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The entomofaunas of roots of *Centaurea maculosa* Lam., *C. diffusa* Lam., and *C. vallesiaca* Jordan in Europe

Niche separation in space and time

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Abstract

Phytophagous insects representing 4 orders, 12 families and 22 species are associated with the roots of *Centaurea maculosa* Lam. (21 insect species), *C. diffusa* Lam. (12 insect species) and *C. vallesiaca* (11 insect species) in Europe. A total of 192 root samples (110 samples of *C. maculosa* and 41 samples each of *C. diffusa* and *C. vallesiaca*) from 71 localities in 8 countries were collected and analysed between 1979 and 1984. Proportions of insect orders in the insect species found on each plant varied considerably between *C. maculosa*, *C. diffusa* and *C. vallesiaca*, but corresponding values for the roots of *C. maculosa* and *C. diffusa* showed a concurrent ranking. A total of 30 parasitoid species were reared from these root feeders and parasitisation levels were generally below 10 %, but reached up to 45 % at two localities. Root feeders (excluding Hemiptera) exploit four distinct root structures on *C. maculosa*, three on *C. diffusa* and only two on *C. vallesiaca* (spatial food niche separation within the plant). Utilization levels of these feeding niches varied greatly between the three host plants. Temporal niche separation does not seem to play a major role in structuring these root feeding insect guilds. Oviposition sites (plants with green leaves) are available throughout the year and larval feeding generally coincides with high levels of water (>60 %) and nitrogen (>1.8 %) content in the roots (autumn and spring). With regard to species introductions into North America for the biological control of these knapweeds, we suggest that at least one (host specific) species should be selected for each of the different root structures. The potential impact of these root feeders on knapweed population growth and equilibrium density is briefly discussed.

1 Introduction

A comprehensive study of the phytophagous insect complex associated with European Cynareae, including *Centaurea* species, was started in 1961 by the Commonwealth Institute of Biological Control (CIBC), Delémont, Switzerland, on behalf of the Canadian Department of Agriculture (ZWÖLFER 1965; BRÖNNIMANN 1962). The purpose of these studies was to find suitable natural enemies for the biological control of spotted and diffuse knapweed, *Centaurea maculosa* Lam. and *Centaurea diffusa* Lam., in North America. Both species were accidentally introduced from eastern Europe in the early 1900s and have become important rangeland weeds in south-western Canada and the north-western United States (HARRIS and MYERS 1984). Three flower head insects imported from Europe, *Urophora affinis* Frld., *U. quadrifasciata* Meig. (Dip., Tephritidae) and *Metzneria paucipunctella* Zell. (Lep., Gelechiidae), were first released into Canada between 1970 and 1973. The root miner *Sphenoptera jugoslavica* Obenb. (Col., Buprestidae) was first released in Canada in 1976. All four biological control agents became established. Despite heavy seed predation, ranging from 60–88 %, and a wide distribution of the flower head insects, no measurable decrease in weed density has so far occurred in Canada (HARRIS and MYERS 1984; J. MYERS, pers. communication).

The present study was carried out between 1979–1984 as part of a second faunistic survey initiated by the CIBC in 1977. The objectives were to investigate the insect species

associated with the roots of *C. maculosa*, *C. diffusa* and the closely related *C. vallesiaca* in their native range in Europe in order to assess their suitability as potential biological control agents.

In this paper, the faunistic aspect of the field survey is presented and spatial (within-plant) and temporal niche separation of these root feeders is described. Here, niche separation refers to differences in resource-use pattern, which may or may not involve niche differentiation (= coevolutionary resource-use displacement [BAZZAZ 1987]). Prospects for the use of the studied root insects as biological control agents are briefly discussed. The structural analysis of the root insect guild is presented elsewhere (MÜLLER 1988a).

2 Host plants, study areas and methods

The genus *Centaurea* (Compositae) consists of around 500 predominantly Mediterranean species. *Centaurea maculosa* is a biennial or a short lived perennial, comprising several subspecies ranging from western Asia to western Europe (DOSTAL 1976). This study concerns only the widely distributed, diploid ($2n = 18$) *C. rhenana* Boreau populations [= *C. maculosa* ssp. *rhenana* (Boreau) Gugler], typical of the continental dryland plant associations (OBERDORFER 1962). The tetraploid ($2n = 36$) *Centaurea biebersteinii* ssp. *biebersteinii* DC (= *C. micranthos* Gmel. ex. Hayek, = *C. maculosa* ssp. *micranthos* Gmel.), is apparently the best match for the tetraploid ($2n = 36$) *C. maculosa* targetted for biological control in North America (SCHROEDER 1986). Unfortunately it could not be included in this survey, because it is mainly distributed in the southern USSR, which was not accessible. In the text below, the name *C. maculosa* will be used for *C. maculosa* ssp. *rhenana*.

