INVASIONS OF LITHOCOLLETINAE SPECIES IN EUROPE - CAUSES, KINDS, LIMITS AND ECOLOGICAL IMPACT (Lepidoptera, Gracillariidae)

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Abstract

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An analysis of the European invasions of the leaf mining Lepidoptera *Phyllonorycter platani* (S t a u d i n g e r 1870), *P. leucographella* (Z e l l e r 1850), *P. issikii* (K u m a t a 1963), *P. robiniella* (C l e m e n s 1859), *P. medicaginella* (G e r a s i m o v 1930) and *Cameraria ohridella* D e s c h k a, D i m i ć 1986. Their possible common ecological requirements as preconditions of invasions, kinds of spread and factors influencing their speed and host impact are discussed. Both positive and negative parts of above species, e.g. increase of species diversity and possible damages are evaluated.

Key words: invasions, *Phyllonorycter*, *Cameraria*, Europe

Introduction

During the 20th century the invasions of several leaf miners of the subfamily Lithocolletinae were observed in Europe. These are *Phyllonorycter platani* (S t a u d i n g e r 1870), *P. leucographella* (Z e l l e r 1850), *P. issikii* (K u m a t a 1963), *P. robiniella* (C l e m e n s 1859), *P. medicaginella* (G e r a s i m o v 1930) and *Cameraria ohridella* D e s c h k a, D i m i ć 1986. As possible invaders also such species as *Phyllonorycter gerasimovi* (H e r i n g 1930) and *P. malella* (G e r a s i m o v 1931) came into consideration (cf. Deschka, 1995). Concerning the last two species the shortage of faunistic records and of their distributional pattern is the main reason, why it is virtually impossible to estimate the possible enlargement of their areas, since their presence there might have been overlooked.

During the invasions of the above six species much attention has been paid to the study of their morphology, bionomics and of the course of their invasions. Since most of these leaf miners cause occasional damage especially in ornamental woods, additional attention was

due to their control. Principi (1953), Bogavac (1959) and some other authors studied the morphology and bionomics of *Phyllonorycter platani*, Emmet (1989), Stigter, van Frankenhuyzen (1991), De Prins (1994) and Baraniak, Walczak (2000) of *P. leucographella*, Deschka (1967) and Kuchlein et al. (2002) of *P. medicaginella*, Whitebread (1990) and Hellrigl (1998) of *P. robiniella*. The morphology, bionomics and population dynamics of *Cameraria ohridella* was investigated by numerous authors, and it is impossible to enumerate of all their papers. Most important are those published e.g. by Deschka, Dimić (1986), Skuhravý (1999), Hellrigl (1999, 2001), Pschorn-Walcher (1994, 1997) and Šefrová, Skuhravý (2000). The distributional dynamics of the individual species was investigated more or less in detail by Borkowski (1973), Deschka (1995), Nash et al. (1995), Agassiz (1996), Hellrigl (1998, 1999), Buszko et al. (2000), Šefrová (2001a) and Šefrová, Laštůvka (2001). Numerous authors presented faunistic data on the gradual invasions and completed the knowledge of their bionomics. Šefrová (1999, 2001b, 2002a, b, c, etc.) devoted special attention to all above six species.

The aim of this paper is the general evaluation of this problem complex, especially concerning the common features of these invasions, and to enclose several questions, e.g.: Do there exist some or certain preconditions for such invasions within the subfamily Lithocolletinae? Have these species some properties making them different from the other related taxa? Have the individual specimens the same preconditions for an invasion? Is the kind of the invasions identical in all these species? Which are the factors influencing the invasions speed, what are the braking and/or limiting factors? How do the invasive leaf miners influence their host plants, the next phytophagous insects on the same food plant and/or the entire communities? Are these species a negative element or a rather enriching local faunistic factor? The explanation of or at least a discussion on the above questions is only possible, if a profound knowledge of the life history and of the environmental requirements of the individual species is available. To enable this way of the discussion, I present at first a brief summary of the known life histories summarized from the available literature and resulting from my own published and unpublished results.

Material and methods

The invasive species were specially studied during the years 1995-2002. The detailed methods of the lab rearings and of field investigations including faunistic data are presented by Šefrová (1999, 2001b, 2002a, b, c) and Šefrová, Skuhravý (2000).

Results

Biological characters of species investigated

Phyllonorycter platani (S t a u d i n g e r 1870) (Fig. 1)

Adult. April – September, 3–4 generations.
Hibernation. Pupa in the fallen leaf.

