections and fragment them along some kind of logical organization. It is not able to reflect the embedment of the objects.

Formal differences of records in columns are not able to emerge. Logical normalisations and physical planning could take a long time in complex relations. Time for reaching the data in big tables can increase.

A part of data structures making spatial indexing possible, for example the KD-tree, the 4-tree, the R+ tree, the BSP-tree are not easily matched into an object-oriented system since they cut the objects into pieces. It contradicts the essence of object-oriented planning that uses complex units [27].

Since the R-tree, the Rective-tree, the KD2B-tree and the Sphere-tree data systems handle the objects as units, they can be used properly in object-oriented modelling [33]. It makes keeping the relation systems possible without breaking the inner connections. Most of the objects in the real world have 1 : M-type relation system. This can be modelled in a higher level of abstraction. Instead of attachment of simple attributes given by the relation database, it makes input of complex attributes possible. The classification builds on the inner connection instead of the type of entity. Origin of objects in the attributes turns traceable. The attribute and the geographical data are not divided. Application of object-oriented models in description and analysis of ecological relations is expected to bring large progress.

Model creation

Prior to actual modelling certain preliminary works must be performed whose aims are to evaluate the resulting situation on the basis of the available data. Based on the calculations made by the preliminary model the optimal execution of the field exploration work, place and method of sample taking as well as planning of perception data types and perceptual frequency must be determined.

Model creation begins with preparation of a conceptual model. In formation of the conceptual model that fundamental principle becomes embodied that generally aim of the model is not to describe the process with detailed mathematical methods, but to reproduce our idea about the problem to be solved, of course in a properly controlled form. In case of the models available today the main question of model creation is not the mathematical description anymore but choosing from amongst the processes to be taken into account. Choosing the proper software the mathematical model in accordance with our decision is available.

Modelling helps to handle the complex problems, but determined by the modeller interactions that one cannot follow in head or by simple calculation methods. In case of numerical resolution methods boundaries of the resolution do not preclude any partial processes, therefore in case of uncertainty one can decide to take the process into account or neglect it on the basis of the calculations made by just the method. The system-like approach of modelling provides that one must take a clear stand on each of the parameters in the mathematical description of the processes. Neglecting a parameter is possible only with changing in the structure of the model.

Most field ecologists are not good at abstraction. If they build a model they often try to incorporate every detail. Most mathematicians are not good at interpretation of their models. Usually they think of “clean models and dirty reality”. However, both abstraction and interpretation are necessary for successful modelling. Many system properties are not represented in the model and some model properties cannot be found in real systems [37]. During the creation of a model the following points of view should be taken into account:

(1) select the optimal level of complexity, but do not try to make a universal model,
(2) plan model development for each time period and area,
(3) if possible, incorporate already existing simulation or stochastic-deterministic models.

In case of ecological models three basic conditions must be cleared. These are as follows:

- type of the object (flora, fauna, etc.) and the volume of the impact to the environment must be determined,
- the medium, in which the processes take part must be determined in space and time,
- situation and response reactions of potential impact receivers must be determined in space and time.

Choosing the software is performed on the basis of choosing conceptional model, and even in this case it would be practical to set up the conceptional model independently from the software, if the available computer program is given.

In the second phase the possible simplifications, proper for the limitations of the software, must be decided on. If the conceptional model defers significantly from the modelling possibilities of the available software, it is not worth starting the detailed elaboration of the model. In case of the single model systems it is advantageous, if the user have scope for action from that point of view how the given software is able to calibrate or validate the environment.

First phase of elaboration of a model is the verification of the software. During verification we examine whether the model gives a properly exact solution in case of the known, and mainly analytically resolvable tasks. Parameters can be independent from time or changeable in time. By spatial extension they can be point-like, linear or spatial-type ones.

During the calibration of the parameters the errors of the parameters are corrected. Aim of calibration is generally not to decrease the deviations to minimum at the measuring point, but to display the character of the process as precisely as the processes taken into account according to the conceptional model and the supposed homogeneity during the parameter estimation make it possible.

Validation means the control of the calibrated model with use of such relevant cases that were not used during calibration: for example, extreme phenomena or simulation of scenario or period left out from calibration. If the results of validation are not satisfactory, the parameters must be modified or even the conceptional model too.

Boundary conditions, characteristics of the medium and the object can be changed according to the chosen scenario. These data are the basis of the evaluation, whose spatial visualization can be performed by geographical information systems.

During post-control material and energy movement as well as the effect of intervention must be traced by establishment of a monitoring network. Data received during the operation of the monitoring must be regularly evaluated, generally by with the help of modelling as well, where the expectable trends can be foretold. Estimation of the parameters of the model must be checked, and if it is not sufficient, the processes taken into account – i.e. the conceptional part of modelling – must be reviewed.

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RELATIONSHIPS BETWEEN CLIMATIC CONDITIONS AND POTATO LATE BLIGHT EPIDEMIC IN EGYPT DURING WINTER SEASONS 1999–2001

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(Received 29th January 2003; accepted 9th June 2003)

Abstract. Late blight is a disease of potatoes caused by *Phytophthora infestans* (Montagne) de Bary, the fungus can destroy virtually 100% of the above-ground parts of susceptible cultivars under favourable environmental conditions and in the absence of any control measures. Sever epidemics of late blight have emerged in both 1999/2000 and 2000/2001 growing seasons. An indicator variable for the occurrence of outbreak during the season based on the number of favourable days in terms of temperature and relative humidity during November to January was used to describe the disease status throughout the tested period. Weather conditions prevailing during potato-growing winter seasons were studied and compared in three potato-growing areas during 1998/1999 and in five growing areas during 2000/2001. Infection efficiency is a function of the environmental conditions and the potato cultivars. Mild and warm nights allow the disease to become established on first-early cultivars. This build-up of inoculums early in the year leads to a tendency for blight to appear in later-planted potato crops in the area sooner than it does in other regions. Wet warm winter seasons were identified as important factors influencing development of the recent late blight epidemics in Egypt. Most of the nights minimum temperature in November and December 1998/1999 were relatively cool in all of potato-growing areas, so, the disease had not built up the inoculums which are needed to start epidemic. While in November and December at 1999/2000 and 2000/2001 growing seasons at Badrashin, Kom Hamada, and Salhia which had relatively warm nights and the rainfall fairly early in November and December 2000/2001 and this occurred again on following days. So, the disease had built up the inoculums for starting epidemic. However, Bosaily and Kafr El-Zayat had cool nights during both seasons.
Keywords: *Phytophthora infestans, epidemic disease, environmental conditions*

Introduction

Potato (*Solanum tuberosum* L.) is one of the most important economic crops in Egypt concerning the production, farm income and exportation.

Potato late blight caused by *Phytophthora infestans* (Mont.) de Bary is still among the most destructive of all plant diseases. Under favourable environmental conditions and in the absence of any control measures, this disease can destroy virtually 100% of the above-ground parts of susceptible cultivars [8]. Infection efficiency is a function of the environmental conditions and the potato cultivars. During periods of favourable weather, many such cycles occur, resulting in an explosive epidemic [6].

Late blight progresses more rapidly under cool, moist conditions than hot dry weather since its spores require water and an appropriate temperature range to germinate. Also, if the conditions for blight are right for extended periods of time earlier in the season there can be a high risk of late blight at that time. The role of the environment in the development of late blight epidemics has been well documented [8, 16, 19]. Cool, wet weather with rainfall and ambient relative humidity (RH) above 90% and temperature of 7 to 21 °C favour late blight development [1, 16, 19].

The aim of this study is to attempt to derive the weather conditions during epidemic 1999/2000–2000/2001 growing seasons, which were favourable to potato late blight outbreak in potato-growing areas, where the disease was observed as an epidemic. Also, comparison of the weather conditions during the studied period in different locations.

Materials and methods

Potato planting dates

Potato was planted in winter (Mehira) season from September to first of October in Badrashin region and from November to first of December in Kafr El-Zayat, Kom Hamada, Bosaily and Salhia.

Survey of potato late blight

General survey in potato fields for late blight disease was carried out during three successive seasons, 1998/1999–1999/2000–2000/2001, in the main potato growing governorates in Egypt i.e. Giza, Behaira, Gharbia and Ismailia (*Fig. 1*). Different locations in each governorate were selected and various potato fields in each location were surveyed using the disease assessment keys, as described by James [10].

Disease assessment as foci

The average area of the foci was determined as the number/feddan and expressed as percentage acreage affected, when the primary stages of epidemic development as foci. The key presented in *Fig. 2* was used and surveyed the crop for foci of infection as follows: 1 = survey the crop and estimate the average number of foci per feddan (N), 2 = determine the average area of the foci (A), 3 = express (1) and (2) as percentage of acreage affected, 4 = use key presented in *Fig. 2* to assess percentage of leaf area affected within the foci, 5 = assessment of late blight by percentage of acreage affected = N × A (m^2)/4200 × 100, and 6 = step 4 × 5 (the output percentage affected with an average infection% within the foci).

Disease assessment as widespread

The key showed in *Table 1* was used when the disease was widespread in the crop. The growth stages were 40–50 days and disease assessment at regular intervals (7–10 days) after the epidemic had started.

Weather data collection

There were several meteorological and agrometeorological weather stations located in potato-growing areas. Over the three seasons, data of environmental conditions in potato areas were collected automatically (electronically) and manually from weather stations in fields of agricultural research stations.

The study areas were covered by 5 weather stations: Badrashin, Kom Hamada, Kafr El-Zayat, Salhia and Bosaily. The equipment and procedure for collecting pertinent environmental data is similar to that described for Blitecast [12].