Centaurea diffusa is a biennial or triennial, of mainly eastern Mediterranean distribution occurring in western Asia, and from the southern USSR to western Germany. It is taxonomically well defined, and North American and European plants appear to belong to the same species. It is a typical plant of the continental steppe and silvo-steppe vegetation in the eastern part of its geographical distribution (SCHROEDER 1986).

In their western distribution area both knapweed species are mainly found in sites disturbed by human activities, such as ruderal areas along roadsides or in abandoned or overgrazed natural pastures. At such locally occurring sites both species often grow in quite dense stands (SCHROEDER 1986).

Centaurea vallesiaca is taxonomically closely related to *C. maculosa* (DOSTAL 1976; HESS et al. 1972) and probably occurs only in the western Alps. It is mainly restricted to south facing, dry and stony slopes in the coline zone (HESS et al. 1972).

The geographic distribution of the studied knapweeds and the main study areas are shown in fig. 1. For *C. maculosa* the survey comprised a total of 110 samples taken at 4 sites in France, 4 in Germany, 15 in Austria, 7 in Hungary, 7 in Romania and 6 in Czechoslovakia. A total of 41 samples of *C. diffusa* were collected from 15 sites in Romania, and 41 samples of *C. vallesiaca* were taken from 11 sites in Switzerland and 2 sites in Italy (fig. 1). Most of the samples were collected in May and June.

Each sample contained 50 to 100 randomly selected plants (see WHABA 1970). The roots, with 5 cm of shoot, were packed in the field between slightly moistened layers of cellulose in styropor boxes. Dissections and rearings were later made in the laboratory to assess the root feeding entomofauna.

Parasitism was studied from larvae collected in the field in June. Host records of the parasitoids were obtained from individually reared host larvae, as well as from mass rearings from roots collected at sites where only one or two species of root feeders were known to occur. Observations on predators were made in the field.

The term "root" is used here to describe the tap root, including the root collar and the central meristem of the rosette.

3 Results and discussions

3.1 The entomofaunas and their taxonomic composition

In our survey 21 phytophagous insect species were found associated with the roots of *C. maculosa*, 12 species with *C. diffusa* and 11 with *C. vallesiaca*. A total of 4 orders, 12 families and 22 species were represented. Neglecting rare species (less than 5 individuals found) there were only 14, 10 and 3 insect species for *C. maculosa*, *C. diffusa* and *C. vallesiaca*, respectively. A list of the species found during our survey and records of two previous surveys are given in table 1.

The large geographic distribution (species-area function) (cf. POLUNIN 1969) and the high number of *Centaurea* spp. present (host speciation rate) most likely account for the high values for herbivore species richness. The high apparency of the rosettes and the rich food resources offered by the roots during winter, together with their poor accessibility, further account for the high number of specialist feeders associated with the roots of *C. maculosa* and *C. diffusa* (MÜLLER 1988a). This interpretation is supported by the small number of insects found in and on the roots of the geographically restricted *C. vallesiaca* populations.

Comparative species compositions, by orders, are given in figure 2. Only species confirmed by field records (including information in SCHROEDER 1986) were used. The proportions of insect orders represented on a plant species varied considerably between *C. maculosa*, *C. diffusa* and the genus *Centaurea* (ten species pooled), but hemipterous and hymenopterous species were always rare. In our survey, 57 % of the root entomofauna on *C. maculosa* and *C. diffusa* occurred on both plants. This percentage rises to 73 % if rare species are excluded, and explains the concurring ranking of proportions of insect orders