Host plant. *Platanus* spp. (introduced).

Origin. Eastern Mediterranean area to Central Asia.

Start of the invasion. Second half of the 19th century.

Course and direction. With more 'jumps', to the north and northwest.

Behaviour of adults. Active at evening and at night, swarming above host trees.

Spread. Wind dispersal, anthropogenic transportation of the fallen leaves with pupae (several tens pupae in the leaf during a gradation).

Causes. Following its introduced host plant.

Fig. 1. *Phyllonorycter platani* is spreading to the north irregularly during the 20th century from the Mediterranean area which it was occupying from the southern Balkans or from Asia Minor at the latest in the second half of the 19th century.

Phyllonorycter leucographella (Z e l l e r 1850) (Fig. 2)

Adult. May, mid-July - end of August, 2 generations.

Hibernation. Larva in the leaf (evergreen host), or pupa.

Host plant. *Pyracantha coccinea* Roem. (introduced ornamental shrub).

Origin. Eastern Mediterranean area to Western Asia.

Start of the invasion. 1970.

Course and direction. With 'jumps' and secondary dispersal centres in various distances; to the north.

Behaviour of adults. Active in the evening and at night, less mobile, resting usually in the growth of the host shrub.

Spread. Transportation of fallen plants, wind dispersal.

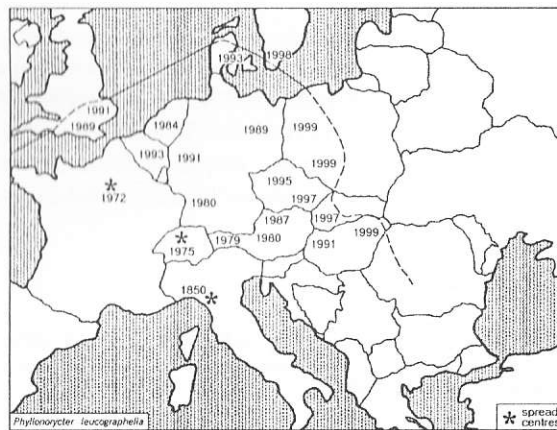Causes. Following its introduced host plant and spread with it.

Fig. 2. The possible spread centres of *Phyllonorycter leucographella* are in northern Italy, in Switzerland and in France, where the species was probably introduced from eastern Mediterranean area or from Asia Minor with its host plant; the distributional data indicate that its spread is not quite continuous and regular.

Phyllonorycter issikii (K u m a t a 1963) (Fig. 3)

Adult. End of May - beginning of August (1-2 summer generations), 2nd decade of August - beginning of May (overwintering generation).

Hibernation. Adult.

Host plant. *Tilia* spp. (autochthonous).

Origin. Eastern Palaearctis, probably introduced in the European Russia.

Start of the invasion. 1980.

Course and direction. Continuous, to the west.

Behaviour of adults. Active in the evening and at night, mobile, hibernation in the bark slots, crevices under bark and in other shelters.

Spread. Wind dispersal, possible anthropogenic transportation of adults during hibernation.

Causes. Introduction into the territory with adequate climate conditions and obligatory host plant.
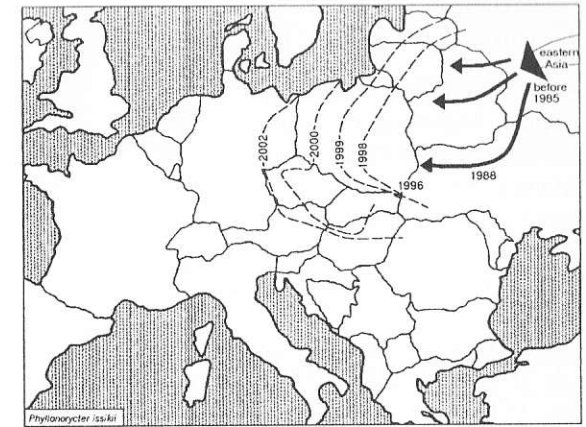

Fig. 3. The spread of *Phyllonorycter issikii* appears to be continuous and comparatively quick in the western direction from the European part of Russia to which it was apparently introduced from eastern Asia before 1980.

Phyllonorycter medicaginella (G e r a s i m o v 1930) (Fig. 4)

Adult. End of April - end of October, 4 or more generations.

Hibernation. Pupa in the fallen leaf.

Host plant. *Medicago* spp., *Melilotus* spp.

Origin. Central Asia to eastern central Europe.