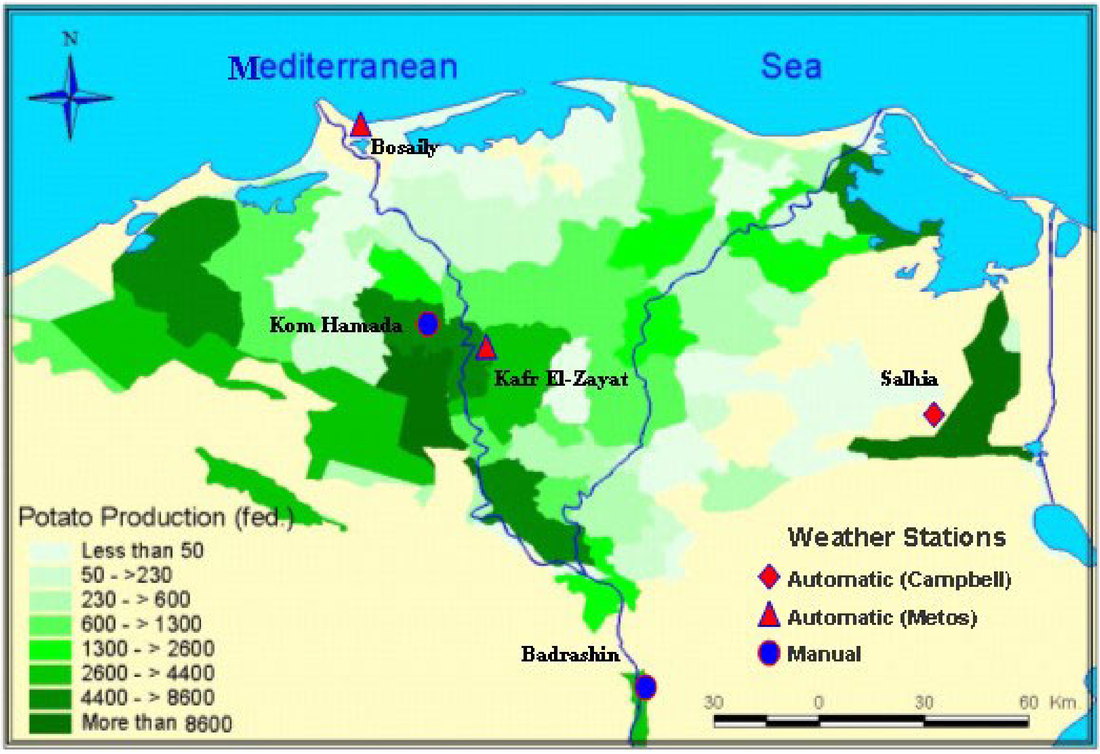


***Figure 1**. Locations in Egypt, where potato fields were surveyed for occurrence of late blight disease during winter growing seasons 1999–2001.*

Collecting weather data automatically

During the three seasons, data of environmental conditions in potatoes fields were collected automatically from weather stations in potato areas. Temperature, relative humidity, leaf wetness in the plant canopy and rainfall were recorded hourly and the data were forwarded via phone-modem connection daily to the Central Laboratory for Agricultural Climate (CLAC) in Dokki. There were automatic weather stations in some regions: Metos electronic weather stations (Metos® Compact, Pessl instruments GmbH., A-8160 Weiz, Austria) in Bosaily and Kafr El-Zayat, Campbell auto station (Campbell Scientific Ltd, CR10X Measurement & Control, USA) in Salhia region. Each weather station consisted of relative humidity sensor, temperature sensor, tipping bucket rain gauge, portable stand, data logger with battery and solar panel, modem and phone. All sensor signals were sampled at 10-min intervals in Campbell Scientific electronic weather station and at 12-min in Metos electronic weather station.

Collection of weather data manually

A thermohygrograph was sheltered in a white wooden house, that recorded temperature (˚C) and relative humidity (%) daily, and the thermohygrograph papers were collected weekly. In Badrashin and Kom Hamada regions, some potato fields were furnished with thermohygrograph, and the thermohygrograph papers were collected weekly.

Estimation of disease characters

The disease severity was used to measure the development of late blight. The degree-day calculation, which called physiological-environmental time scale used as an environmental quality or combination of quantities (environmental units).

Disease progress curves

The progress of late blight in potatoes was estimated by the observations of epidemics, as exemplified by Fry [7]. The graph paper, statistics and computers, were used for fitting the disease progress curves [11]**.** Simple and polynomial regression models are common forms of this type of model. Statistical modelling of disease progress data for potato late blight was represented as $Y = f(t)$, where y is disease severity, t is time, $f(t)$ is some function of time.

Results and discussion

Survey of potato late blight

Survey of potato for incidence of late blight was carried out in several fields in three locations in Egypt (Badrashin, Kafr El-Zayat and Bosaily) during three consecutive winter seasons 1998/1999, 1999/2000 and 2000/2001, and in two locations (Kom Hamada and Salhia) during two winter seasons 1999/2000 and 2000/2001. There were some differences between disease severities at those locations. The obtained result indicated that the disease severity was very low in all surveyed localities at Badrashin, Kafr El-Zayat, and Bosaily, where severities were ranged from 9–20%, in 1998/1999. The highest severities of blight were at Badrashin, Kom Hamada and Salhia, where severities ranged from 85–97% and 97–100% in 1999/2000, 2000/2001, respectively. However, disease severity was low in Kafer El-Zayat and Bosaily, where severities ranged from 10–25%.

The results of the present study showed that disease incidence varied between the three seasons and different locations. In most areas surveyed, the most affected area by late blight was at Giza, Behaira and Ismailia. The highest severity of late blight in many fields indicated that these fields were grown under favourable weather conditions [5, 8, 14, 15].

Monitoring of weather conditions

The weather data was plotted in *Figs. 3–7*. Daily total rainfalls are included in each figure. In all figures, horizontal lines were included to indicate the thresholds of temperature (min. 10 °C, max. 25 °C), relative humidity (85%) and rainfall (2 mm).

Most of the nights (minimum temperature) in November and December 1998/1999 were relatively cool in all of potato-growing areas, so, the disease had not built up the inoculums which are needed to start epidemic [3, 4]. There was a big contrast in this regard with November and December 1999/2000-2000/2001 at Badrashin, Kom Hamada and Salhia, which had relatively warm nights. However, Kafr El-Zayat and Bosaily had cool nights during both seasons. We note also that the rainfall came fairly early in November and December 2000/2001 and occurred again on following days. De Weille [2] reported that after three or four days from infection at the first leaf spot occur, the number of diseased leaves will soon begin to increase. Thus for a period extending from November and December 1999/2000-2000/2001, warm and humid nights were the usual occurrence at most of stations in growing areas which had

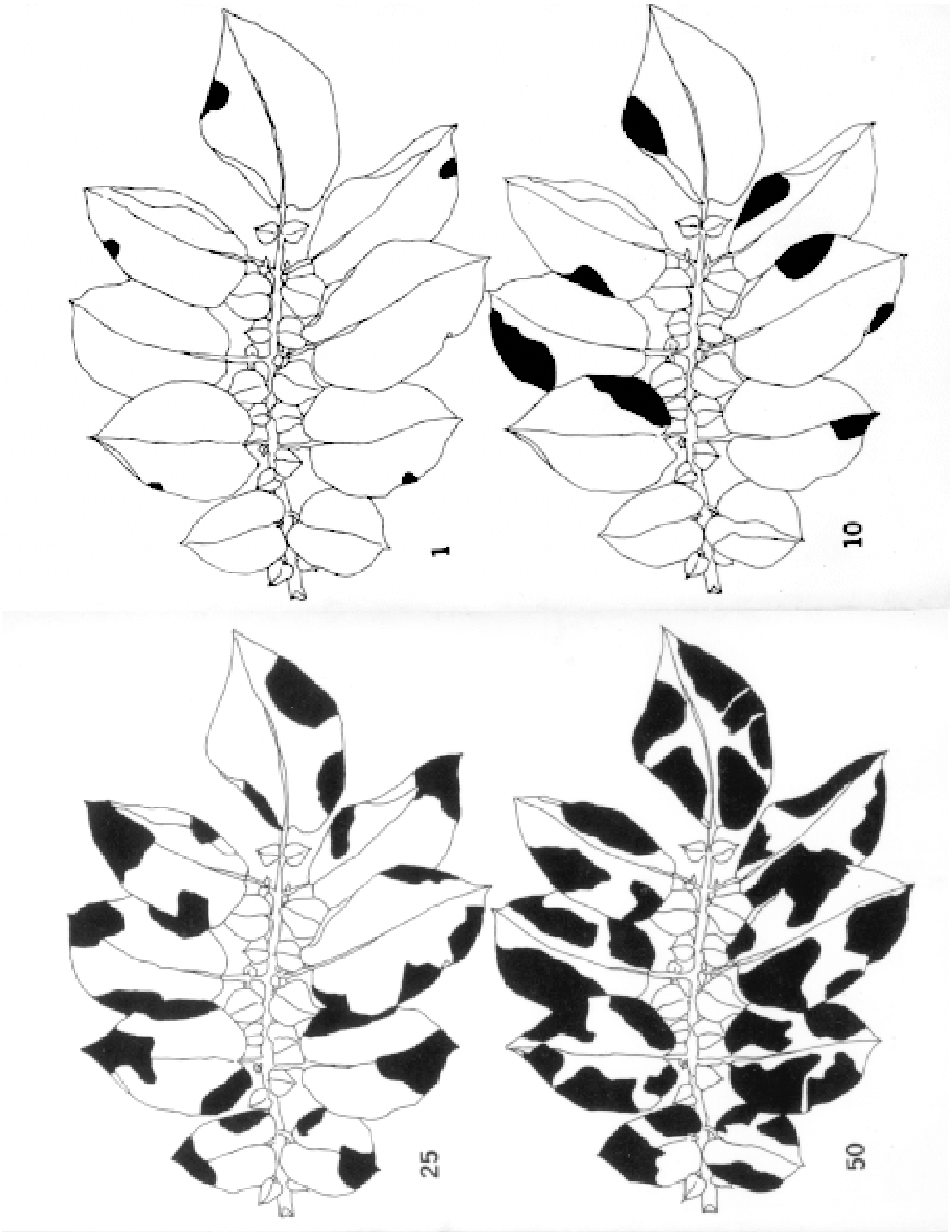


Figure 2*. Assessment of percentage of leaf area affected by late blight within the foci, it scaled as 1, 10, 25 and 50% (James, 1947* [10]*).*

outbreak of late blight. An important part of the climatological model for the development of *Phytophthora infestans* is the continuation of high humidity into each morning after sunrise. Such a continuation would normally be most favoured by the presence of complete fog or cloud cover. Then it is reasonable to expect that, in the potato crops themselves, leaf surfaces would have been wet for at least a few hours during most nights in this period [2]. Similar results were obtained by Ullrich [17]

***Table 1**. Assessment key* for the last stages of late blight epidemic when infection is widespread.*

Blight (%)	Nature of infection
0	No disease observed.
0.1	A few scattered plants blighted; not more than 1 or 2 spots in 12-yard radius.
1	Up to 10 spots per plant; or general light infection.
5	About 50 spots per plant; up 1 to 10 leaflets infected.
25	Nearly every leaflet infected, but plants may smell of blight; field looks green although every plant is affected.
50	Every plant affected and about 50% of leaf area destroyed; field appears green, flecked with brown.
75	About 75% of leaf area destroyed; field appears neither predominantly brown nor green.
95	Only a few leaves on plants, but stems are green.
100	All leaves dead, stems are dead or dying.

* Disease assessment keys, which described by James (1947) [10] in British Mycological Society Manual.

found from the laboratory investigations that 50% infection result was obtained in 4.5 hours of leaf wetness. In the temperature interval between 10°C and 21°C, obtained about equal degree of infection. However, Hyre [9] considered temperature below 7.2 °C or above 25.5 °C to be unfavourable for blight development.