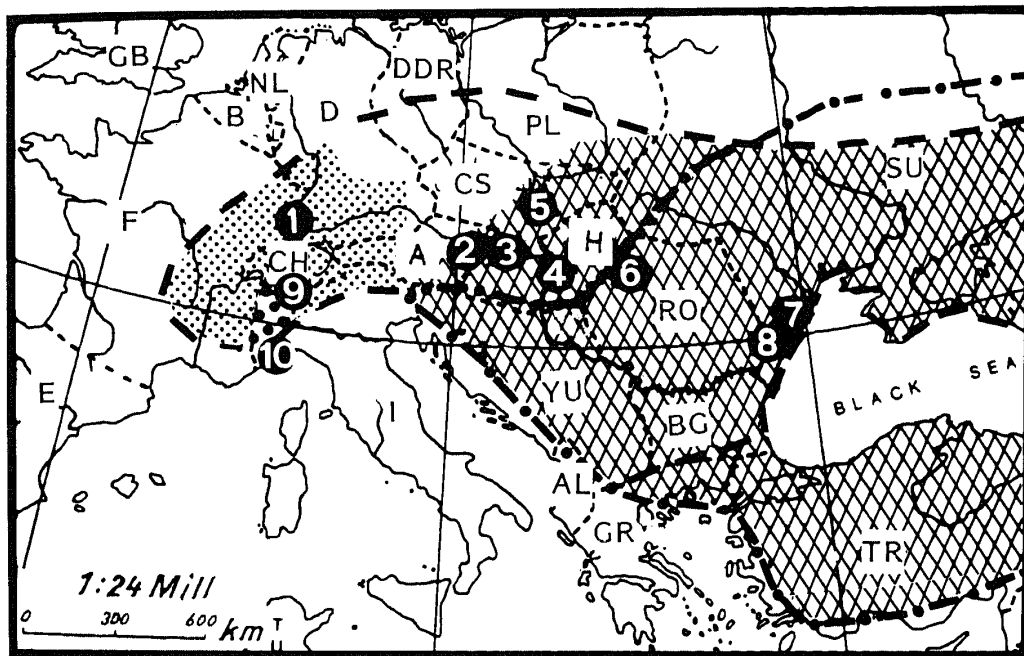


Fig. 1. Geographic distribution of the studied *Centaurea* species (based on records in DOSTAL 1976), and main study areas. Host plant distribution: --- *C. diffusa* Lam., -- *C. rhenana* Boreau (including all ssp.) [= *C. maculosa* ssp. *rhenana* (Boreau) Gugler], [] *C. maculosa* Lam. ssp. *maculosa* [= *C. stoebe* ssp. *maculosa* (Lam.) Hayek], [] *C. biebersteinii* ssp. *biebersteinii* (= *C. micranthos* S. G. Gmelin ex Hayek, = *C. maculosa* ssp. *micranthos* Gmel.), [] *C. vallesiaca* Jordan. Study areas and collection sites: *Centaurea maculosa*: 1 = Alsace and S-German Rhine Valley: Kembs, Blodelsheim, Geisswasser, Reguisheim, Rheinweiler, Markt, Istein, Neuenburg; 2 = NE-Austria: Dürnstein, St. Michael, Neudorf, Sollenau, Plankenberg, Siegersdorf, Eggendorf, Nickelsdorf, Gattendorf, Streitenhofen, Weiden, Donnerskirchen, Felixdorf, Schwechat, Mönchshof; 3 = NW-Hungary: Fertőrákos, Balf, Sopron, Sumeg, Czakvar; 4 = Central Hungary: Budapest, Pilis; 5 = Slovakia: Detva, Haj, Hacheva, Debrad, Borka, Rosenau; 6 = W-Romania: Lugaçu de Jos, Poieni, Vadu Crisului, Cluj; 7 = E-Romania: Nufaru, Victoria, Jassi. – *Centaurea diffusa*: 8 = E-Romania: Somova, Tulcea, Victoria, Agighiol, Horia, Babadag, Constanta, Mamaia, Mineri, Malcoci, Nalbant, Murighiol, Jurilovka, Mangalia, Slava Rusa. – *Centaurea vallesiaca*: 9 = Swiss Valais: Brigerbad, Lalden, Hochtenn, Bitsch, Mörel, Naters, Baltschieder, Baltschieder, Salgesch, Raron, Fully; 10 = NW-Italy (Liguria): Villa Faraldi, Diano Marina (host plant record needs to be verified)

Table 1. Phytophagous insect species associated with the roots of *Centaurea maculosa*, *C. diffusa* and *C. vallesiaca* in Europe

	Emergence period	Host range ¹	<i>maculosa</i>	<i>Centaurea</i> ² <i>diffusa</i>	<i>vallesiaca</i>
APHIDOIDEA (total species)			2	2	0
<i>Chomaphis centaurea</i> CB		S	L	—	—
<i>Protaphis alexandrea</i> (Nevs)		S	—	F	—
<i>Sminthurodes betae</i> Westw.		S	+	+	—
<i>Trama centaureae</i> CB		S	+	+	—
LEPIDOPTERA (total species)			8	3	6
Tortricidae					
<i>Pelochrista medullana</i> Zell.	13. VI.—30. VII.	S	+	+	—
<i>Celypha rurestrana</i> Dup.		S			(+)
<i>Cnephasiella incertana</i>	6. V.—7. VII.	G			(+)
<i>Cnephasia communana</i>	8. V.—10. V.				(+)
Cochylidae					
<i>Agapeta zoegana</i> L.	23. V.—13. IX.	S	+		
<i>Stenodes straminea</i> Haw.	2. V.—5. VI.	S	+	+	+
<i>Stenodes meridiana</i> Stgr.	3. VII.—3. VIII.	S	+		
Phycitidae					
<i>Epischmia prodromella</i> Hb.	10. VI.—13. VI.	G			(+)
<i>Myctegretis achatinella</i> Hb.	25. VII.—30. VII.	G	(+)		
Pterolonchidae					
<i>Pterolonche inspersa</i> Stgr.	4. VII.—13. VIII.	S	+	+	(+) ²
Gelechiidae					
<i>Pleurota pyropella</i> Den. und Schiff.	7. VI.—9. VI.	G	(+)		
Galeriidae					
<i>Melisoblaptes zelleri</i> de Joan	23. VI.—2. VII.	G	(+)		
COLEOPTERA (total species)			9	5	2
Curculionidae					
<i>Cleonus piger</i> Scop.	3. VII.—15. VII.	S	+	+	
<i>Cyphocleonus achates</i> Fahr.	31. VI.—27. VII.	S	+	+	
<i>Cyphocleonus tigrinus</i> Panz.	6. VII.	G	(+)	F	
<i>Peritelus sphaeroides</i> Germ.			(+)		(+)
<i>Apion penetrans</i> Germ.	16. VI.—13. VII.	S	+	+	
<i>Apion onopordi</i> Kirby	14. V.—18. VII.	S	+	+	+
<i>Apion orientale</i> Gerst.	7. VII.—13. VII.	S	(+)		
<i>Apion alliariae</i> Herbst	1. VII.—2. VII.	S	(+)		
Buprestidae					
<i>Spenoptera jugoslavica</i> Ob.	23. VI.—21. VII.	S	+	+	
DIPTERA (total species)			2	2	3
Anthomyiidae					
<i>Pegohylemyia centaureae</i>	5. V.—8. VI.				
Hennig	12. V.—17. V.	S	+	(+)	+
<i>Pegomya</i> sp.	14. V.—16. V.				(+)
<i>Delia platyura</i> Meigen		G			(+)
Agromycidae					
<i>Melanagromyza aeneiventris</i> F.		G		F	
Syrphidae					
<i>Cheilosia proxima</i> Zett.	25. VI.—12. VII.	S	+	(+)	
Total species			21	12	11
(excluding rare species)			14	10	3