Start of the invasion. 1950.

Course and direction. Continuous, slow, to the west.

Behaviour of adults. Active by day, in the evening and at night, less mobile, resting in the growth of the host plant.

Spread. Wind dispersal and active passages on short distances.

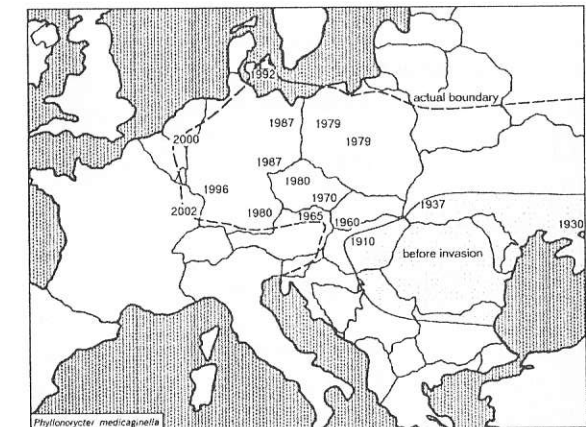Causes. Enlargement of the area to the west without obvious anthropogenic causes.

Fig. 4. *Phyllonorycter medicaginella* spread continuously and slowly to the west without apparent anthropogenic influence from the fifties of the 20th century.

Phyllonorycter robiniella
(C l e m e n s 1859) (Fig. 5)

Adult. End of June - beginning of August, beginning of August - mid-September (1-2 summer generations), mid-August - mid-May (overwintering generation).
Hibernation. Adult.
Host plant. *Robinia pseudacacia* L., *Robinia* spp.
Origin. North America, introduced into Switzerland before 1980.
Start of the invasion. 1980.
Course and direction. With 'jumps' and secondary dispersal centres in various distances; more to the north, northeast and east.
Behaviour of adults. Active at dusk and at night, swarming above host trees, very mobile, predisposed for the wind dispersal.
Spread. Wind dispersal (continuous), anthropogenic transportation of adults during hibernation (origin of distant secondary dispersal centres).
Causes. Introduction into the territory with the introduced original host plant and with the corresponding climate conditions.
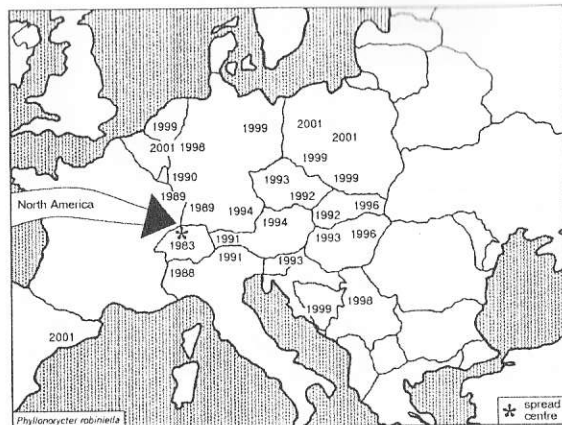

Fig. 5. *Phyllonorycter robiniella* shows an irregular spread from the district of Basle, where it was introduced from North America probably before 1980.

Cameraria ohridella
D e s c h k a & D i m i ć 1986 (Fig. 6)

Adult. Mid-April - beginning of October, 2-3 generations.
Hibernation. Pupa in the fallen leaf.
Host plant. *Aesculus hippocastanum* L. (in Europe; original host plant unknown).
Origin. Probably eastern Palaearctis, probably introduced into the southern Balkans (Macedonia, Albania, western Bulgaria or northern Greece) before 1980.
Start of the invasion. 1980.
Course and direction. Continuous, more or less in all directions.
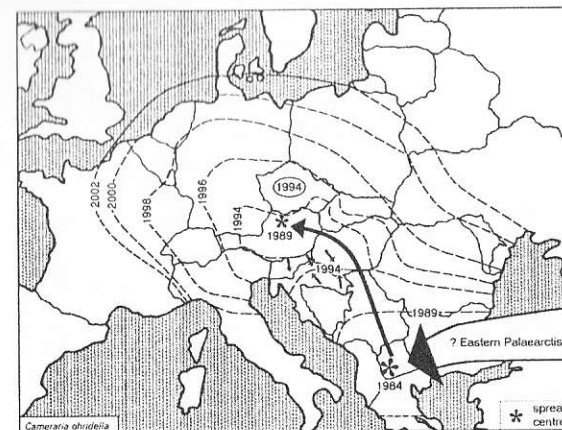Behaviour of adults. Active in the