Estimation of disease progress curves

Late blight epidemic started shortly after the rainy season started and progressed steadily in most of potato-growing areas in Egypt during winter seasons 1999–2001 (*Figs. 8–9*). The progress of late blight in potato fields, the x (disease severity) increased from $0 \leq x_0 \leq$ 0.1–1.0% after 70 days during non-epidemic year, while during epidemic year, the x increased from $0 \leq x_0 \leq$ 40–45% after 70 days from planting date. Obviously x_0 locates the curve at time zero.

***Table 2.** Polynomial models* for analysis of disease progress data for different potato-growing areas during winter seasons 1999–2001.*

Locality	Growing season	Polynomial model	R^2
Badrashin	1999	$y = -0.0021\,x^6 + 0.0648\,x^5 - 0.7391\,x^4 + 3.7252\,x^3 - 7.5435\,x^2 + 4.8013\,x$	0.9931
	2000	$y = -0.0167\,x^5 + 0.2984\,x^4 - 1.3962\,x^3 + 1.7216\,x^2 + 0.3354\,x$	0.9882
	2001	$y = -0.0187\,x^5 + 0.4707\,x^4 - 4.5362\,x^3 + 21.649\,x^2 - 38.598\,x + 20.933$	0.996
Kom Hamada	2000	$y = -0.0004\,x^6 + 0.0011\,x^5 + 0.1015\,x^4 - 0.7938\,x^3 + 2.0318\,x^2 - 1.5881\,x$	0.9989
	2001	$y = 4E\text{-}05\,x^6 + 0.0002\,x^5 - 0.0246\,x^4 + 0.0761x^3 + 2.4781\,x^2 - 3.847\,x$	0.997
Kafr El-Zayat	1999	$y = -1E\text{-}05\,x^6 + 0.0005\,x^5 - 0.0096\,x^4 + 0.0804\,x^3 - 0.2268\,x^2 + 0.1732\,x$	0.9842
	2000	$y = 0.0003\,x^6 - 0.0074\,x^5 + 0.0573\,x^4 - 0.1333\,x^3 + 0.0224\,x^2 + 0.1161$	0.9773
	2001	$y = -0.0007\,x^6 + 0.0226x^5 - 0.2607\,x^4 + 1.2986\,x^3 - 2.3776\,x^2 + 1.3166\,x$	0.9875
Bosaily	1999	$y = -0.0001\,x^6 + 0.0037\,x^5 - 0.0404\,x^4 + 0.2169\,x^3 - 0.4949\,x^2 + 0.3514\,x$	0.9829
	2000	$y = -0.0002\,x^6 + 0.0062\,x^5 - 0.0853\,x^4 + 0.5492\,x^3 - 1.4162\,x^2 + 1.1327\,x$	0.9639
	2001	$y = -0.0003\,x^6 + 0.0108\,x^5 - 0.1277\,x^4 + 0.6224\,x^3 - 0.8596\,\mathrm{x}^2 + 0.1744\,x$	0.9776
Salhia	2000	$y = -0.0004\,x^6 + 0.0011\,x^5 + 0.1015\,x^4 - 0.7938\,x^3 + 2.0318\,x^2 - 1.5881\,x$	0.9989
	2001	$y = 4E\text{-}05\,x^6 + 0.0002\,x^5 - 0.0246\,x^4 + 0.0761\,x^3 + 2.4781\,x^2 - 3.847\,x$	0.997

*Statistical analysis with polynomial regression using MINITAB statistical program.
y: disease severity, x: days after planting, R^2: coefficient of determination between x and y variables.

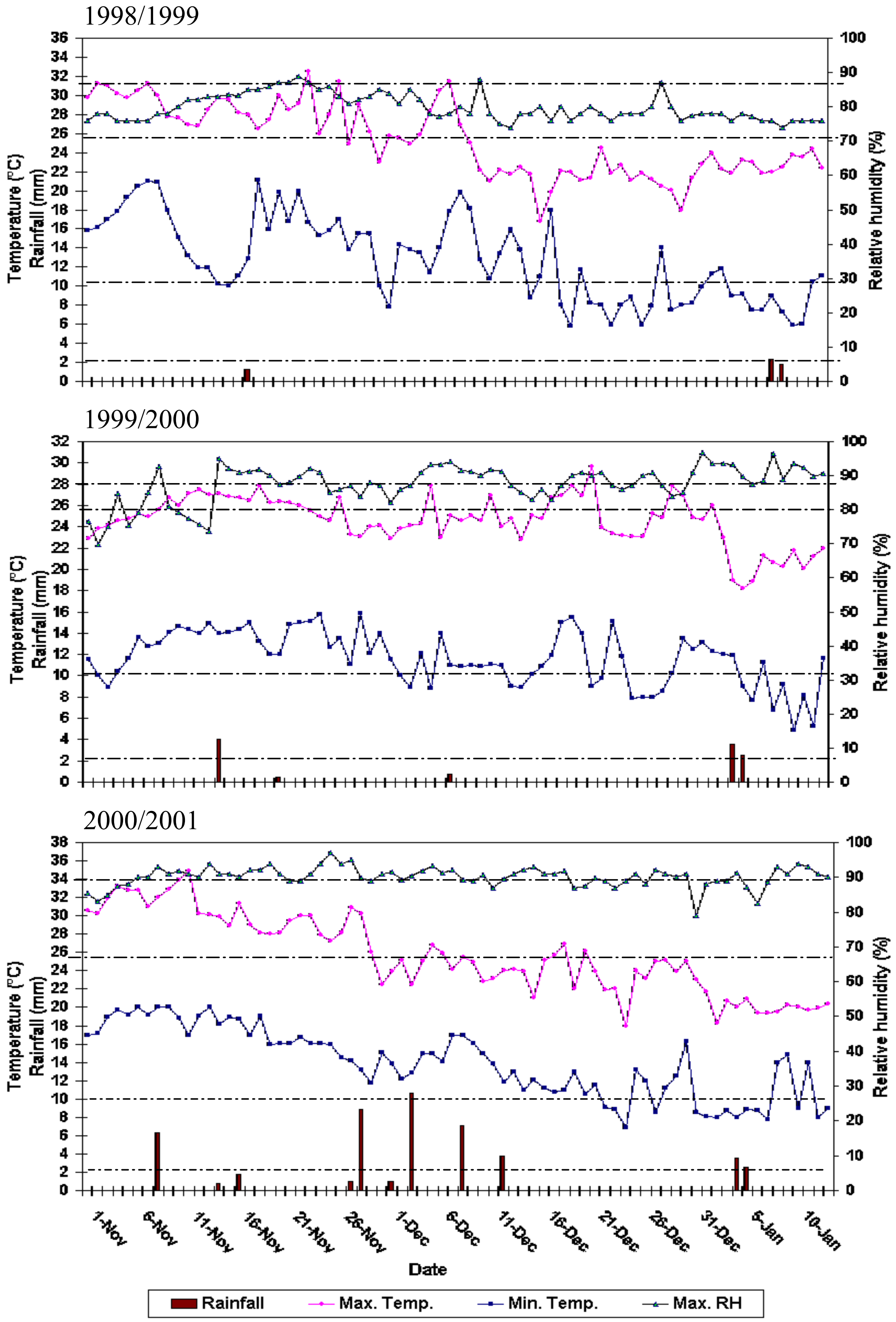


Figure 3. *Daily rainfall (mm), maximum and minimum daily temperature (°C), and maximum daily relative humidity (%) during winter seasons 1999–2001 in Badrashin region.*

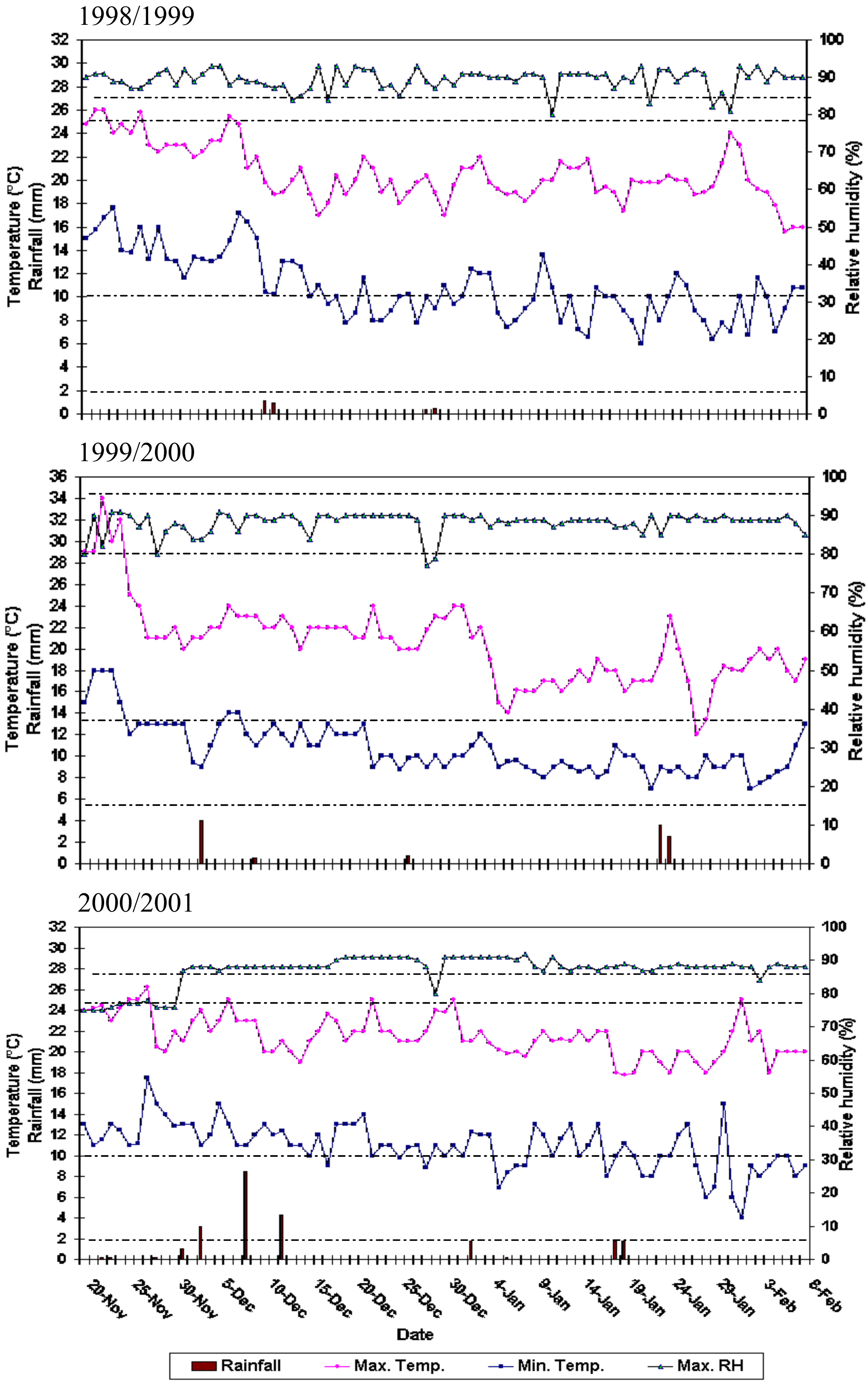


Figure 4. *Daily rainfall (mm), maximum and minimum daily temperature (°C), and maximum daily relative humidity (%) during winter seasons 1999–2001 in Kafr El-Zayat region.*