¹ S = Specialist feeder: restricted at least to the tribe Cynareae, G Generalist feeder. — ² + Own survey record, (+) Rare species (less than 5 individuals). Additional records listed by SCHROEDER, (1986): L = Literature record, F = Field record.

found on the roots of these two knapweeds. The roots are predominantly attacked by moths and weevils, whereas flies (mainly tephritids) dominate the corresponding flower head guilds (ZWÖLFER 1977, 1980).

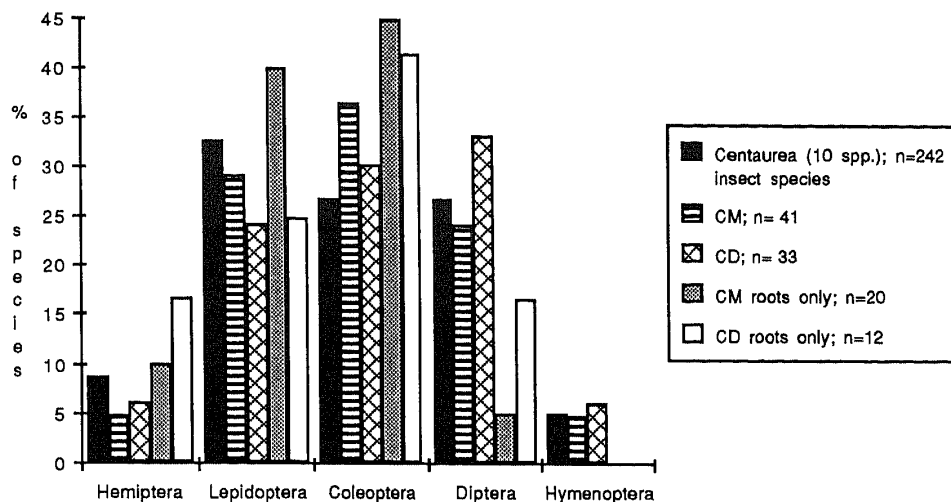


Fig. 2. Taxonomic composition of insect faunas on *C. maculosa* (CM), *C. diffusa* (CD), *C. vallesiaca* (CV) and the genus *Centaurea*¹. – ¹ Data from LAWTON and SCHROEDER (1978), who analyzed ZWÖLFER's (1965) Cynareae data

3.2 Predators and parasitoids

Elaterid larvae were the most frequently and widely observed predators, being absent only from the Swiss Valais. The two staphylinid predators *Ontholestes haraldi* (Epph.) and *Xantholinus linearis* (Ob.) were also collected from *C. maculosa* and *C. diffusa* roots originating from various regions. Plants attacked by moths and Cleonini weevils were often infested by the saprophagous sciarid flies *Bradysia* spp. Such secondary attack may have a considerable impact on plant performance by increasing the susceptibility to disease (pers. observations) as well as to abiotic factors such as drought (OHNESORGE 1976).

Root feeders are both concealed and protected by the soil layer and, in addition, 3 of the 10 more common insect species on the roots of *C. maculosa* and *C. diffusa* produce a gall-like enlargement of the tap root. In a recent analysis of parasitoid species richness on British phytophagous insects, HAWKINS and LAWTON (1987) found a low parasitoid load associated with such well concealed herbivores: thus few parasitoid species might be expected for the studied root feeders. However, a total of 30 parasitoid species were reared and identified, including 2 tachinid flies, 11 ichneumonid and 13 braconid wasps, and 4 other hymenopterous species (table 2).

