

How do lepidopteran seasonal guilds differ on some oaks (*Quercus* spp.) – A case study

M. TURČÁNI¹, J. PATOČKA^{1†}, M. KULFAN²

¹Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Prague, Czech Republic

²Department of Zoology, Comenius University, Mlynská dolina, Bratislava, Slovakia

ABSTRACT: The differences between oak lepidopteran communities were studied in Slovakia in 1993 and 1994. Sampling was undertaken between April and October on 3 oak species (*Quercus robur*, *Q. petraea*, *Q. rubra*). Biological traits of larvae were examined in order to explain differences in seasonal guilds among oaks. Communities varied in structure and abundance. Species richness in four seasonal guilds (flush, late spring, summer and autumn feeders) had a similar pattern on each of the studied oak species. The guild of flush feeders had the richest species assemblage, followed by the late spring feeder guild and both guilds were significantly richer than the summer feeder guild and autumn feeder guild.

Keywords: lepidopteran larvae communities; Slovakia; oaks; seasonal guilds

Oaks (*Quercus* spp.) are represented in Slovakia (Central Europe) by eight native and one introduced species; they are distributed in the warmest part of the country from an altitude of about 100 m up to 1,000 m a.s.l. More than 250 lepidopteran species have been recorded feeding on *Quercus* spp. (PATOČKA 1980; PATOČKA et al. 1999).

The life history traits of Lepidoptera in Central Europe and basic information about the species habitat preferences are relatively well known. Habitat preferences and community structure of Lepidoptera in Slovakia were studied earlier by PATOČKA (1980) and PATOČKA et al. (1962, 1999) and STOLINA et al. (1985), but their assessment relied mainly on direct observations and qualitative characteristics rather than on quantitative statistical analyses. Habitat preference was simplified and expressed by “forest types” (units of forest taxonomy) – areas where the ecological optima of these species were found. These studies showed habitat preferences of the most abun-

dant defoliators: *Lymantria dispar*, *Operophtera brumata*, *Erannis defoliaria*, *Tortrix viridana*, *Aleimma loeflingiana*, *Archips xylosteana* and several others. The occurrence of outbreaks was used as an indicator of habitat preference (the outbreak is defined as an increase in abundance to an extent where feeding causes visible defoliation, usually heavier than 30–40%). The role of other species as elements in forest ecosystems, the relationships among species, and their formation into guilds on various oak species have remained speculative.

PATOČKA (1954) divided the lepidopteran species on oaks in Slovakia into four seasonal guilds. The first was from budburst till the beginning/middle of June. It is estimated that 80–90% of the total number of caterpillar species recorded on oaks is present at that time. The caterpillars in this guild overwinter as larvae or eggs or hatch from those laid in early spring. The second guild mainly consists of leaf miners (*Stigmella* spp., *Phyllonorycter* spp. and

Supported by the Ministry of Agriculture of the Czech Republic, Project No. QH 71094 *The Use of Dendrochronology in the Reconstruction of Fluctuation Cycles of Nun and Gypsy Moths in Central Europe*.

Table 1. Number of species, number of specimens and seasonal diversity and evenness of Lepidoptera collected at four sites in 1993 and 1994

Site/host tree	Site 4 (<i>Q. rubra</i>)		Site 1 (<i>Q. petraea</i>)		Site 2 (<i>Q. robur</i> 1)		Site 3 (<i>Q. robur</i> 2)	
	1993	1994	1993	1994	1993	1994	1993	1994
Year of study	1993	1994	1993	1994	1993	1994	1993	1994
Number of species	15	25	29	43	46	57	56	67
Number of specimens	23	44	87	139	216	372	264	347
Maximum seasonal diversity (Shannon-Weaver index)	1.9	2.4	1.7	2.2	2.2	2.7	2.6	2.9
Maximum seasonal evenness (Pielou's index)	1.00	1.00	0.96	0.97	0.97	0.98	0.97	0.98

Tischeria spp. and also some smaller free feeders like *Cyclophora* spp.). Some larger species from the first guild like *L. dispar*, *Orthosia* spp. or *Biston stratararius* often complete their development at this time. The third guild occurs in August–September. It consists partially of the second generation of the first guild for example *Pandemis* spp., *Cyclophora* spp. and *Pseudoips prasinanus*. Finally, the fourth guild (October–November) consists of the second flight period of leaf miners in the genera *Stigmella*, *Tischeria* and *Phyllonorycter* and the mostly univoltine genus *Ectoedemia*. Recent studies of KULFAN et al. (1997) and KULFAN and DEGMA (1999) showed that species diversity and evenness differed significantly between oak species and time of the year.

Our effort was focused on understanding the mechanisms that explain variance in lepidopteran communities in various seasonal guilds on different oaks. The main study goals were:

- (1) To investigate patterns of lepidopteran communities on three oak species across a year;

- (2) To analyze the similarity of seasonal guilds at various sites represented by different oaks.

STUDY SITES AND METHODS

A dataset was collected during May to October in 1993 and 1994. Samples were taken every 20 days (nine times per season, the last sampling was excluded from statistical assessment due to the zero number of larvae in almost all samples) using a beating tray (25 beatings per sample). There were nine sample intervals each year. Sampling started on 30 April, 7–10 days after budburst, and finished on 7 October in both years. Branches at eye height, about 1 m in length, were beaten during each sampling period. Approximately 99.5% of 1,518 collected larvae were identified *in situ* to the species level; others were identified after rearing in a laboratory to the adult stage. GERASIMOV (1952) and PATOČKA (1954, 1980) were used as identification references. A systematic list of species includ-