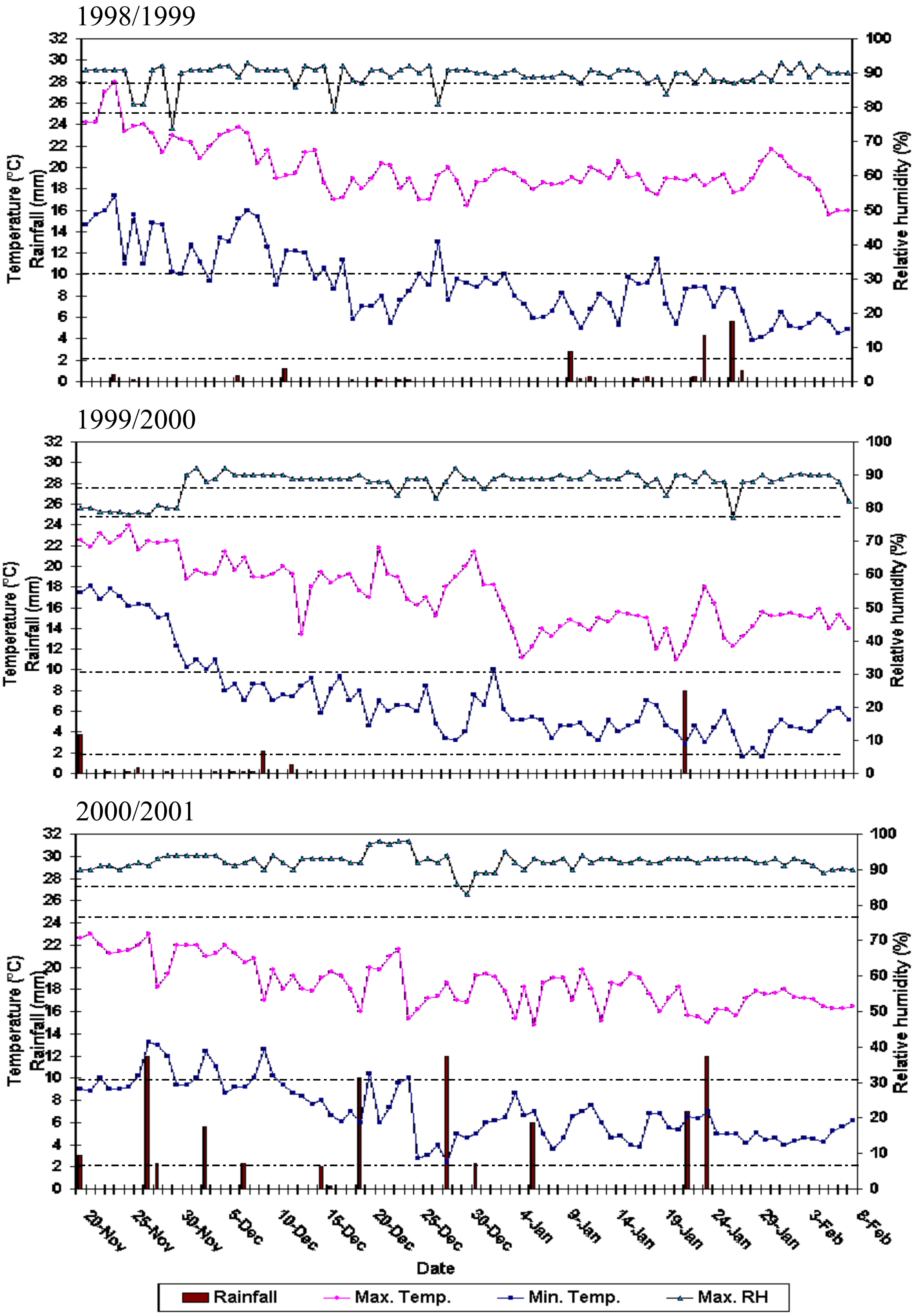
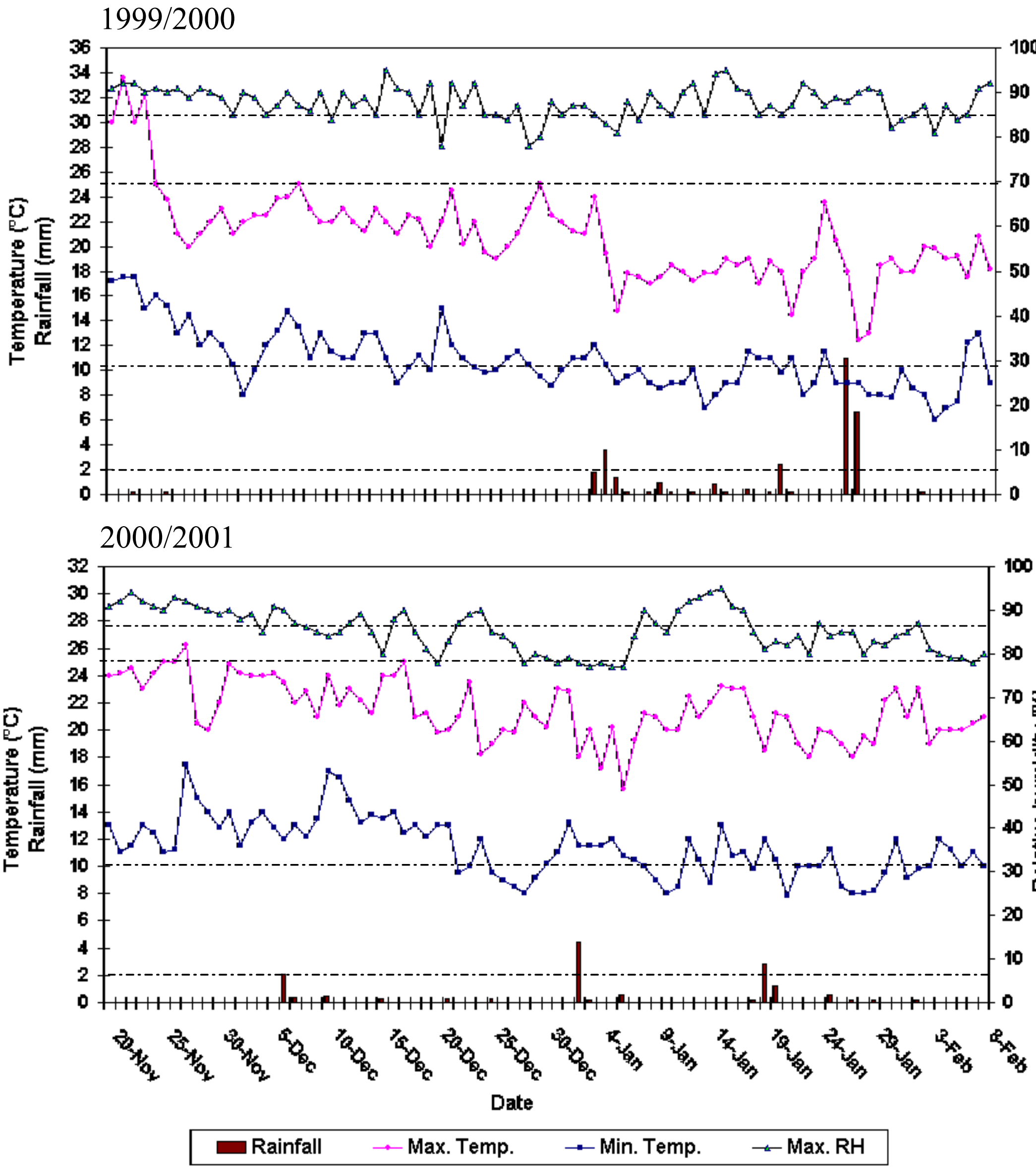


Figure 5. *Daily rainfall (mm), maximum and minimum daily temperature (°C), and maximum daily relative humidity (%) during winter seasons 1999–2001 in Bosaily region.*


1999/2000

2000/2001

Figure 6. Daily rainfall (mm), maximum and minimum daily temperature (°C), and maximum daily relative humidity (%) during winter seasons 2000–2001 in Kom Hamada region.

A plot of potato late blight values vs. time – a disease progress curve – summarizes the effect of host, pathogen, and environment on epidemic development. Thus the same pathogen in the same environment and in the same host species produced both positively and negatively skewed progress curves [11, 18].

Statistical analysis of disease progress curves

MINITAB statistical program was used for fitting the best model to describe the relationships between time (days after planting) and observing disease severity. The model based on the observed set of data about the mechanism of disease increase. Polynomial regression models are common forms of this type of model.