In general, parasitisation of an individual host species never exceeded 15 % in any one locality, and no parasitoid species was found at more than six sites. An exception was the egg-larval parasitoid *Chelonus intermedius* Ths. which parasitised 45 % of *A. zoegana* larvae in one site in Hungary. Eggs of this moth are the most exposed to parasitoids, as they are laid on the rosette leaves. Parasitism of the weevils *Cyphocleonus achates* (Fahr.) and *Cleonus piger* Scop. by the braconid *Vipio tentator* Rossi and the ichneumonid *Aritranis fuscicornis* Tschek. also attained up to 45 % in some populations in eastern Romania and Austria. Both of these wasps attack late instar larvae and overwinter within the root (STINSON et al. 1988).

As parasitisation and predation was studied only in late larvae and pupae, their role in structuring the studied root insect guild remains unknown.

Table 2. Parasitoids reared from *Centaurea* root feeders

Parasitoid species	Emergence period	Host ¹	Regions ²	Level of parasit. ³	Life history ⁴
DIPTERA					
Tachinidae					
<i>Zenxia cinerea</i> Meigen	10. VII.-12. VII.	?	A	2×	so, I, ovolarviparous
<i>Solieria pacifica</i> Meigen	22. VII.-25. VII.	?	A/H	2×	so, I, ovolarviparous
HYMENOPTERA					
Ichneumonidae					
<i>Centeterus confector</i>	31. V.-29. VI.	?	A/H	low	so, I, larval
<i>C. nigricornis</i> Thoms	29. V.-8. VI.	?	CH	low	so, I, larval
<i>C. elongator</i> Berth.	24. V.-1. VI.	?	CH	low	so, I, larval
<i>Scambus brevicornis</i> (Grav.)	23. VII.	?	A/H	low	so, E, larval
<i>Pimpla spuria</i> Grav.	24. V.-31. V.	S	CH	med.	so, I, pupal
<i>Exeristes roborator</i> (F.)	11. VIII.-9. IX.	?	CH	low	so, E, larval
<i>Glypta sculpturata</i> Grav.	1. VII.-13. IX.	A	RO, A	med.	so, I, larval
<i>G. bifoveolata</i> Grav.	17. VII.-24. VIII.	A	RO	4×	so, I, larval
<i>Lissonota bivittata</i> Grav.	7. VII.-10. VII.	M	RO	4×	so, I, larval
<i>Hyposoter</i> sp.	13. VII.-20. VII.	A	A	2×	so, I, larval
<i>Artrianis fuscicornis</i> Tschek.	V.-VI.	CY, CL	RO, A, A/H	low	so, I, larval
Braconidae					
<i>Apanteles</i> cf. <i>laevigatus</i>	?	?	A/H	2×	I, larval
<i>Bracon epiriptus</i> Marsh.	17. V.-31. V.	S	CH	low	gr, E, larval
<i>B. larvicida</i> Wesm.	16. VI.-15. VII.	A	RO	low	gr, E, larval
<i>B. minutator</i> F. var. <i>trucidator</i> M.	11. VII.-16. VII.	S	CH	4×	gr, E, larval
<i>B. praeternissus</i> Marsh.	6. VI.-30. VI.	A, P	RO, A	low	gr, E, larval
<i>B. grandiceps</i> Thoms.	29. VI.-5. VII.	A, S	H, CH	med.	gr, E, larval
<i>B. erraticus</i> Wesm.	15. IX.-29. VI.	S	CH	low	gr, E, larval
<i>Bracon</i> sp.	VI.-VII.	SP	RO ⁵⁾	med.	gr, E, kills med-sized p.
<i>Vipio tentator</i> Rossi	V.-VI.	CY, CL	RO, A, A/H	med.	I, larval
<i>Chelonus annulipes</i> Wesm.	6. VI.-30. VII.	A	RO, A/H	low	so, I, egg-larval
<i>C. intermedius</i> Ths.	18. VI.-31. VII.	A	A/H	high	so, I, egg-larval
<i>C. sculpturatus</i> Szepi.	10. VI.-26. VII.	A, P	RO, A/H	med.	so, I, egg-larval
<i>Dacnusa tarsalis</i> Thoms.	6. V.-9. V.	?	A/H	2×	so, larval

Pteromalidae					
<i>Chlorocytus? loagare</i> (Walk.)	23. VIII.-2. VII.	?	A, A/H	3×	so, E?
<i>Trichomalus</i> sp.					
<i>bracteatus</i> (Walk.)	28. VII.-5. IX.	?	A/H	2×	so, E?
Eucyrtidae					
<i>Copidosoma</i> sp.	24. VI.-24. VII.	A, P	RO, A, A/H	med.	gr, I, polyembryonic
Chalcidoidea		SP	RO ⁵	med.	gr, I, larval