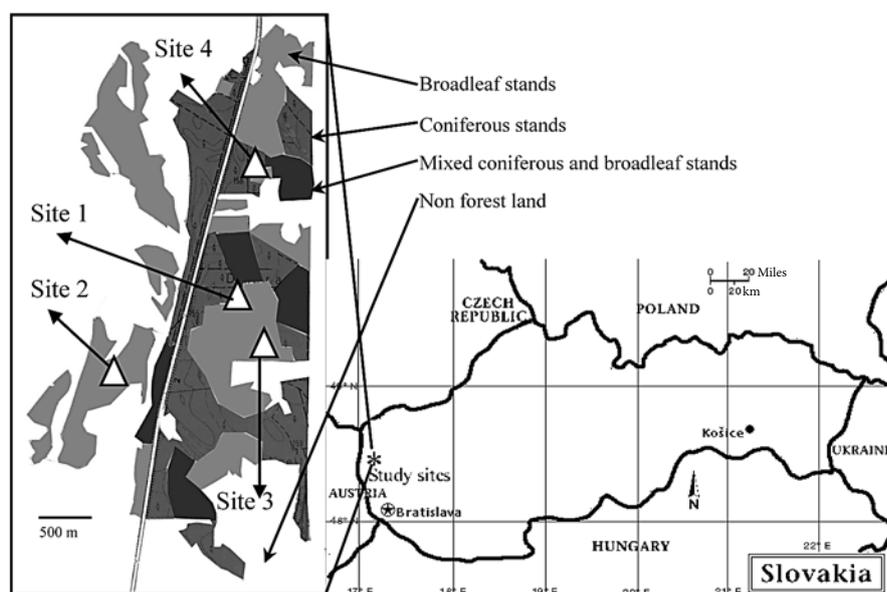


Fig. 1. Location of the forest complex and individual study sites

ing selected life history traits can be found in the Appendix (Table 1A).

The study area in Western Slovakia was between 48°25' and 48°30'N and 17°09' and 17°11'E (Fig. 1). Four sites were selected representing two stands of *Q. robur*, one stand of *Q. petraea* and one of *Q. rubra*, all plots were in the same vicinity. The maximum distance between any two sites was about 2 km.

Site 1 (*Q. petraea*): A 25 years old artificially planted stand of *Q. petraea*. Planted in dense rows and surrounded by Scotch pine (*Pinus sylvestris*). Sparse understorey. Site elevation about 160 m. The site represents the plant association *Quercus-Pinetum* Kripel 1965.

Site 2 (*Q. robur* 1): A natural close growing hardwood plain forest with the dominant species *Q. robur*. The site was located in the vicinity of the Moravia River. The age of trees was estimated to be about 100 years. Site elevation 150 m. The stand represents the plant association *Fraxino-Ulmetum-Quercetosum* Somsak 1959.

Site 3 (*Q. robur* 2): Similar to the previous site and forming a fringe of *Q. robur* stands along a cultivated area. The age of the trees was estimated to be 120 years. Site elevation 160 m. The site represents the plant association *Frangulo-alni-Quercetum* Michalko 1989. Both *Q. robur* stands had rich understorey vegetation.

Site 4 (*Q. rubra*): The introduced *Q. rubra* is planted among stands of Scotch pine. The site represents the plant association *Quercus-Pinetum* Kripel 1965.

Leaf-mining Lepidoptera were excluded from this study as only free-living species sensitive to sampling using a beating tray were collected.

In statistical analyses we summarized the number of individuals in each family to determine if there were any visual differences in the host preference. We also calculated diversity (Shannon-Weaver index) and evenness (Pielou's index) of Lepidoptera larvae on each site. Then we separated species into four seasonal guilds and tested the differences in the number of species and individuals in guilds. This was done separately for each oak to compare if the pattern was similar. To test differences, matrixes of presence/absence (species) or abundance (individuals) were constructed. The sum from two samplings entered the analysis for each guild. All species in each guild were entered into the matrix separately, where the rows were species and the columns indicated the presence/absence of species or number of individuals. Data were transformed as $\log(x + 1)$ prior to analysis. ANOVA was performed to evaluate differences among seasonal guilds. This was done separately for each tree species.

The species were divided into seasonal guilds by determining when they were most abundant. Polyvoltine species were sorted into seasonal groups based on the time when the most abundant generation was found. For example a bivoltine species was treated as a summer feeder if its individuals were found only in the summer generation during our study. Seasonal guilds were usually well defined. Only in the case of late spring feeders (LSF) there were two subgroups:

- (a) Flush feeders (FIF) that continued feeding in June;
- (b) species that started feeding in June.

The former subgroup was included in the group of late spring feeders because they feed mainly on developed and mature leaves.

The classification of the species was as follows: FIF – species present as larvae that overwintered or just hatched. These species were in synchrony with budburst and were feeding almost exclusively on new foliage from the end of April to the end of May and the beginning of June; LSF – species feeding mainly on developed and recently matured foliage (usually the end of May up to the end of June and the beginning of July); summer feeders (SF) – feeding on mature leaves at the beginning of July to the beginning of August; and autumn feeders (AF) – this group hatched in the second half of August and the beginning of September and was feeding on the toughest leaves.

RESULTS

The number of species and individuals varied considerably between sites and years. *Quercus rubra* had the lowest number of species and individual specimens followed by *Q. petraea* with the richest communities being found on *Q. robur* (Table 1). The total number of larvae on *Q. rubra* was 23 in 1993 vs. 44 in 1994, on *Q. petraea* 87 in 1993 vs. 139 in 1994 and on *Q. robur* 216 and 372 in 1993 and 372 and 347 in 1994. On *Q. rubra* and *Q. robur* the maximum species diversity was found in spring and on *Q. petraea* in early spring or late spring, respectively. The evenness was quite stable at all sites.