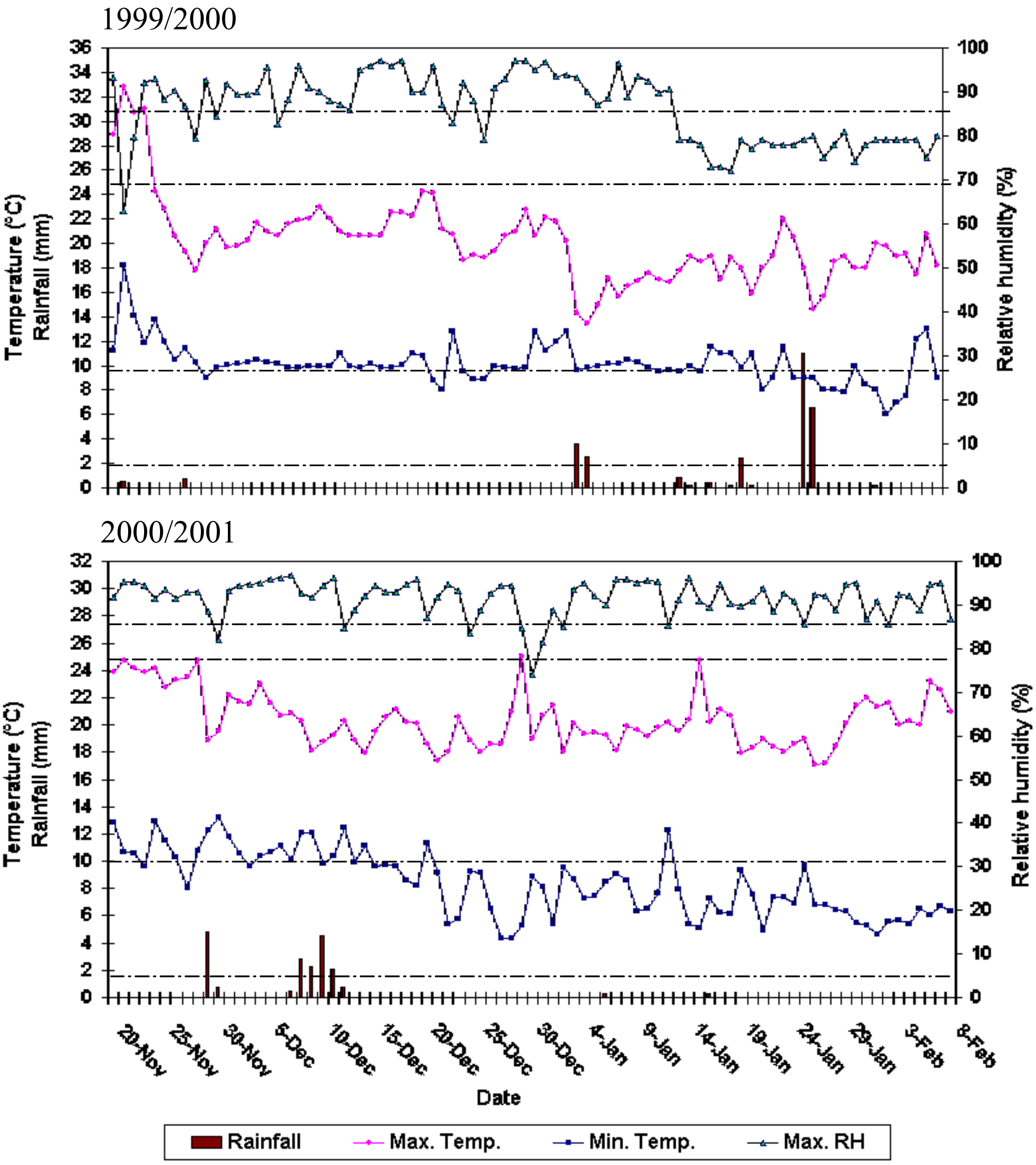


Figure 7. *Daily rainfall (mm), maximum and minimum daily temperature (°C), and maximum daily relative humidity (%) during winter seasons 2000–2001 in Salhia region.*

Statistical modelling of disease progress data for potato late blight represented as $y = f(x)$, where y is disease severity, x is time (days after planting); $f(x)$ is function of time. The function of time has been described as $y = b_0 + b_1 x + b_2 x^2 + \ldots + b_q x^q$, in which the b's are unknown parameters estimated from the data and x is days after potato planting. The equations of disease progress curves for the growing area have been shown in *Table 2*. Models of this type are called polynomials. Although parameters are constants, their estimates are random variables; the estimated parameters characterize epidemics.

The increase in blight in a field of potatoes during epidemic years follows a compound-interest pattern of development [18], resulting in a sigmoid-shape disease progress curve. All models are simplification of reality.

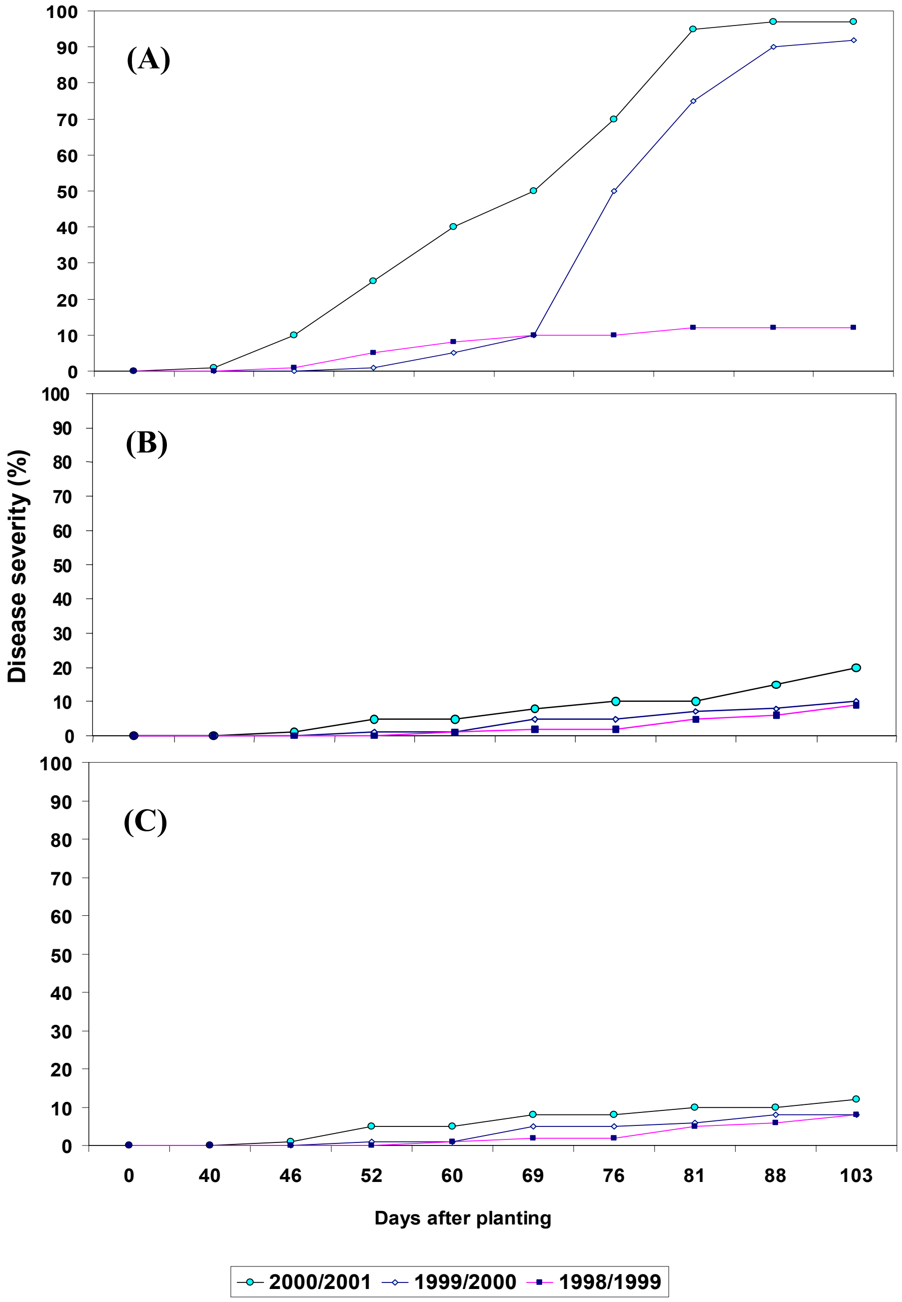


Figure 8. *Late blight progress curves on potato in* (A) *Badrashin,* (B) *Kafr El-Zayat and* (C) *Bosaily growing area during three winter seasons 1999–2001. Visual disease severity assessments weekly.*

Conclusion

Late blight epidemic started shortly after the rainy season started and progressed steadily in most of potato-growing areas in Egypt during winter seasons 1999–2001.

Blight appeared consistently earlier in South-Delta (Badrashin) than elsewhere, because the potatoes had been planted 25–30 days before planting date of other potato-growing area in winter season.

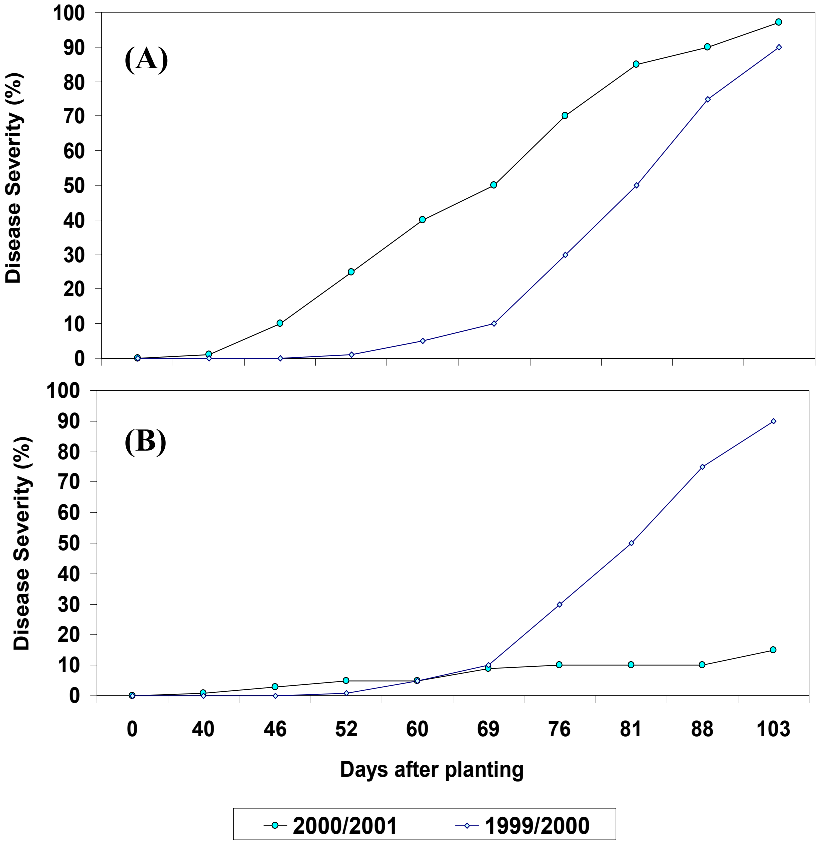


Figure 9. *Late blight progress curves on potato in* (A) *Kom Hamada and* (B) *Salhia growing area during two winter seasons 1999–2001. Visual disease severity assessments weekly.*

From the disease progress curves it can be seen, late blight epidemic started shortly after rainy season and progressed steadily in most of potato-growing areas in Egypt during epidemic winter seasons 2000–2001.

Potato blight forecasting is important to protect the potato yield. If the favourable weather conditions can be forecast and communicated to the growers early with sufficient time for a control sprayed, the crop will be protected.