Fig. 6. *Cameraria ohridella* spreads from its two distributional centres – in Macedonia and in Upper Austria; its continuous and multidimensional spread was partly broken by the massifs of the Alps and of the Carpathians, and in the southern direction by the limited use of its food plant.

morning, in the evening and at night, swarming above host trees, very mobile, predisposed for the wind dispersal, observed at light in large distances from the host.
Spread. Wind dispersal, possible anthropogenic transportation of leaves with pupae (but distant secondary dispersal centres not observed).
Causes. Invasion following introduction into the corresponding climate conditions with the occurrence of acceptable host (introduced in the territory of the invasion).

Discussion

At least six species of the leaf mining moths of the subfamily Lithocolletinae invaded Europe during the last 100 years outnumbering invasions of any other group of small moths. The question arises, whether these species of Lithocolletinae posses some special preconditions tending to the introduction and/or invasion. It is obvious that the introduction and the following spread of any animal species is due to a coincidence of special circumstances and chances (cf., e.g. Elton, 1958, or Agassiz, 1996). It seems, however, that the existence of preconditions should be presumed, e.g.: 1. The mining caterpillars pupate in the leaves and the pupae can be transported with the fallen leaves by various anthropogenic factors on short or very long distances. 2. The occasional gradations may occur in most species, and only one dry leaf with a high number of pupae can be sufficient for the origin of a new population. 3. Some species hibernate as adults in various crevices or in very tight little rooms simulated by artificial containers, transport boxes etc. easily transported by different vehicles. 4. If some of such species reach a new territory in this way, and if they are confronted with a similar climate and host plant, then the following spread is accelerated by wind resulting from the wing adaptation and from the negligible weight of the moths.

A next question arises after the first one. Have just these species some properties in common enabling their introduction and the following invasion compared with the other related taxa? The above characters or properties favouring the species of the subfamily Lithocolletinae compared with other microlepidopteran species show that such preconditions are inherent to most species of this group. If we analyse the course etc. of the studied invasions, it seems that there do not exist any additional common properties. It shows that most of the Lithocolletinae has more or less developed preconditions for the introduction and the invasion, but also that each of the invasions has its specific run and departure points. The species *Phyllonorycter robiniella* and *Cameraria ohridella* and/or *Phyllonorycter issikii* (Figs 3, 5, 6) respectively were introduced from very long distances into an area of adequate climate and with a corresponding host plant. *P. platani* and *P. leucographella* (Figs 1, 2) enlarged their areas following their host plants after their introduction. *P. medicaginella* (Fig. 4) seems to enlarge its distributional area regardless of the area of its host plants.

The next question – if all individuals of the same species have the identical preconditions – should be confronted with the generally known fact that, for genetic, demographic and environmental reasons, each successful population has to comprise several hundreds of

fertile and mating individuals capable of reproduction. But only few individuals, or just a single female (in extreme cases) are responsible for the start of a large-sized invasion following their introduction. It seems therefore that certain differences might exist rather between individuals regardless of similar invasive chances, and that only individuals showing optimum genetic fitness can start the next invasion. Unfortunately, unsuccessful introductions and invasions remain usually unrecognised and the number of useless 'experiments' cannot be registered even within the same species.

Do all species spread in the same way? Which are the factors responsible the speed of invasions, or which are, on the contrary, limiting factors. The study results indicate that the distributional factors are partly different in different species. Several authors were dealing with these problems generally (cf., e.g. Deschka, 1995, or Agassiz, 1996). The most important factors influencing the speed of invasions in the species investigated are summarized in Table 1. Each factor shows an empiric scale of 0–3 according to its importance, and the resulting amount is comparable with the distributional speed of the individual species.

It shows that the decisive distributional way of these species is the wind dispersal. This can be associated with some additional possibilities, e.g. the anthropogenic transfer of pupae in fallen leaves (P. platani, Cameraria ohridella), a transportation of host plants with the caterpillars (Phyllonorycter leucographella) or the anthropogenic transfer of moths hibernating in crevices of various objects (P. issikii, P. robiniella). The wind dispersal causes a more or less continuous spread reflecting the wind directions and the orographic barriers of high mountain ranges (the Alps and the Carpathians), whereas anthropogenic vectoring imitates 'jumping' resulting in secondary distributional long distance focus or island areas. The decisive factor exhibits its influence on the general character of an invasion (a continuous distributional process in P. issikii and Cameraria ohridella, Figs 3, 6, compared with some its irregularities in P. leucographella and P. robiniella shown in Figs 2, 5). The success of the wind dispersal and the distributional speed are influenced by the population density of the both species and its host plant. The considerable distributional speed and the continuous spread (Phyllonorycter issikii, Cameraria ohridella, Figs 3, 6) are obviously due to: 1. The continuous distributional pattern of the host plant. 2. The long-term high abundance of the species in question. If the distributional pattern of the host plant is insular (Pyracantha, Platanus), the success of the wind dispersal is lower, but it