A comparison of larval abundance classified into families showed the absence (Psychidae, Tineidae, Bucculatricidae, Gracillariidae, Ypsolophidae, Oecophoridae) or scarcity (Coleophoridae) of smaller species on *Q. rubra* and low numbers on *Q. petraea* in both years (Figs. 2a,b). The Geometridae were the most abundant family in both years of study, followed by Lymantriidae in 1993 and Noctuidae in 1994. Only species of the families Coleophoridae,

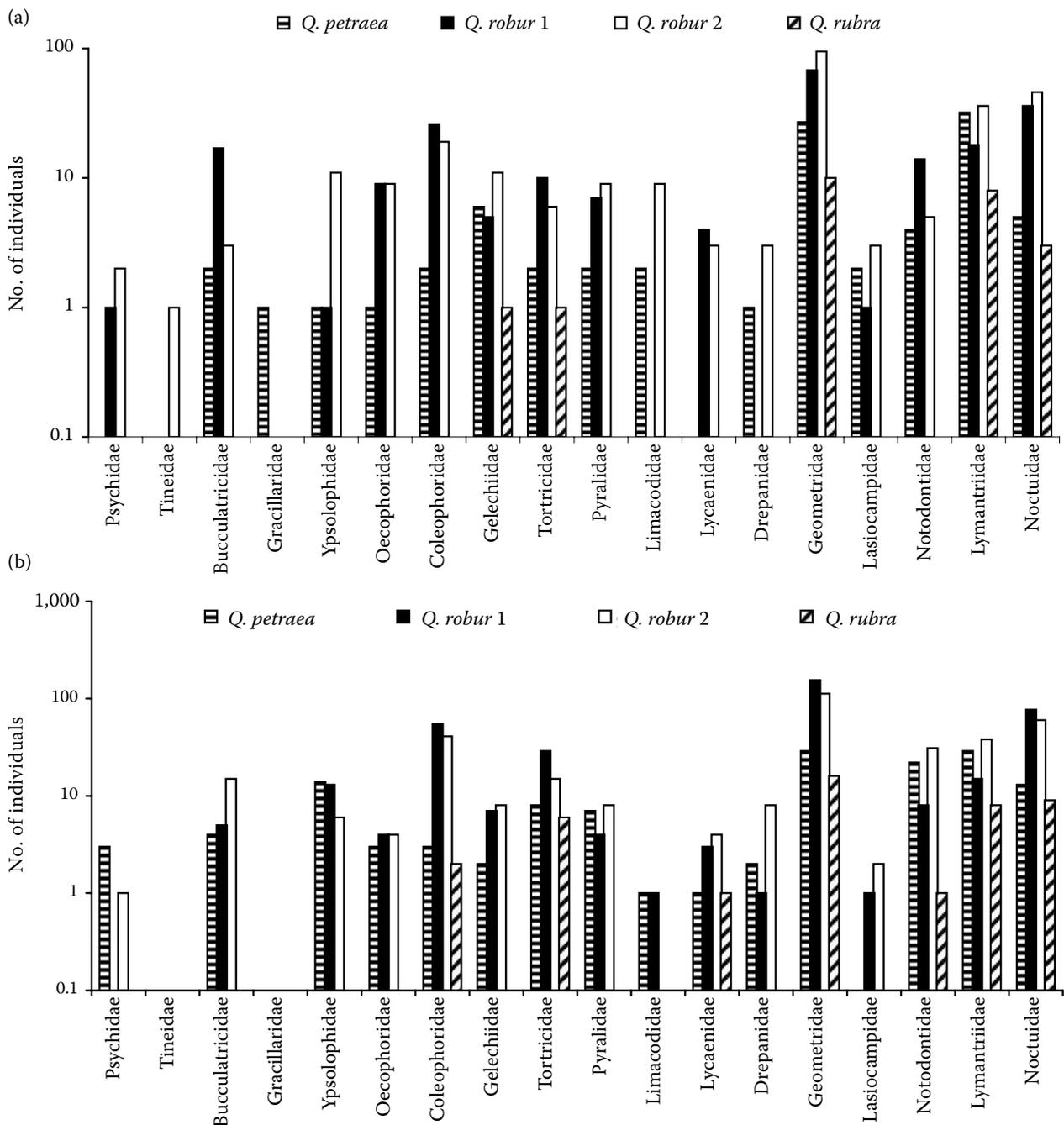


Fig. 2. Comparison of larval abundance per family at 4 sites in 1993 (a) and in 1994 (b)

Gelechiidae, Tortricidae, Lycaenidae, Geometridae, Lymantriidae and Noctuidae were found on *Q. rubra* during this study. Lycaenidae, Geometridae, Notodontidae, Lymantriidae and Noctuidae represent larger Lepidoptera (pupa 10 to 30 mm in length) which are generally widely polyphagous (PATOČKA, TURČÁNI 2005).

Coleophoridae, Gelechiidae and Tortricidae represent small Lepidoptera which are much more sensitive to food quality and foliage architecture because of their size and feeding strategies. Individuals from these families were generally absent on

Q. rubra (only *Teleoides paripunctellus* and *Pandemis corylana* were found in 1993). *T. paripunctellus* spins two leaves together and feeds on the internal epidermis + mesophyll, the external epidermis remains untouched. *P. corylana* spins together several leaves and is more abundant on *Q. robur*, which has leaves arranged in clusters. In 1994, single individuals of *Coleophora ibipennella* and *C. lutipennella* were found on *Q. rubra* but they were more abundant on other oak species. Several polyphagous tortricid species were also found on *Q. rubra* that year.