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TEMPORAL-SPATIAL PATTERN OF TRUE BUG ASSEMBLIES (HETEROPTERA: GERROMORPHA, NEPOMORPHA) IN LAKE BALATON

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(Received 10th December 2002; accepted 9th May 2003)

Abstract. The present study was carried out at lake Balaton during 1999 and 2000, collecting Heteroptera species from 44 sampling sites. The different basins and the surrounding streams were compared based on temporal-spatial patterns of bug assemblies. The dominance and constancy values of the present species were used in the analysis. The Szemes Basin shows the least values of diversity and the streams have the greatest values.

Keywords: *aquatic bugs, semiaquatic bugs, freshwater, community, pattern-analysis,hydrobiology*

Introduction

The lake Balaton is reckoned among the most frequently examined lakes in the world, but the knowledge of its ecosystem is still imperfect. Beside the lake scientists have to pay attention also to the catchment areas.

Hydrocenological researches on Nepomorpha or Gerromorpha in Hungary have been being in progress for decades [1, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 29, 30, 33], but few of them have been dealing with ecological pattern analysis [5, 6, 16, 29].

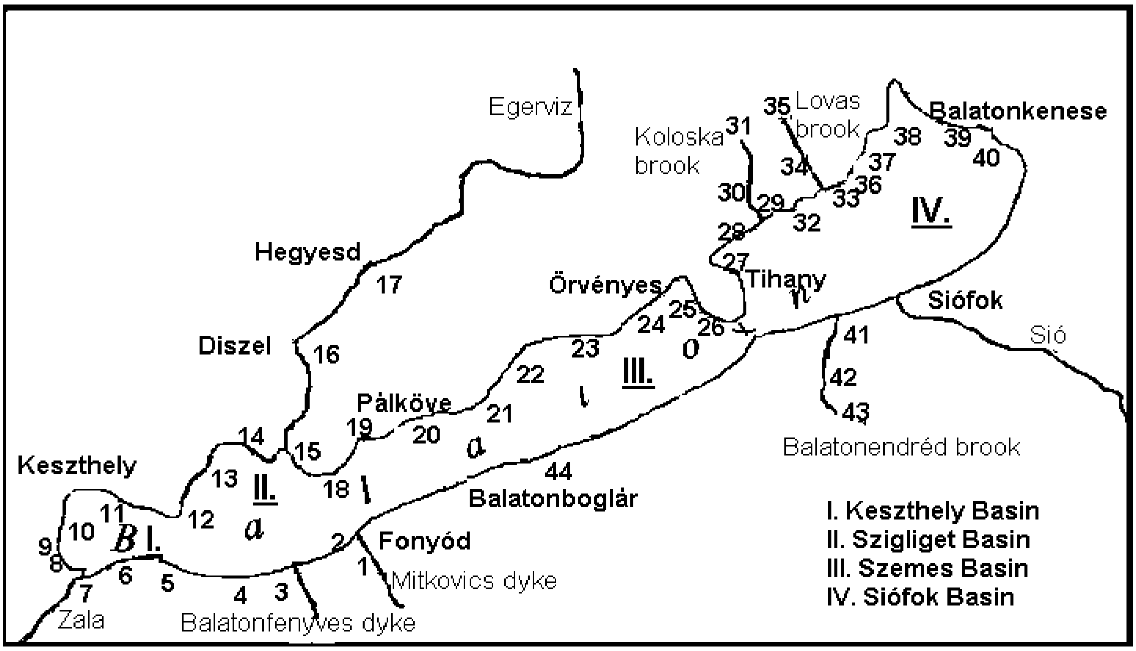
The exploration of the pattern in time and space of the Heteroptera communities beside the supply of data for basic research can contribute to reply some practical questions too. Based on former observations bugs can be suitable to show the change of their environment, so they can use to indicate the change in time and space of the water quality [3, 5, 7, 8, 10, 12, 13].

Consequently the goal of the fieldwork was to collect informations for the development of a monitoring system of the biological water quality.

Materials and methods

The sampling sites were designated in the north and south shoreline of lake Balaton and along the bank of streams flowing into the Balaton (Mitkovics stream, Balatonfenyves stream, River Zala, Egervíz stream, Koloska stream, Lovas stream, Balatonendréd stream). 204 samples were collected from the 44 sampling sites (*Fig. 1*) in 1999 and 2000.

Insects were collected by hand net. The obtained semiquantitative sample shows well the ratios of the species, but do not give information about the real quantity of the species. The works of Benedek [2], Hufnagel and Vásárhelyi [17], Jansson [18,19], Péricart [20], Savage [24], Soós [25], Štusák [26], Vepsäläinen and Krajewski [31], and



1. Alsóbélatelep, Mitkovics dyke
2. Alsóbélatelep, next to the beach
3. Balatonfenyves dyke, at the narrow-gauge railway
4. Balatonmáriafürdő
5. Balatonberény I.
6. Balatonberény II.
7. River Zala
8. Fenékpuszta I.
9. Fenékpuszta II.
10. Keszthely
11. Vonyarcvashegy, Szent Mihály Hill
12. Balatongyörök
13. Szigliget bay, Anglers camping
14. Szigliget bay
15. Egervíz, at the mouth
16. Egervíz, at Diszel
17. Egervíz, at Hegyesd
18. Badacsonylábdihegy
19. Ábrahámhegy
20. Pálköve
21. Balatonszepezd I.
22. Balatonszepezd II.
23. Balatonakali, near to the Dörgicse railway station
24. Örvényes, next to the beach
25. Sajkod, beach
26. Sajkod, far away from the beach
27. Diós-Gödrös
28. Balatonfüred, near to the pier
29. Koloska brook, at the mouth
30. Koloska brook
31. Koloska brook, at the spring
32. Palóznak bay, at Csopak
33. Lovas brook, at the mouth
34. Lovas brook, at Lovas
35. Lovas brook, at the spring
36. Alsóörs I.
37. Alsóörs II., Riviera camping
38. Balatonalmádi
39. Balatonkenese, at Törökverő
40. Balatonakarattya, at the sewage farm
41. Balatonendréd brook, at the mouth
42. Balatonendréd brook, at Bocsida field
43. Balatonendréd brook, at the spring
44. Between Balatonlelle and Balatonszemes

***Figure 1.** The sampling sites at lake Balaton and surrounding streams*

Vásárhelyi [32] were used for identification of bugs. The detailed summary of the collecting methods can be found in Bakonyi's [1] and Hufnagel's [10] dissertations. At all place and time, habitat and water quality characteristics were measured. These data were published formerly [3, 4]. The four basins of Balaton and the streams were compared in this work. After the identification of the collected imagos and larvae zoocenological tables were made which were analysed using multivariate statistical methods. By means of Syn-Tax program package [21, 22, 23] ordinations (PCoA, PCA) and classifications (hierarchical clustering) were used for reconnaisance of the similarity patterns. In addition number of species, number of individuals, dominance, constancy values were calculated. The measurement of the biodiversity has many problems. This analysis was made based on the methodological recommendations by Hufnagel et al. [14]. Comparing the basins of Balaton and the surrounding streams Rényi's diversity ordering was applied with the help of NuCoSA program package [27, 28].

Results

As a result of our study 31 Heteroptera species were found in Balaton and in the examined streams (*Table 1*). Next to the species the constancy and dominance values are indicated in *Table 1*. The serial numbers of bugs were used in multivariate statistical methods to identify them. During the examination in 147 from the 204 samples were found Heteroptera species and 4247 bugs were identified. The basins of Balaton were compared to streams based on Heteroptera species. The streams unambiguously differ from all basins of Balaton. The main difference among the basins was between the Szemes Basin and Szigliget Basin (*Fig. 2*).

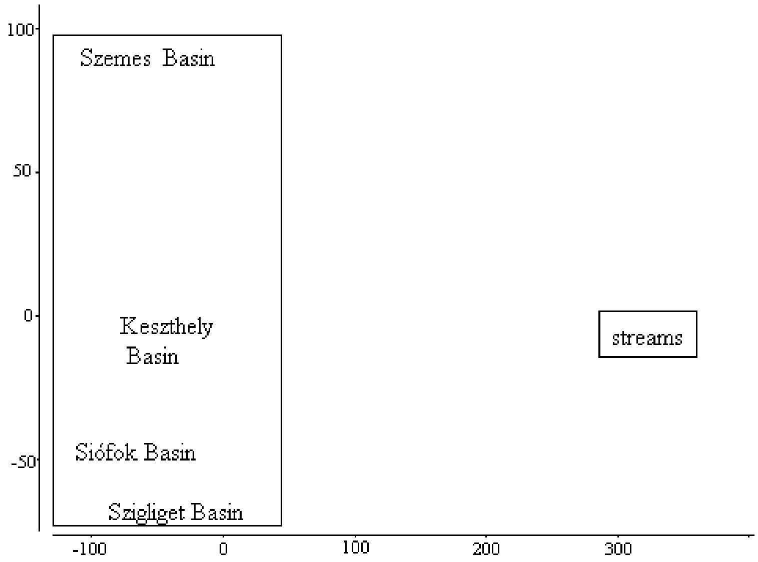


Figure 2. *The result of the ordination on the basins of Balaton and streams.*

Fig. 3 shows the result of the ordination on the Heteroptera species of Balaton and streams. From the living water to still water continuity is on the vertical axis (axis 2), while the number of individuals can be found on the axis „z". In the figure we can sepatate some groups of the Heteroptera species, according to the followings. The I marks the species with high number of individuals, the II marks the group of medium number of individuals, and the III marks the small number of individuals. To the group I/1 belongs only *Aquarius paludum*, which is a typical species of the standing waters. *Sigara striata* (group I/2) can be found in the streams or in the standing water, *Gerris lacustris* in the group I/3 was collected in the streams with high number of individuals. *Gerris argentatus* and *Micronecta meridionalis* belong to the II/1 group, these species are mainly typical of the Siófok Basin, while *Plea leachi* and *Cymatia coleoptrata* (II/2) characterize the Szemes Basin. The species in II/3 (*Sigara lateralis, Ilyocoris*

Table 1. *The collected Heteroptera species and their constancy (c%), dominance (d%) and serial number (No.).*