may increase during the periods of the population outbreaks. That is why Phyllonorycter platani, partly P. leucographella and P. robiniella 'pushed' their distributional limits in the way of 'jumps'. The species of lower abundance and of lower tendency to the wind dispersal spread distinctly slower (P. medicaginella, Fig. 4). The long-term invasion speed of the individual species depends on the coincidence and on the realization of the above factors, but it is not proportional to the sum of their importance (compare Table 1). P. issikii the host tree of which is distributed continuously shows therefore the most rapid spread. On the contrary, the species with the slowest changes of their areas are P. platani the host tree of which occurs very individually and solitary, and P. medicaginella the host plants of which are continuously distributed, but its adults are only little mobile and therefore resistant to the wind dispersal (Figs 1, 3, 4).

The abundance and, as a consequence, the distributional speed is limited by the biotic antagonists. Considerable differences are observed between the individual species studied. All species are attacked by a wide spectrum of oligophagous parasitoids (e.g. nearly 40 species in Cameraria ohridella – cf. Deschka, 1995; Pschorn-Walcher, 1997; Stolz, 1997; Grabenweger, Lethmayer, 1999; Hellrigl, Ambrosi, 2000; Heitland, Freise, 2000). The parasitation size is rather different in the individual species regardless of the parasitoid species number showing maximum 10 % in C. ohridella up to 80 % and more in Phyllonorycter leucographella (cf. also Emmet, 1989 and Mey, 1991). The limiting factors are usually climatic or other environmental requirements of the individual species or the limited areas of the host plants and/or the geographic barriers. While the invasion of P. platani reached probably already its limits and the invasion of P. leucographella closes to it, the next four species continue their spread.

How the individual species do influence their host plants, the other phytophagous insects on the same host plant (competition possibility) and, finally, the entire communities? Cameraria ohridella shows (in this regard) a special position keeping its continuously high population density on the maximum environmental level, obviously due its specific ecological adaptations (Šefrová, Laštůvka, 2001). This causes undoubtedly a distinct impact on the host tree, which loses its assimilation capacity up 8–10 weeks before the usual leaf fall. Combined with the other factors, especially with shortage of water, this might cause a decreased limit of growth, of number of fruits etc. But any kind of dying away in trees was not observed even in a long-term aspect. The population density of the other species studied is governed by both biotic factors, especially by parasitoids (Phyllonorycter leucographella) and by their combination with the weather impact (density decrease especially due to the mortality during the winter). Their gradations are usually short time (P. platani, P. robiniella, P. leucographella) and their influence on the host plant is negligible. In some cases the density is (locally) constantly high (P. medicaginella), but regeneration capacity of the host plant also prohibits any visible damage. Four of the species studied (P. leucographella, P. platani, P. robiniella and Cameraria ohridella) are miners of introduced plants similarly as a minimum number of (similarly allochthonous) specialized phytophagous insects eliminating any reasonable discussion of this phenomenon. That is why these leaf miners obviously influence essentially neither the other plant species nor any entire autochthonous

Table 1. Factors responsible for the distributional outbreaks of the species studied; their importance corresponds to the scale of 0 to 3

Factor / Species	Wind dispersal	Anthropogenic transportation			Density		Σ	Spread [km.a⁻¹]
		adult	pupa	host	moth	host		
Phyllonorycter platani	2	0	2	0	0-3	0	4-7	15
P. leucographella	1	0-1	0	3	1	1	6-7	60
P. issikii	3	2	0	0	1-2	3	9-10	110
P. medicaginella	1	1	0	0	1-2	3	6-7	20
P. robiniella	3	2	0	0	1-3	1-3	7-11	10-40
Cameraria ohridella	3	2	2	0	3	2	12	60-70

communities. The next species – *Phyllonorycter medicaginella* – behaves like an autochthonous species and no negative influence was observed on the relative *P. insignitella* (Z e l - l e r 1846), which shows rather similar bionomics and ecology. As for *P. issikii* it seems that this species might be integrated among the other specialized phytophagous insects in *Tilia* spp. without any negative impact on these trees.