¹LEPIDOPTERA - A: *Agapeta zoegana*; P: *Pelochrista medullana*, S: *Stenodes straminea*; M: *St. meridiana*. COLEOPTERA - CY: *Cyphocleonus achates*; CL: *Cleonus piger*; SP: *Sphenoptera jugoslavica* (data from ZWÖLFER 1976). - ² Host collected from RO: E-Romania, H: Central Hungary; A/H: E-Austria/NW-Hungary; A: Central Austria (Wachau); CH: Swiss Valais. - ³ Level of parasitisation (% of the hosts attacked in the indicated regions): number of records for <5 records; low: <5%; medium: 5-30%; high: 31-50%. - ⁴ so/gr: solitary/gregarious; E/I: Ecto/Endoparasitoid. - ⁵ Data from ZWÖLFER (1976); collected additionally from Bulgaria and Greece.

3.3 Niche separation in space








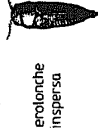


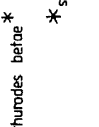
The members of the root-feeding entomofauna associated with the three knapweed species exploit different root structures. Figure 3 illustrates the more common insect species feeding in or on these roots and shows their larval food niches. Five food-niches, each utilized by different insect species, can be distinguished (MÜLLER 1988a).

Figure 4 shows the overall utilization of these niches by the more common insect species. The cumulative number of sites (samples, which correspond roughly to the geographic range, cf. LAWTON and SCHROEDER 1977) at which specific food niche exploiters (cf. fig. 3) were collected showed the same ranking for four feeding-niches as the cumulative values for relative abundances of larvae. Data were too few to extend this analysis to external feeders.

Apion spp. account for the high utilization of the root collar on *C. maculosa*. The central meristem of the rosette remained unexploited in *C. diffusa*, and the root cortex and the root cylinder in *C. vallesiaca*. Geographic isolation with a corresponding limited species pool of potential exploiters may be mainly responsible for this. The two dominant species on *C. vallesiaca*, *Stenodes straminea* Haw. and *Apion onopordi* Kirby, however, produced the highest abundance levels recorded (number of individuals per 100 roots).

3.4 Niche separation in time

An overview of the temporal niche separation is given in fig. 5. All common root feeders, with the exception of *Cleonus piger*, pass the winter as larvae within the roots. Feeding occurs mainly in autumn and spring when water and nitrogen content of the roots is high (data from MÜLLER 1984). The summer generations of the moth *Agapeta zoegana* L. (Hungary and Romania) develop mainly on plants that remained in the rosette stage. As such plants are present throughout the year, the availability of oviposition sites does not play a major role in the basic structuring of the root insect guilds. This is in contrast to the flower head guild, where there is a critical limited window of time during which successful oviposition can occur (ZWÖLFER 1985, 1988). Experiments to study the effect of various combinations of infestation times for pairs of root feeders (e.g. gall formers and miners) on larval development and gall formation to predict specific species associations are presently being carried out. The biennial *C. maculosa* and *C. vallesiaca* are usually attacked only once by root feeders, in the rosette stage in late summer. The North American short lived perennial *C.*

Root structures infested by phytophagous insect species	Centaurea		Feeding niches		Insect species
	mac.	diff.	mac.	vall.	
1. Central meristem of rosette <i>Stenodes straminea</i> Haw. <i>Pegophylomyia centaureae</i> Hennig	+	+	+	+	 <i>Stenodes straminea</i> *  <i>Pegophylomyia centaureae</i>
2. Root collar <i>Apion penetrans</i> Germer <i>Apion onopordi</i> Kirby <i>Apion orientale</i> Gerst. <i>Apion allianiae</i> Herbst <i>Cheilosia</i> sp.	+	+	+	+	 <i>Apion</i> spp.  <i>Cheilosia</i> sp. *
3. Central vascular tissue <i>Cyphocleonus achates</i> (Fabr.) <i>Cleonus piger</i> Scop. <i>Sphenoptera jugoslavica</i> Ob. <i>Pterolonche inspersa</i> Stg.	+	+	+	+	 <i>Cyphocleonus achates</i> *  <i>Cleonus piger</i>  <i>Sphenoptera jugoslavica</i>  <i>Pterolonche inspersa</i>
4. Root cortex <i>Agapeta zoegana</i> L. <i>Pelochrista medullana</i> Sgr.	+	+	+	+	 <i>Agapeta zoegana</i> *  <i>Pelochrista medullana</i>
5. External on root <i>Trama centaureae</i> CB <i>Sminthurus betae</i> Westw.	?	+	?	?	 <i>Sminthurus betae</i> *