Taxa	*c*%	*d*%	No.
Gerromorpha			
Gerridae			
Aquarius paludum paludum (Fabricius, 1794)	34.80	16.84	6
Gerris argentatus (Schummel, 1832)	25.98	9.07	5
Gerris asper (Fieber, 1860)	7.84	1.53	3
Gerris lacustris (Linnaeus, 1758)	16.67	7.82	2
Gerris odontogaster (Zettersedt, 1828)	8.33	0.64	4
Gerris thoracicus (Schummel, 1832)	6.86	1.37	1
Veliidae			
Microvelia reticulata (Burmeister, 1835)	7.35	1.27	7
Velia saulii saulii (Tamanini, 1947)	1.96	0.54	8
Velia caprai caprai (Tamanini, 1947)	1.47	0.35	9
Mesoveliidae			
Mesovelia furcata (Mulsant & Rey, 1852)	7.35	0.87	10
Hydrometridae			
Hydrometra gracilenta (Horváth, 1899)	0.98	0.05	11
Hydrometra stagnorum (Linnaeus, 1758)	5.39	1.46	12
Nepomorpha			
Nepidae			
Nepa cinerea (Linnaeus, 1758)	12.25	4.05	13
Ranatra linearis (Linnaeus, 1758)	6.37	0.45	28
Notonectidae			
Notonecta glauca glauca (Linnaeus, 1758)	17.16	4.87	14
Pleidae			
Plea minutissima minutissima (Leach, 1817)	16.18	6.26	15
Corixidae			
Callicorixa praeusta praeusta (Fieber, 1848)	1.47	0.09	16
Corixa punctata (Illiger, 1807)	0.49	0.02	21
Cymatia coleoptrata (Fabricius, 1777)	14.22	4.73	27
Hesperocorixa linnaei (Fieber, 1848)	14.22	5.30	22
Hesperocorixa sahlbergi (Fieber, 1848)	0.98	0.05	23
Micronecta meridionalis (Fieber, 1860)	7.35	5.63	26
Micronecta minutissima (Linnaeus, 1758)	0.49	0.02	25
Micronecta pusilla (Horváth, 1895)	1.47	0.99	24
Paracorixa concinna (Fieber, 1848)	0.49	0.02	31
Sigara falleni (Fieber, 1848)	12.75	1.51	18
Sigara lateralis (Leach, 1817)	6.37	2.94	17
Sigara limitata (Fieber, 1848)	0.49	0.09	30
Sigara nigrolineata nigrolineata (Fieber, 1848)	3.43	4.24	20
Sigara striata (Linnaeus, 1758)	29.41	11.30	19
Naucoridae			
Ilyocoris cimicoides cimicoides (Linnaeus, 1758)	25.98	5.63	29

cimicoides, Hesperocorixa linnaei, Nepa cinerea, N. glauca, S. nigrolineata) are mostly in streams. *Gerris asper, Microvelia reticulata, Velia caprai, Mesovelia furcata, Hydrometra gracilenta, Callicorixa praeusta, Sigara falleni, Corixa punctata, Hesperocorixa sahlbergi, Micronecta pusilla, Micronecta minutissima, Ranatra linearis, Sigara limitata, Paracorixa concinna* (group III/1) characterize the standing water, but they were collected in small cuantity of individuals. *Gerris odontogaster* and *Velia saulii saulii* were found both in the streams and in the basins, while the *Gerris*

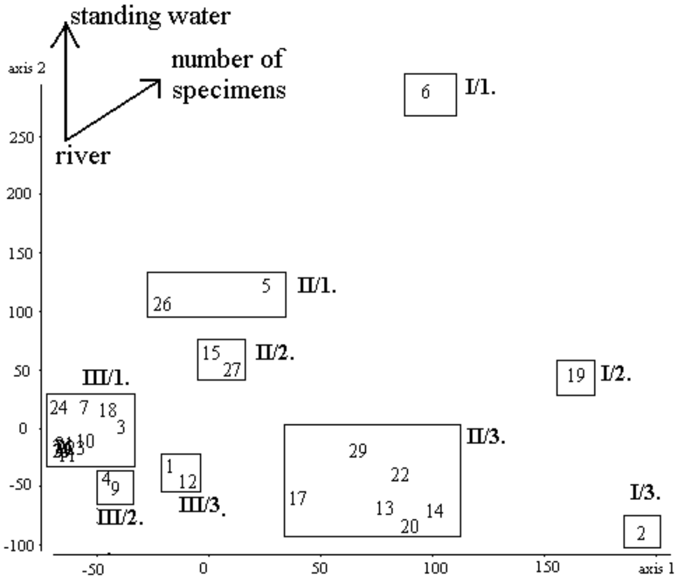


***Figure 3.** The result of the ordination on the Heteroptera species of Balaton and streams.*

thoracicus and *Hydrometra stagnorum* were collected only from the streams (groups III/2 and III/3).

Among the Heteroptera species the *Aquarius paludum* and the *Cymatia coleoptrata* are typical of the Szemes Basin, the *Micronecta meridionalis* and the *Gerris argentatus* are mainly peculiar to the Szigliget Basin and the Siófok Basin. The *Gerris lacustris, Notonecta glauca, Sigara lateralis, Sigara nigrolineata, Hesperocorixa linnaei, Nepa cinerea, Sigara striata* and *Ilycoris cimicoides* are characteristic of the streams. But none of the Heteroptera species are unique in the Keszthely Basin (*Fig. 3*).

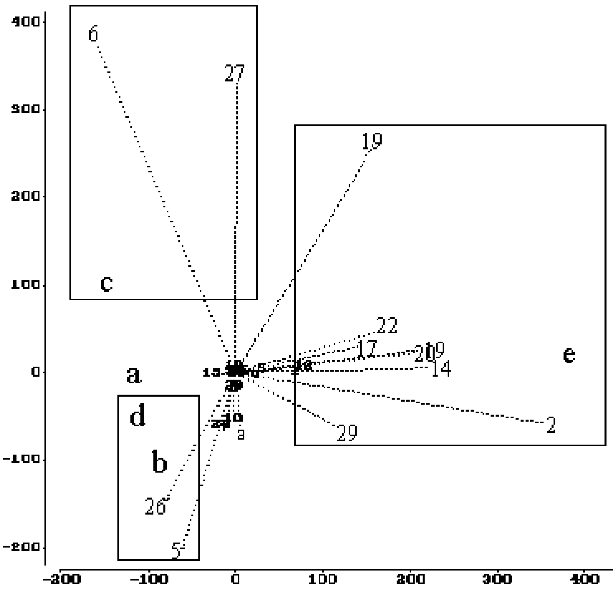


***Figure 4.** The result of the PCA on the Heteroptera species of Balaton and streams.* a: *Keszthely Basin,* b: *Szigliget Basin,* c: *Szemes Basin,* d: *Siófok Basin.*

Various diversity indices were used for characterization the basins and streams. The average number of species and the avarege number of individuals can be seen in *Fig. 5*.

The values of the average number of species and the number of individuals are the greatest in the streams and the least in the Szemes Basin. The average number of species compared to the average number of individuals has the greatest value at the Szigliget Basin (*Fig. 6*). Rényi's diversity ordering was used by means of NuCoSA program package and the values are given in *Fig. 7*. The decreasing lines show the run of thediversity values of the basins and streams on different parameters. Number 1 marks the Keszthely Basin, number 2 is the Szigliget Basin, number 3 is the first group of Szemes Basin, number 4 is the second group of Szemes Basin, number 5 marks the Siófok Basin, number 6 and number 7 are the two groups of streams. Because of the high number of sampling sites in the Szemes Basin and along the streams these were divided into 2–2 parts to get more homogeneous samples.

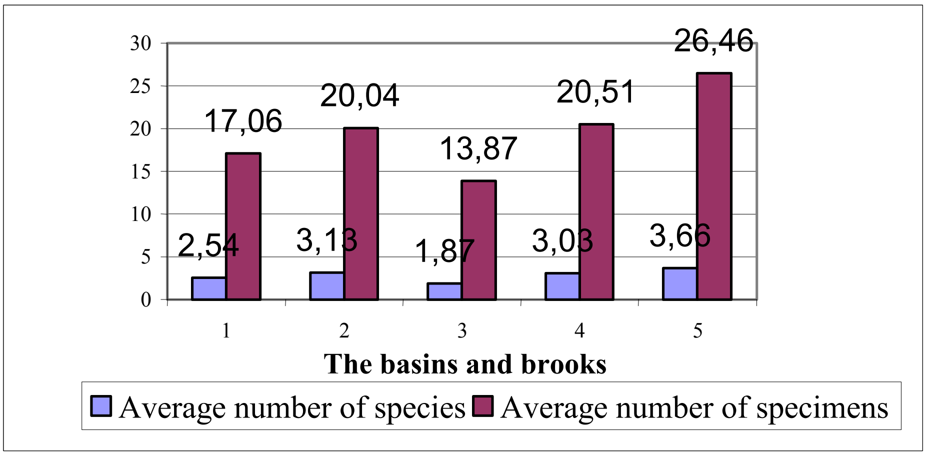


Figure 5. *The average number of species and average number of individuals of Heteroptera in lake Balaton and streams.* 1: *Keszthely Basin,* 2: *Szigliget Basin,* 3: *Szemes Basin,* 4: *Siófok Basin,* 5: *streams.*

Figure 6*. The number of species divided by the number of individuals of Heteroptera in lake Balaton and streams.* 1: *Keszthely Basin,* 2: *Szigliget Basin,* 3: *Szemes Basin,* 4: *Siófok Basin,* 5: *streams.*

If a diversity profile runs above another one means that this sample is more diverse in respect both of the rare and the frequent species. If two lines cross each other the samples can not be ordered accordig to the diversity. By inreasing the scale parameter the frequent species have more influence on the value of the Rényi's diversity. In our survey the Szemes Basin has the less diversity and the first group of the streams shows the greater diversity. The diversity of the Siófok Basin is less than the values of the others. The Keszthely Basin, the Szigliget Basin and the second group of the streams show similar diversity patterns.

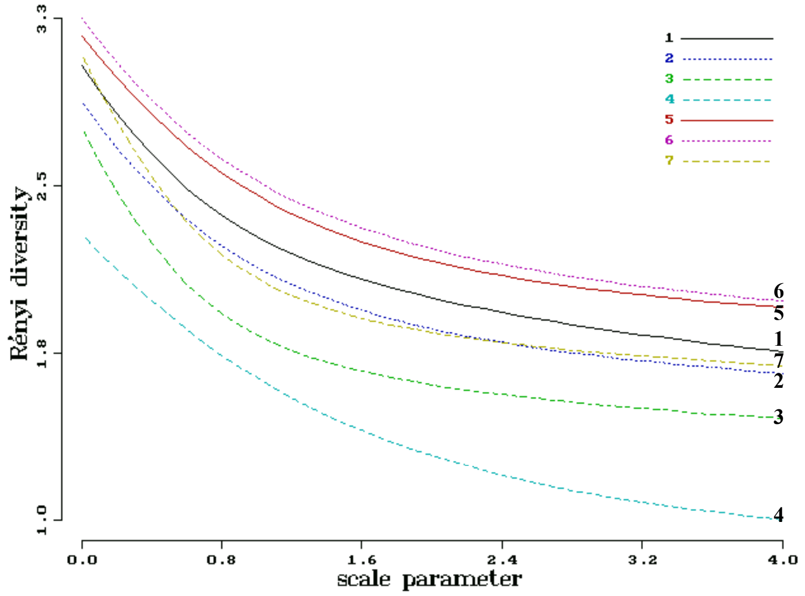


Figure 7. *The result of diversity ordering on basins and streams.* 1: *Keszthely Basin,* 2: *Szigliget Basin,* 3: *the first group of the Szemes Basin, 4: the second group of the Szemes Basin,* 5: *Siófok Basin,* 6: *the first group of streams,* 7: *the second group of streams.*

Discussion

31 Heteroptera species were found and 4247 bugs were identified in this work. The Heteroptera fauna of the streams is basically different from the fauna of lake Balaton, but also the four basins have differencies in their bug assemblies. The highest values of number of individuals and number of species of bugs were found in streams according to the environmental heterogenity. Among the streams was found both fast flowing parts without reed and slow flowing parts - with almost still water character - with reed. The reason of the differentation of the fauna in the basins is the quality of the founded reed. From the point of view of Heteroptera fauna the sampling sites can be analysed using multivariate statistical methods or diversity indices. Using these methods the cenological patterns were revealed. For the more precise description of the structure of the communities the examination of the food nets could be important. Besides it is essential to examine further sampling sites and collect further data.