Table 1A. A systematic list of the species recorded during this study with a short description of life-history traits (the system according to LAŠTŮVKA 1998)

Taxon	Host specificity	Ballooning	Feeding strategy	Voltinism	Pupa length (mm)
Psychidae					
<i>Canephora hirsuta</i> (PODA, 1761)	polyphagous	no	sac/case bearing	univoltine	14–17
<i>Dahlica</i> sp.	mosses, lichens, algae	no	sac/case bearing	univoltine	4–6
<i>Protitia betulina</i> (ZELLER, 1839)	mosses, lichens and algae	no	sac/case bearing	polyvoltine	6–7
<i>Psyche casta</i> (PALLAS, 1767)	polyphagous	no	sac/case bearing	univoltine	5–6
Tineidae					
Tineidae sp.	organic material	no	galleries	uni- to polyvoltine	6–10
Bucculatricidae					
<i>Bucculatrix ulmella</i> ZELLER, 1848	<i>Quercus</i> spp., <i>Castanea sativa</i> , <i>Fagus sylvatica</i>	no	miner only at early stages	bivoltine	3–4
Gracillariidae					
Gracillariidae sp.	<i>Quercus</i> spp.	no	miner; later conical spun leaf	bivoltine	5–6
Ypsolophidae					
<i>Ypsolopha alpella</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp., mainly <i>Q. pubescens</i> group	no	free living	univoltine	6–7
<i>Ypsolopha ustella</i> (CLERCK, 1759)	Fagaceae, <i>Quercus</i> spp.	no	free living	univoltine	7–8
Oecophoridae					
<i>Carcina quercana</i> (FABRICIUS, 1775)	<i>Quercus</i> spp., <i>Fagus sylvatica</i>	no	spun leaves	univoltine	7–9
Chimabacchidae					
<i>Diurnea fagella</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf woody plants, polyphagous	no	spun leaves	univoltine	10–14
<i>Diurnea lipsiella</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf woody plants, polyphagous	no	spun leaves	univoltine	9–12
Coleophoridae					
<i>Coleophora ibipennella</i> ZELLER, 1849	<i>Quercus</i> spp.	no	miner from sac at early stages only	univoltine	7–9
<i>Coleophora kuehnella</i> (GOEZE, 1783)	<i>Quercus</i> spp.	no	miner from sac at early stages only	univoltine	7–9

Table 1A to be continued

Taxon	Host specificity	Ballooning	Feeding strategy	Voltinism	Pupa length (mm)
<i>Coleophora lutipennella</i> (ZELLER, 1838)	<i>Quercus</i> spp.	no	miner from sac	univoltine	7–9
Gelechiidae					
<i>Teletodes paripunctellus</i> (THUNBERG, 1794)	<i>Quercus</i> spp., <i>Betula</i> spp.	no	spun leaves, skeletonize	univoltine	4–6
<i>Teletodes luculellus</i> (HÜBNER, 1813)	<i>Quercus</i> spp.	no	spun leaves, skeletonize	univoltine	4–5
<i>Teletodes decorellus</i> (HAWORTH, 1812)	<i>Quercus</i> spp.	no	spun leaves, skeletonize	univoltine	4–6
Limacodidae					
<i>Apoda limacodes</i> (HUFNAGEL, 1766)	<i>Quercus</i> spp., <i>Fagus sylvatica</i>	no	free living, young skeletonize	occasionally bivoltine	8–9
Tortricidae					
<i>Tortrix viridana</i> LINNAEUS, 1758	<i>Quercus</i> spp., <i>Q. robur</i> and <i>Q. pubescens</i> mainly	no	spun leaves, fold leaf margin	univoltine	8–12
<i>Aleimma loeflingiana</i> (LINNAEUS, 1758)	<i>Quercus</i> spp., <i>Q. petraea</i> and <i>Q. pubescens</i> mainly	no	spun leaves	univoltine	7–9
<i>Acleris ferrugana</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp., <i>Carpinus betulus</i> and other broadleaf woody species	no	spun leaves, skeletonize as young	univoltine	7–8
<i>Tortricodes alternellus</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf trees, <i>Quercus</i> spp. mainly	no	spun leaves	univoltine	9–10
<i>Exapate congelatella</i> (CLERCK, 1759)	polyphagous on broadleaf trees	no	spun leaves	univoltine	8–10
<i>Eulia ministrana</i> (LINNAEUS, 1758)	polyphagous on broadleaf woody plants	no	spun leaves	univoltine	12
<i>Ptycholoma lecheanum</i> (LINNAEUS, 1758)	polyphagous on broadleaf woody plants	no	spun leaves	univoltine	10–13
<i>Archips xylosteana</i> (DENIS & SCHIFFERMUELLER, 1775)	polyphagous on broadleaf trees, occasionally coniferous	no	transversely rolled leaf	univoltine	11–14
<i>Choristoneura hebenstreitella</i> (MÜLLER, 1764)	polyphagous on broadleaf trees	no	spun leaves	univoltine	13–17
<i>Pandemis corylana</i> (FABRICIUS, 1794)	Fagaceae g. sp., Corylaceae g. sp. etc.	no	spun leaves	mostly bivoltine	11–14
<i>Pandemis cerasana</i> (HÜBNER, 1786)	polyphagous on broadleaf sometimes coniferous woody plants, often <i>Quercus</i> spp.	no	spun apical leaves	mostly bivoltine	11–14
<i>Pandemis heparana</i> (DENIS & SCHIFFERMUELLER, 1775)	polyphagous on broadleaf woody plants	no	spun leaves	uni- to bivoltine	12–15
<i>Spilonota ocellana</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf trees and shrubs	no	buds, spun shoots	uni- to bivoltine	7–9
<i>Zeiraphera isertana</i> (FABRICIUS, 1794)	<i>Quercus</i> spp.	no	spun leaves, sometimes entomophagous	univoltine	8–9