* shown in feeding-niche

C. Purseglove

Fig. 3. Spatial (within-plant) niche separation of the more common insect species associated with the roots of *Centaurea maculosa*, *C. diffusa* and *C. vallesiaca* in Europe (modified from MÜLLER 1988a)

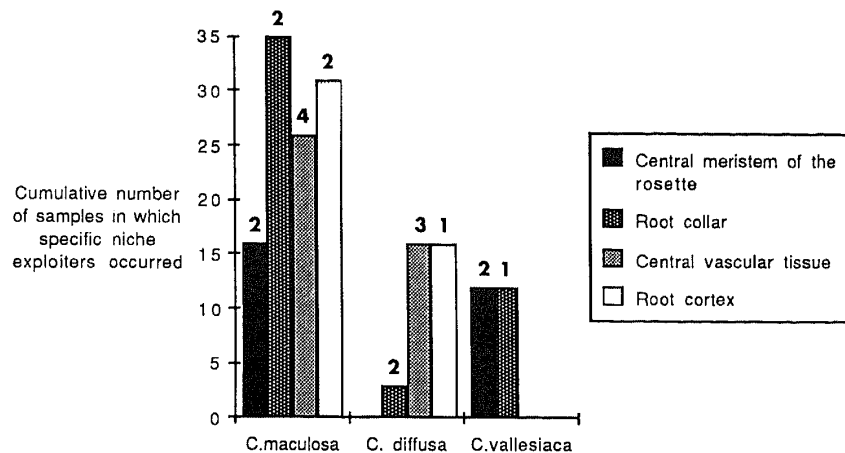


Fig. 4. Utilization of the different root tissue structures of *Centaurea maculosa*, *C. diffusa* and *C. vallesiaca* by their more common insect species. A total of 40 samples from 22 sites were analysed for *C. maculosa*, 18 samples from 7 sites for *C. diffusa* and 16 samples from 4 sites for *C. vallesiaca*. Values above the columns give the numbers of root feeding species exploiting that niche

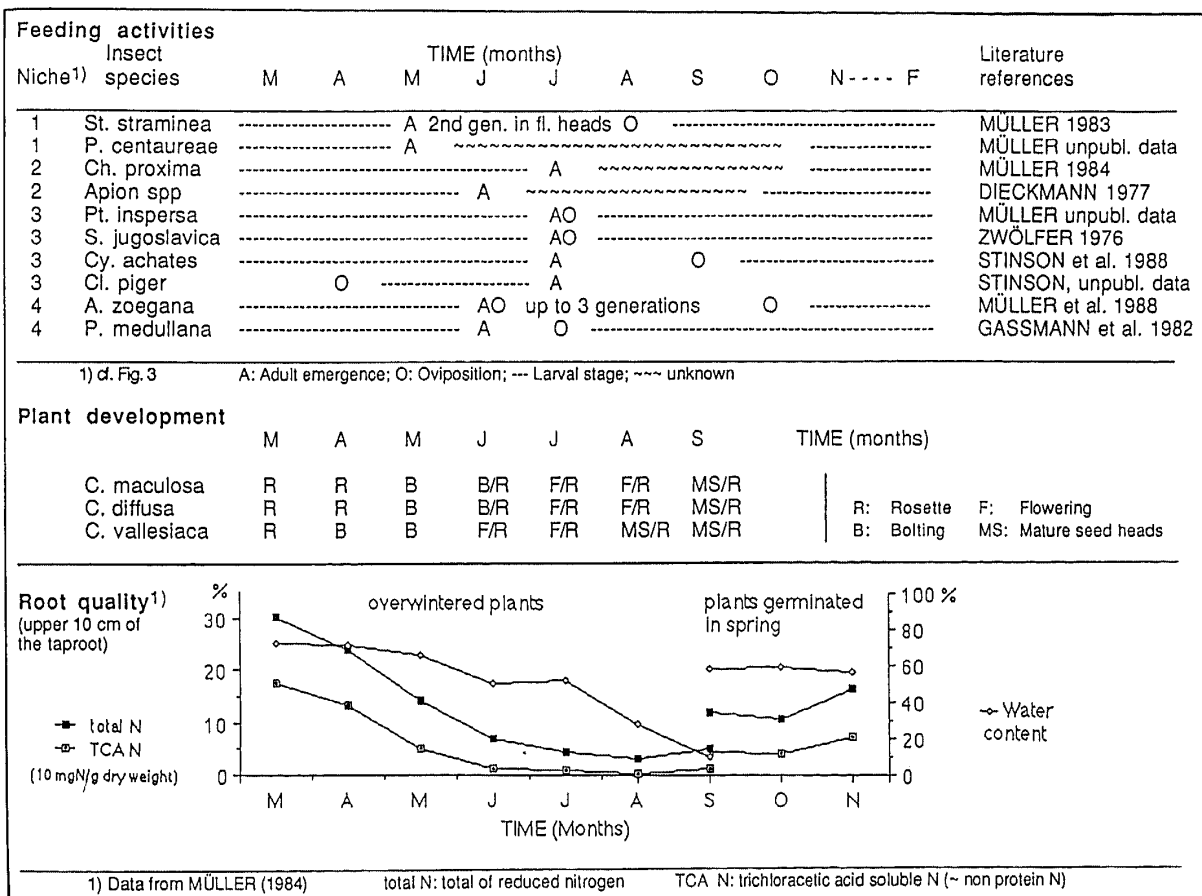


Fig. 5. Feeding activities of knapweed root insects in relation to plant development and root quality parameters

maculosa, however, may be attacked during several subsequent years (MÜLLER 1988b; STINSON et al. 1988).