The last question, if namely the above species are a negative element or if they actually enrich central European fauna is combined with the previous facts. This problem should be discussed in a wider context and it obtains a subjective character. Generally, such introductions, as the above species, enrich undoubtedly the species diversity of any landscape similarly as their introduced food plants do. Such species as *Phyllonorycter leucographella*, *P. platani*, *P. robiniella* and *Cameraria ohridella* represent, however, together with their food plants, 'exotic' elements involving both subjective and objective evaluation: e.g. taking into consideration the purely ornamental function of their food plants and, at the same time, the negative effect of their presence in the autochthonous phytocoenoses; and similarly, it is ambiguous, if such leaf miners should be considered their pests, or on the other hand, their limiting (control) factors (e.g. in *Robinia pseudacacia*). We may argument that the invasions of such species as *Phyllonorycter issikii* and especially *P. medicaginella* represent actually positive enriching of the local fauna, because they result from the continuous, both natural and anthropogenic changes accompanying the development of plant and animal communities for thousand years and, thus, becoming inherent members of communities to which the term "natural" is often attributed.

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Šefrová H.: **Invaze druhů podčeledi Lithocolletinae v Evropě – příčiny, způsoby, limity a ekologický vliv.**

Provedli jsme analýzu evropských invazí druhů *Phyllonorycter platani* (S t a u d i n g e r 1870), *P. leucographella* (Z e l l e r 1850), *P. issikii* (K u m a t a 1963), *P. medicaginella* (G e r a s i m o v 1930), *P. robiniella* (C l e m e n s 1859) a *Cameraria ohridella* D e s c h k a & D i m i ć 1986 vycházející z literárních údajů i vlastních víceletých výzkumů. Jsou diskutovány možné společné vlastnosti těchto druhů, jejich předpoklady k invazi, způsoby jejich šíření, faktory ovlivňující rychlost invaze a vlivy na hostitele. Je zhodnocen pozitivní i negativní význam těchto druhů, tj. vliv na zvyšování druhové diverzity i jejich možná škodlivost.

DEGRADATION OF SEMINATURAL PASTURES BY LOCAL OVERMANURING WITH CATTLE OR SHEEP EXCRETA

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Abstract

Novák J., Slamka P.: Degradation of seminatural pastures by local overmanuring with cattle or sheep excreta. Ekológia (Bratislava), Vol. 22, No. 2, 143–151, 2003.

The aim of the research was to investigate the effect of overmanuring by NPK nutrients on soil and sward degradation within the framework of 10 sites of pasture ecosystems during the years 1995-2000. The sites were situated in submountain and mountain areas of Slovakia (the Western Carpathians), where Walachian way of grazing still survives. Soil samples from strongly overmanured sites where animals stayed long while having regular rest from the overgrazed pastures (young cattle) and the areas folded by sheep were analysed. There were found the high contents of NPK nutrients in them. The contents of nutrients fluctuated within the following range: from 3912 to 8652 mg.kg^{-1} for total nitrogen (N_t), 131 to 216 mg.kg^{-1} for phosphorus (P) and 527 to 1880 mg.kg^{-1} for potassium (K). Content of humus on the investigated areas ranged from 5.3 to 13.6 %. Low ratio of C:N (6.9:1 to 9.9:1) resulting from C_{ox} and N_t values reflects good nutrient pool. However the concentration of K in soil exceeding 500 mg.kg^{-1} is considered to be negative in pasture ecosystem. There is no need to fertilise soils degraded in this way with K and P as has been recommended in the older agricultural literature, because the content of K and P in these soils is high. The high concentrations of NPK in soil were tolerated mainly by ruderal weeds (*Rumex obtusifolius, Arctium lappa, Urtica dioica, Cirsium arvense, Aegopodium podagraria, Anthriscus sylvestris, Capsella bursa-pastoris, Chenopodium bonus-henricus, Anthemis arvensis, Stellaria media, Geranium pusillum, Geranium pratense, Glechoma hederacea*) an by some good quality forage grasses. During the years weed grassland communities by dominance of *Rumex obtusifolius* (6-43 %) has been established at the overmanured sites. There is a need for seeking methods suitable for soil and botanical degradation removing.

Key words: animal excreta, botanical degradation, livestock resting place, NPK nutrients, overmanuring, pasture ecosystem, soil degradation