Table 1A to be continued

Taxon	Host specificity	Ballooning	Feeding strategy	Volitism	Pupa length (mm)
<i>Ancylis mitterbacheriana</i> (DENIS & SCHIFFERMUELLER, 1775)	Fagaceae, especially <i>Quercus</i>	no	longitudinally folded leaf	mostly bivoltine	6–8
<i>Pammene albuginana</i> (GUENÉE, 1845)	<i>Quercus</i> spp. – galls of Cynipidae	no	internal galleries	univoltine	7–9
Pyralidae					
<i>Elegia similella</i> (ZINCKEN, 1818)	<i>Quercus</i> spp.	no	web nest	mostly univoltine	7–8
<i>Phycita roborella</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp.	no	web nest	univoltine	10–12
<i>Conobathra repandana</i> (FABRICIUS, 1798)	<i>Quercus</i> spp.	no	web nest	polyvoltine	9–10
<i>Conobathra tumidana</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> , prefers <i>Q. cerris</i> and <i>Q. pubescens</i>	no	web nest	univoltine	8–10
<i>Acrobasis consociella</i> (HÜBNER, 1813)	<i>Quercus</i> spp.	no	web nest	univoltine	9–10
Lasioleptidae					
<i>Phylloidesma tremulifolia</i> (HÜBNER, 1810)	broadleaf woody species, often <i>Quercus</i> spp.	no	free living	univoltine	20–25
<i>Pocilocampa populi</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees	no	free living	univoltine	12–16
Lycanidae					
<i>Neozelephyrus quercus</i> (LINNAEUS, 1758)	<i>Quercus</i> spp.	no	free living	univoltine	9–10
Drepanidae					
<i>Watsonalla binaria</i> (HUFNAGEL, 1767)	<i>Quercus</i> spp.	no	free living	univoltine	8–12
Geometridae					
<i>Semiothisa alternaria</i> (HÜBNER, 1799)	polyphagous on woody species	no	free living, skeletonize as young	uni- or bivoltine	12–16
<i>Plagodis dolabraria</i> (LINNAEUS, 1767)	<i>Quercus</i> spp., <i>Fagus sylvatica</i>	no	free living, skeletonize as young	uni- or bivoltine	12–14
<i>Ennomos autumnarius</i> (WERNERBURG, 1859)	broadleaf woody species	no	free living	univoltine	22–26
<i>Selenia tetralunaria</i> (HUFNAGEL, 1767)	polyphagous	no	free living, skeletonize as young	bivoltine	12–16
<i>Colotois pennaria</i> (LINNAEUS, 1761)	polyphagous on broadleaf trees	yes	free living	univoltine	13–17
<i>Apocheima pilosaria</i> (DENIS & SCHIFFERMUELLER, 1775)	polyphagous on broadleaf trees	yes	free living,	univoltine	14–17
<i>Biston strataria</i> (HUFNAGEL, 1767)	<i>Quercus</i> spp. and other broadleaf trees	yes	free living	univoltine	18–23
<i>Biston betularia</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees, sometimes herbs	probably no	free living, skeletonize as young	polyvoltine	18–24

Table 1A to be continued

Taxon	Host specificity	Ballooning	Feeding strategy	Voltinism	Pupa length (mm)
<i>Agriopsis leucophaearia</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp. mainly	yes	free living	univoltine	9–12
<i>Agriopsis marginaria</i> (FABRICIUS, 1776)	<i>Quercus</i> spp. mainly, also other broadleaf trees	yes	free living	univoltine	10–14
<i>Agriopsis aurantiaria</i> (HÜBNER, 1799)	polyphagous on broadleaf trees and <i>Larix</i> spp.	yes	free living	univoltine	10–16
<i>Erannis defoliaria</i> (CLERCK, 1759)	polyphagous on broadleaf trees	yes	free living	univoltine	12–16
<i>Paradarisa similaria</i> (HUFNAGEL, 1767)	broadleaf trees	no	free living, skeletonize as young	univoltine	10–12
<i>Hypomecis roboraria</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf woody species, <i>Quercus</i> spp. mainly	no	free living, skeletonize as young	uni- or bivoltine	14–24
<i>Hypomecis punctinalis</i> (SCOPOLI, 1763)	broadleaf woody species	no	free living, skeletonize as young	uni- or bivoltine	13–18
<i>Ectropis crepuscularia</i> (DENIS & SCHIFFERMUELLER, 1775)	polyphagous on herbs and low woody trees	no	free living, skeletonize as young	uni- or bivoltine	11–16
<i>Lomographa tenerata</i> (DENIS & SCHIFFERMUELLER, 1775)	mainly on <i>Prunus</i> spp. and <i>Padus avium</i>	no	free living, skeletonize as young	mostly univoltine	10–11
<i>Campaea margaritata</i> (LINNAEUS, 1767)	broadleaf trees	no	free living, skeletonize as young	polyvoltine	12–15
<i>Alsophila aceraria</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp. mainly, also other broadleaf trees	yes	free living	univoltine	8–9
<i>Alsophila aescularia</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp. mainly, also other broadleaf trees	yes	free living	univoltine	9–10
<i>Hemitea aestivaria</i> (HÜBNER, 1799)	broadleaf woody species	no	free living, skeletonize as young	occasionally bivoltine	11–13
<i>Cyclophora linearia</i> (HÜBNER, 1799)	<i>Fagus sylvatica</i> , <i>Quercus</i> spp., <i>Vaccinium</i> spp.	no	free living, skeletonize as young	bivoltine	11–14
<i>Chloroclysta miata</i> (LINNAEUS, 1758)	<i>Vaccinium</i> spp., Salicaceae g. sp., Betulaceae g. sp., <i>Quercus</i> spp. occasionally	no	free living	univoltine	12–13
<i>Epirrita dilutata</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf woody species	yes	free living	univoltine	10–12
<i>Operophtera brumata</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees, sometimes coniferous and <i>Vaccinium</i> spp.	yes	free living or spun leaves	univoltine	7–9
<i>Eupithecia dodoneata</i> GUENÉE, 1857	<i>Quercus</i> spp.	no	free living	univoltine	5–7
Notodontidae					
<i>Phalera bucephala</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees	no	free living, gregariously	mostly univoltine	24–30
<i>Drymonia dodonaea</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp., rarely <i>Fagus sylvatica</i> , <i>Betula</i> spp.	no	free living	uni- or bivoltine	14–16
<i>Ptilodon capucina</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees	no	free living	uni- or bivoltine	16–18