Acknowledgements. The research was carried out by means of Department of Systematic Zoology and Ecology of the Eötvös Loránd University. I am grateful to Dr. Levente Hufnagel for his kind help. This work was supported by Pro Renovanda Cultura Hungariae Foundation.

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Almaši et al.:
BOLESTI, ŠTETOČINE I KOROVI KUKURUZA I NJIHOVO SUZBIJANJE

DISEASES, PESTS AND WEEDS OF MAIZE AND THEIR CONTROL
Školska knjiga, Novi Sad, 2002

reviewed by É. ERDÉLYI
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The book is written in Serbo-Croatian. It consists of 5 chapters: agricultural engineering of maize, diseases of maize, maize pests, weeds in maize, motorization for protection. The middle three (most spacious) chapters have abstracts in English. At the end of each chapter we find colour pictures and plenty of references mostly from the Carpathian basin.

Maize is one of the most important cultivated plants in the world. This book is probably – at least in Europe – the most detailed work about plant protection of maize until now. It is written – 695 pages with 38 coloured picture-tables – by a group of 14 authors from different Universities and Institutes of several cities of Yugoslavia, that shows the importance of maize growing in Serbia.

The *first chapter* shortly informs us about importance of maize growing in general, hybrids and agricultural engineering of maize cultivation (no English abstract).

The *second chapter* is mainly written in accordance with numerous results on maize diseases obtained for the last 50 years in Serbia. This topic is divided into three parts:

(1) Parasitic Diseases
  - caused by fungi – these are the most distributed and economically most important,
  - caused by viruses – maize dwarf mosaic virus, beet mosaic virus and barley yellow dwarf virus are the most important in Serbia,
  - spiroplasm, phytoplasm – which have not been detected yet in the country, and
  - bacteria – it has insignificant economic importance in Serbia.

(2) Non-parasitic Diseases.
(3) Integrated Maize Protection.

A brief analysis of disease spread, deleteriousness and symptoms, biology and epidemiology of parasites, as well as control measures are presented. Beside parasites present in the country, some parasites that could endanger maize production in Serbia are also described. These diseases are classified into the following groups:

- Diseases of seeds and seedlings: a result of inadequately organised seed production, cropping practices and especially of too deep and early planting.
- Leaf spots: Beside some other insignificant types of leaf spots, Northern corn leaf blight was registered in Serbia. This type of leaf spot caused forced plant maturation – the greatest damages in the country – and a radical solution was the development of local resistant maize hybrids and their introduction into production.
- Diseases of above ground organs.

ISSN 1589 1623

- Root and stalk rots: one of the most spread and most deleterious maize disease in Serbia, which appeared quite frequently in the first generation of the local hybrids.
- Ear mouldiness: introduction of hybrid forms and application of mineral fertilisers significantly increased the damages resulting from ear mouldiness. In addition to direct damages (which recently has occurred in stored maize) significant losses arise from mycotoxins forming in mouldy ears (zearalenone and T2 toxine were the most frequently found). Such ears cause the development of mycotoxicoses in domestic animals (i.e. in hog breeding).

Maize yield significantly varied over years, regions and locations of the country as a result of adverse effects of abiotic factors. This chapter presents symptoms of injuries caused by chemicals, abnormal changes due to other causes, meteorogical and edaphic factors. These factors very often interact and often depend on applied cropping practices. The importance of crop rotation, soil tillage, fertilising, seeds, planting and irrigation within the integrated plant protection is also discussed. Problems regarding maize resistance to parasitic diseases and the role of biotechnology in parasite, pest and weed control are presented, as well. Maize parasitic diseases are described in details in this chapter. A great importance of the resistant hybrids within the integrated maize plant protection is underlined. This chapter presents the methods of artificial plant inoculations by various parasites, source of resistance and mode of inheritance, as well as several other topics related to this problem. Parasite, pest and weed biotechnical control is also described in this chapter. The following topics were especially emphasized: plant tissue culture, DNA recombinant technology, resistance of transformed plants to viruses, fungi and insects and importance of maize breeding and genetics for resistance to herbicides.

The content of the *third chapter* encompasses the following divisions: Introduction, Retrospective view on maize pests in Yugoslavia (Serbia and Montenegro), Field maize pests, Maize storage pests, Integrated maize pest control, References, Summary and List of pest Latin names. This chapter is based on 570 papers about maize pests of national and international authors. The field maize pests encompass about 70 more significant or important pest species. Noxiousness for certain pests and their control, biological and ecological aspects are presented. About 20 species of maize storage pests were observed. The studies of Yugoslavian authors claim, that approximately 130 species of various animal classes (25 are economically important) attack and damage maize during its growth. According to their number, and especially to their economic importance, insects are the most significant maize pests in Serbia. Insects are followed by mammals, nematodes, birds and mites. We can reed about pests damaging the underground parts of maize, parts close to soil surface, pests dangerous to sown seeds, about leaf and stalk pests and pests damaging generative organs of maize (tassels and ears). Great areas under maize are suitable for mass reproduction of pests, particularly, specific maize pests, which are closely related to this crop. This phenomenon very often occurs in smallholdings. Areas under small grain cereals, most often used as preceding crops (wheat is predominant) of maize, contribute to mass production of click beetles that are also dangerous maize pests. The greatest attention in the text on control of certain maize pests was paid to non-chemical methods (cropping practices, biological measures, growth of resistance hybrids). These actions and measures are important links within the integrated maize pest control. Larvae of western corn rootworm and click beetles are the most dangerous among the mentioned species. Crop rotation is the most important control measure for these two pests. Irrigation of commercial maize results higher yield. This procedure is a very important method to decrease reproduction and noxiousness of several pests, but it increases reproduction of some others. Several tables present effects of certain cropping practices on abundance of more important pests: crop rotation, sowing time, crop weediness, irrigation and soil management. Chemical maize pest control in Serbia is mostly applied against click beetles and maize leaf weevil. Fields under maize in the one-crop system shall be treated with insecticides in order to control western corn rootworm. One of the tables presents economic thresholds of noxiousness, pointing out the necessity of performing a particular chemical control. The data refer to all important pests in several countries. Due to systematic monitoring of pest distribution, abundance and development on account of forecasting the degree of their occurrence, it is possible to achieve more efficient and more economic protection of maize against pests, which will contribute to lesser application of pesticides. If all areas are surveyed for the number of larvae, great savings can be accomplished. Preventive actions (mechanical cleaning, improvement of storage premises, preventive chemical treatments), grain control at receipt, cleaning, cooling, drying, planned relocation of maize and temperature control, grain mass status during storing have priority within the integrated maize pest control. In case when pests attack maize they decide whether chemical or physical and mechanical measures should be taken.

The *fourth chapter* is written about weeds in maize field. Weeds are usual companions of cultivated plants. The most recent results on weed research in maize crops in Serbia reveal that there are 213 weed species, weed-ruderal and ruderal plants. Among these, the weed-ruderal species are the most distributed. The perennial species of geophytes and hemicryptophytes are less distributed. Their ability to reproduce vegetatively allows their intensive propagation and recalcitrance on cultivated soils. The seasonal dynamics are clearly expressed in the composition of the maize crop weed community. We can learn from the authors that our knowledge of the biology and ecology of weeds, as well as the structure of maize weed communities and their fluctuations which are dependent on environmental and agroecological conditions, are important when planning and undertaking weed control measures. This is particularly true with respect to the use of herbicides whose rational and efficient application should be based on the all-inclusive knowledge of floristic and phytocelonic relationships of weed vegetation. On the basis of this, as well as our knowledge of the biological characteristics of weeds, it is possible to choose the type, amount, timing and method of herbicide application in order to achieve maximum weed control efficiency with a minimum negative effect to the cultivated plant, environment and man. Weed control is a complex of various complimentary methods for their elimination. It should be conducted thoroughly in time and space on both cultivated plant and non-cultivated soils. The authors suggest to coordinate the measures with the biological and ecological characteristics of both maize and weeds in order to be more successful. Weed control is of preventive nature on non-cultivated and cultivated soils. Agriculture measures provide favourable conditions for cultivated plants and help weed control. They include primary and additional soil tillage, inter-row cultivation as well as other methods which increase maize yield and eliminate weeds. Chemical measures involve herbicide application, substances which directly eliminate weeds. Herbicide application has many advantages, but have certain negative effects on cultivated plants, man and his environment. For weed control in maize crops in Serbia 39 active substances with 134 products of herbicides are used. Weed control in maize crops includes the use of selective herbicides of both contact and translocational activity. Their application involves soil treatment prior to, during and immediately after sowing and before crop and weed germination. It is underlined, that due to the heterogeneous agroecological conditions of certain maize growing regions in Serbia, as well as the floristic composition and structure of weed communities of maize crops, herbicide application must be specific and well planned at each location. For this reason, rational solutions for herbicide application should be found for each location. This includes minimum labor and expences with a maximum positive effect in weed control and the elimination of negative effects for the cultivated plant, man and his environment.

In the *fifth chapter* we can read about machines and their maintenance used in maize cultivation, especially in plant protection (mechanical, chemical and other special protection). This chapter does not have an English abstract.

The plant protection of maize is very important. The goal of the authors was to provide us with a quick update. They achieved it with the good structure of chapters and subdivisions.

This book is very practical and can be useful for experts working in different fields: agronomy, plant protection, production of insecticides etc., and also for lecturers, students and Ph.D. students of agriculture universities. Using these results in plant protection of maize we can reduce damage, heavy losses in production in an economically and ecologically accepted way and with the smallest possible risk. The project was supported and sponsored by many agricultural organizations and companies. Their list and advertisements can be seen as a final chapter of 40 pages at the end of the book.