Table 1A to be continued

Taxon	Host specificity	Ballooning	Feeding strategy	Voltinism	Pupa length (mm)
<i>Spatalia argentina</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp.	no	free living	uni- or bivoltine	15–18
Noctuidae					
<i>Moma alpinum</i> (OSBECK, 1778)	<i>Quercus</i> spp. mainly	no	free living, skeletonize as young	univoltine	13–15
<i>Acronicta psi</i> (LINNAEUS, 1758)	polyphagous on woody plants	no	free living	uni- or bivoltine	16–18
<i>Amphipyra pyramidea</i> (LINNAEUS, 1758)	polyphagous on trees	no	free living	univoltine	16–22
<i>Cosmia trapezina</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees	no	free living	univoltine	13–14
<i>Agrochola laevis</i> (HÜBNER, 1803)	broadleaf trees, oaks mainly adult larva: herbs	no	free living	univoltine	11–13
<i>Eupsilia transversa</i> (HUFNAGEL, 1766)	polyphagous on broadleaf woody plants, herbs	no	free living	univoltine	14–17
<i>Lithophane ornitopus</i> (HUFNAGEL 1766)	broadleaf trees, oaks mainly	no	free living	univoltine	14–16
<i>Dichonia convergens</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp.	no	free living	univoltine	14–16
<i>Orthosia incerta</i> (HUFNAGEL, 1776)	polyphagous on broadleaf woody plants	no	free living	univoltine	15–18
<i>Orthosia cruda</i> (DENIS & SCHIFFERMUELLER, 1775)	broadleaf trees, oaks mainly	no	free living	univoltine	10–13
<i>Orthosia miritosa</i> (DENIS & SCHIFFERMUELLER, 1775)	<i>Quercus</i> spp. mainly	no	free living, gregariously	univoltine	13–15
<i>Orthosia opima</i> (HÜBNER, 1809)	polyphagous	no	free living	univoltine	15–17
<i>Orthosia cerasi</i> (FABRICIUS, 1775)	polyphagous on broadleaf woody plants	no	free living	univoltine	13–16
<i>Orthosia munda</i> (DENIS & SCHIFFERMUELLER, 1775)	polyphagous on broadleaf trees	no	free living	univoltine	16–19
Pantheidae					
<i>Colocasia coryli</i> (LINNAEUS, 1758)	broadleaf trees	no	free living, skeletonize as young	uni- or bivoltine	14–15
Lymantridae					
<i>Orgyia recens</i> (HÜBNER, 1819)	broadleaf woody species	no	free living	occasionally bivoltine	12–16
<i>Orgyia antiqua</i> (LINNAEUS, 1758)	polyphagous on woody plants, <i>Vaccinium</i> spp., Rosaceae mainly	no	free living	bi- or trivoltine	9–12
<i>Calliteara pudibunda</i> (LINNAEUS, 1758)	broadleaf trees, prefers <i>Fagus sylvatica</i>	no	free living	univoltine	18–25
<i>Euproctis similis</i> (FUESSLY, 1775)	<i>Quercus</i> spp., <i>Ulmus</i> spp., <i>Salix</i> spp. and Rosaceae	no	nests	univoltine	10–13

Table 1A to be continued

Taxon	Host specificity	Ballooning	Feeding strategy	Voltinism	Pupa length (mm)
<i>Lymantria dispar</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees, <i>Quercus</i> spp. mainly	yes	free living	univoltine	18–28
<i>Parocneria detrita</i> (ESPER, 1785)	<i>Quercus</i> spp.	no	free living	univoltine	11–13
Nolidae					
<i>Nycteola revayana</i> (SCOPOLI, 1772)	<i>Quercus</i> spp.	no	sparsely spun leaves, skeletonize as young	mostly bivoltine	9–11
<i>Pseudoips prasinanus</i> (LINNAEUS, 1758)	polyphagous on broadleaf trees	no	free living, skeletonize as young	uni- or bivoltine	13–15

Differences among seasonal guilds in species number and abundance were quite uniform for all oaks. In 1993 the number of FIF was significantly higher than the number of species in other seasonal guilds, except for *Q. petraea*, where differences between FIF and LSF were not significant (Fig. 3a). In 1994, the FIF guilds had significantly more species on all oaks (Fig. 3b). This pattern was also similar for the number of individuals (Figs. 3c,d). The only exception was an insignificant difference between FIF and LSF on *Q. petraea* in 1993 (Fig. 3c).

DISCUSSION

Lepidopteran communities account for a high proportion of all arthropods in tropical (LOWMAN, WITTMAN 1996) and temperate forests (SUMMERSVILLE et al. 2003), understanding the variables that determine the species diversity and composition should provide information of high ecological and economic importance. However, the extent to what the level of species diversity found on any particular host tree differs from random expectation remains unclear. Another unanswered question is why large differences among Lepidoptera communities are found on taxonomically closely related host species growing in the same vicinity.

The lepidopteran community structure may be influenced by many factors originating from different environmental parameters such as pressure from natural enemies to differences among individuals of the same host tree. HUNTER et al. (1997) found that the budburst phenology of individual oaks was a dominant factor determining the spatial distribution of *O. brumata* and *T. viridana*. The extent to what this pattern (differences in lepidopteran communities among crowns of the same host species) is a result of the random distribution of lepidopteran individuals has been tested recently (CRIST et al. 2003). Some information is known about the spatial effect on the species distribution in small areas (< 1 km). Lastly, lepidopteran communities vary significantly between seasons (SUMMERSVILLE, CRIST 2003; SUMMERSVILLE et al. 2003). SUMMERSVILLE et al. (2003) also studied how lepidopteran communities in temperate forests are structured. They determined several important mechanisms that play a role in forming arboreal communities, e.g. seasonal variation influenced caterpillar communities most significantly; the similarity of larval assemblages is not closely related to phylogenetic relationships among host trees (they studied three tree genera). Another message from this study is that the host specificity of Lepidoptera may be less prevalent than previously

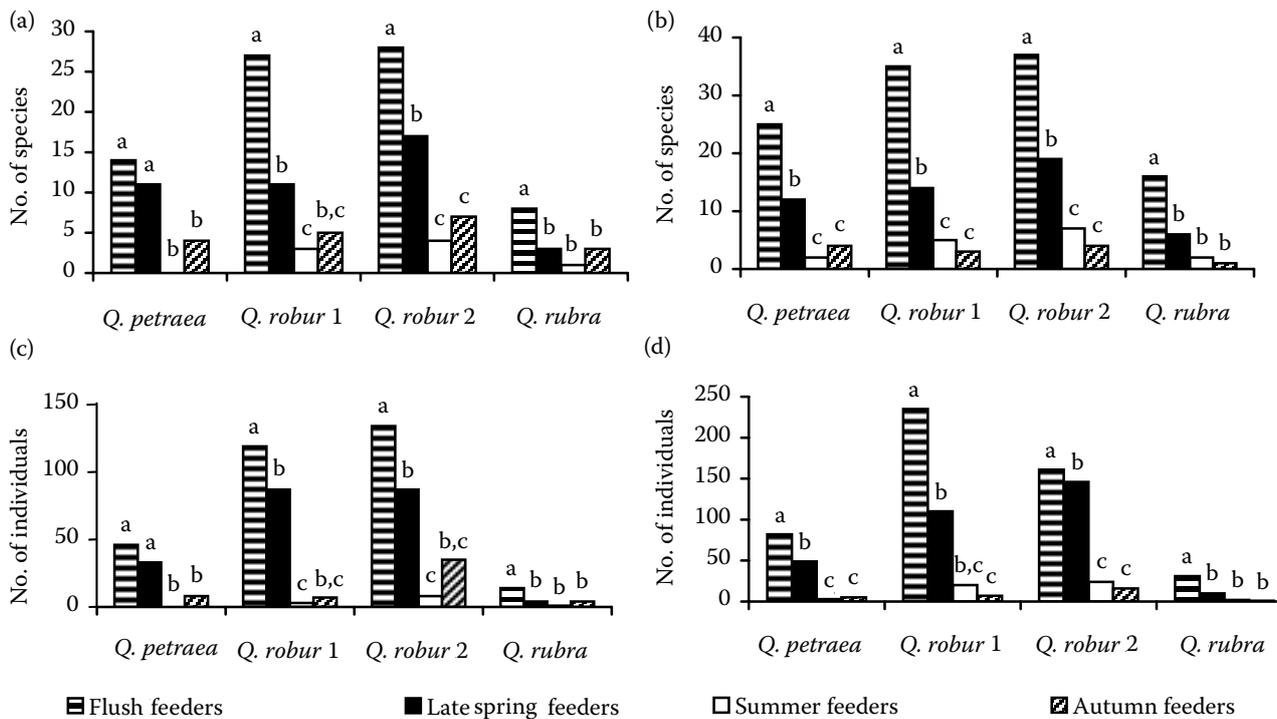


Fig. 3. Differences in the number of species and individuals in seasonal guilds: (a) comparison of species in 1993; (b) comparison of species in 1994; (c) comparison of individuals in 1993; and (d) comparison of individuals in 1994. The columns designated by different letters are significantly different ($P < 0.05$) among the seasonal guilds on individual oak species (ANOVA, LSD test)

thought. They also suggested that resource specialization may occur at the taxonomic level of the host genus or family (also suggested by STORK et al. 1997). In our study, we focused on the genus *Quercus* and found quite large differences in richness and also in the species composition on oaks.

Results also showed a steady decrease in the number of species and individuals from early spring to autumn. This pattern is well known from the “*Quercus* type” of host tree (NIEMELÄ, HAUKIOJA 1982). These authors suggested that this effect was due to a decline in available resources. Another theory was presented e.g. by FEENY (1970), KAMATA and IGARASHI (1996), who stated that tougher leaves with a higher concentration of tannin contributed to the lower richness of Lepidoptera later in the oak and beech growing season. In addition, a recent study by FORKNER et al. (2004) confirmed a negative correlation between some specialist oak feeders and condensed tannins in the canopy of *Q. alba* and understorey of *Q. velutina*. Their results generally indicated a negative response from both specialists and generalists to condensed tannins. We have no information about condensed tannins from our study sites, but the number of species and individuals was significantly higher early in spring on almost all the oak species studied; only *Q. petraea* was excluded from this general pattern.

This different pattern on *Q. petraea* in some seasons may be attributable to budburst which occurred later than on *Q. robur* and *Q. rubra* and resulted in a low number of early hatching species which by comparison were abundant on *Q. robur*. At the *Q. robur* sites there was also a better food supply due to the presence of other early flushing tree species (*Betula* spp., *Ulmus* spp., *Salix* spp.). Polyphagous species may survive on these early flushing species and later move to *Q. robur*. Significant differences were found between LSF and both SF and AF at majority, but there were no significant differences between SF and AF. Both SF and AF guilds were of low abundance and species number. While oaks produce the majority of their leaves in spring, there is also some production of “May sprouts” (Lammas shoots?) or leaf regeneration after defoliation events in late May or early June. This is a source of fresh food in early summer and is used as a niche by specialized species (e.g. *Minutia lunaris*).

CONCLUSIONS

This study documents the types of communities found on three different oak species. We found that the number of species in four seasonal guilds (flush, late spring, summer and autumn feeders) had a similar pattern on each of the studied oaks:

the highest number of species was found among FIF, a significantly lower number of species among LSF and both these groups supported a significantly higher number of species than summer and autumn feeders with several exceptions. The differences between SF and AF were found not to be significant. The same pattern was also found for the number of individuals. The only exception was an insignificant difference between FIF and LSF on *Q. petraea* in some seasons, insignificant difference between LSF and AF on *Q. robur* in some seasons and permanent insignificant difference between LSF, SF and AF on *Q. rubra*.

Acknowledgements

We would like to thank the reviewers who gave us useful comments and improved the quality of the manuscript. Thanks also to Dr. SHINSAKU KOJI, who gave us valuable comments and recommendations on early versions of the manuscript and to ALAN FLYNN and Dr. PETER FEDOR, who checked the English.

References

- CRIST T.O., VEECH J.A., SUMMERVILLE K.S., GERING J.C., 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist*, 162: 734–743.
- FEENY P., 1970. Seasonal changes in oak leaf tannins and nutrient as a cause of spring feeding by winter moth caterpillars. *Ecology*, 51: 565–581.
- FORKNER R.E., MARQUIS R.J., LILL J.T., 2004. Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*. *Ecological Entomology*, 29: 174–187.
- GERASIMOV A.M., 1952. *Nasekomye cheschuekrylye I.*, 2, Gusenitsy. Moskva, Leningrad, Izdatel'stvo AN SSSR: 339.
- HUNTER M.D., VARLEY G.C., GRANDWELL G.R., 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: A classic study revisited. *Proceedings of the National Academy of Sciences*, 94: 9176–9181.
- KAMATA N., IGARASHI I., 1996. Seasonal and annual change of a folivorous insect guild in the Siebolds beech forests associated with the outbreaks of the beech caterpillar, *Quadricalcarifera punctatela* (Motschulsky) (Lep., Notodontidae). *Journal of Applied Entomology*, 120: 213–220.
- KULFAN M., DEGMA P., 1999. Seasonal dynamics of lepidopteran larvae communities diversity and equitability on oaks in the Borská nížina Lowland. *Ekológia*, 18: 100–105.
- KULFAN M., ŠEPTÁK L., DEGMA P., 1997. Lepidoptera larvae communities on oaks in SW Slovakia. *Biologia*, 52: 247–252.
- LAŠTŮVKA Z. et al., 1998. Checklist of Lepidoptera of the Czech and Slovak Republics. Brno, Konvoj: 117.
- LOWMAN M.D., WITTMAN P.K., 1996. Forest canopies: methods, hypotheses, and future directions. *Annual Review of Ecology and Systematics*, 27: 55–81.
- NIEMELÄ P., HAUKIOJA E., 1982. Seasonal patterns in species richness of herbivores: Macrolepidoptera larvae on Finnish deciduous trees. *Ecological Entomology*, 7: 169–175.
- PATOČKA J., 1954. *Húsenice na duboch v ČSR*. Bratislava, Štátne pôdohospodárske nakladateľstvo: 262.
- PATOČKA J., 1980. *Die Raupen und Puppen der Eichen-schmetterlinge Mitteleuropas*. Monografie Angewandte Entomologie 23. Hamburg und Berlin, Paul Parey: 188.
- PATOČKA J., TURČÁNI M., 2005. *Lepidoptera Pupae of Central Europe*. Stenstrup, Apollo Books.
- PATOČKA J., ČAPEK M., CHARVÁT K., 1962. Contribution to research of canopy fauna of insects on oaks in Slovakia with special regard to Lepidoptera. *Biologické práce VIII/5*. Bratislava, SAV: 154.
- PATOČKA J., KULFAN J., TURČÁNI M., 1999. Schmetterlinge (Lepidoptera) als Eichenschädlinge. In: PATOČKA J., KRISTÍN A., KULFAN J., ZACH P. (eds), *Die Eichenschädlinge und ihre Feinde*. Zvolen, Institute for Forest Ecology of SAV: 152–250.
- STOLINA M. et al., 1985. *Ochrana lesa*. Bratislava, Príroda: 480.
- STORK N.E., DIDHAM R.K., ADIS J., 1997. Canopy arthropod studies for future. In: STORK N.E., ADIS J., DIDHAM R.K. (eds), *Canopy Arthropods*. London, Chapman and Hall: 551–561.
- SUMMERVILLE K.S., CRIST T.O., 2003. Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region and patch size. *Oikos*, 100: 134–148.
- SUMMERVILLE K.S., CRIST T.O., KAHN J.K., GERING J.C., 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. *Ecological Entomology*, 28: 747–757.

Received for publication May 13, 2009
Accepted after corrections August 4, 2009

Sezonní gildy housenek na některých dubech (*Quercus* spp.) – Případová studie

ABSTRAKT: V letech 1993 a 1994 byly na Slovensku studovány rozdíly společenstev motýlů na dubu. Vzorky byly odebrány ze tří druhů dubů (*Quercus robur*, *Q. petraea*, *Q. rubra*) od dubna do října. Byly zkoumány bionomické vlastnosti housenek, na jejichž základě byl vysvětlován rozdíl v sezonních společenstvech jednotlivých dubů. Společenstva vykazovala variabilitu ve struktuře i abundanci. Druhová pestrost čtyř společenstev (defoliátoři časného jara, pozdního jara, léta a podzimu) vykazovala podobný vzor na všech studovaných druzích dubů. Společenstvo časného jara bylo druhově nejbohatší, následovalo společenstvo pozdních jarních defoliátorů, přičemž obě skupiny byly statisticky významně bohatší než společenstva letních a podzimních defoliátorů.

Klíčová slova: společenstva motýlích housenek; Slovensko; duby; sezonní gildy

Corresponding author:

Prof. Ing. MAREK TURČÁNI, Ph.D., Česká zemědělská univerzita v Praze, Fakulta lesnická a dřevařská,
165 21 Praha 6-Suchdol, Česká republika
tel.: + 420 224 383 738, fax: + 420 234 381 860, e-mail: turcani@fld.czu.cz