A distinct temporal niche separation occurs between the herbivore guilds of the roots and the flower heads of these knapweeds. The larval activities of the members of these two guilds succeed one another. The root feeders develop in the nutrient rich tap roots in the autumn and spring. In summer, when the quality of the roots declines, the flower heads and seeds are exploited.

3.5 Morphological comparison of attacked and unattacked plants

In the field, impact of herbivores on plant performance is difficult to distinguish from phenotype specific oviposition preferences and requires careful experimentation. Plants attacked by the moths *A. zoegana* and *Pterolonche inspersa* Stgr., and the weevils *C. piger* and *C. achates* are generally larger (larger root crown diameter, higher number of shoots) than uninfested plants (table 3), but were significantly smaller after subsequent develop-

Table 3. Morphological comparison of attacked and unattacked plants in the field

Locality Insect species	Roots n	Root collar diameter (mm)	Shoots n	Max. shoot diameter (mm)
Pilis (Hungary)				
<i>Agapeta</i>	72	12.68 b ¹	2.11 b	5.71 a
<i>Pterolonche</i>	104	12.66 b	1.80 b	6.34 ab
controls	56	7.23 a	1.14 a	7.16 b
Dürnstein (Austria)				
<i>Agapeta</i>	19	21.21 b	7.79 b	3.84 a
<i>Cyphocleonus</i>	19	12.74 b	6.53 b	3.68 a
controls	53	5.69 a	3.42 a	3.45 a
Steinfeld (Austria)				
<i>Agapeta</i>	56	7.55 b	2.45 a	4.50 b
<i>Cleonus</i>	24	10.13 c	4.75 b	4.13 ab
<i>Pterolonche</i>	14	9.57 bc	4.00 ab	4.64 ab
controls	64	5.03 a	2.27 a	3.64 a

¹ ANOVA; values followed by the same letter are not significantly different (p = 0.05, Scheffé F-Test).

ment (MÜLLER 1984). However, nothing can be said about the causes of such associations. Higher mortality risk due to root infestation of small plants compared to larger plants (MÜLLER 1983), preference of larger (more apparent) plants for oviposition (STINSON et al. 1988), or compensation or overcompensation of infested plants [increased number of shoots after herbivory (MÜLLER 1983)] lead to the observed associations. POWELL and MYERS (1988) studied the effect of *S. jugoslavica* at its release site in British Columbia on *C. diffusa* and, although they found a reduced survival of seedlings and rosettes, delayed reproduction and reduced seed output in infested plants compared to controls, there was only intermittent damage to the knapweed populations. Experiments with potted plants showed that mining of a single larva of *A. zoegana* destroyed small plants, that several larvae could develop on the same plant and that the larvae searched for additional plants if they depleted their food supply before termination of larval development (MÜLLER et al. 1988; MÜLLER 1988b). The impact of *A. zoegana* and *C. achates* on the survival, phenology and seed production of diploid *C. maculosa*, and its consequences on population biology of spotted knapweed are presently being studied in more detail in laboratory and field experiments by one of us (H. M.).

4 Conclusions

As a result of this survey, and accompanying host specificity studies and experiments to assess the effectiveness of selected species, three moths, *Agapeta zoegana*, *Pelochrista medullana* and *Pterolonche inspersa*, and a weevil *Cyphocleonus achates* were recommended for introduction into the USA and Canada (GASSMANN et al. 1982; MÜLLER et al. 1988; STINSON et al. 1988). The first releases were made in 1983 (*A. zoegana*), 1985 (*P. medullana*) and 1987 (*P. inspersa* and *C. achates*). *Agapeta zoegana*, *P. medullana* and *P. inspersa* are now established in Canada, and *A. zoegana* in the USA (MÜLLER 1988c).

There are no indigenous root herbivores known to attack the two target weeds in North America. An appropriate strategy for introductions of agents against these knapweeds is to select one species for each of the different niche types, since it was shown earlier that species which develop in different tissues of the root coexist at random or showed positive associations (MÜLLER et al. 1988; MÜLLER 1988a). In addition, a positive correlation between species packing (number of root-feeding species per knapweed population) and infestation rates (percent of roots attacked) was found in more stable habitats (i.e. similar to the infested areas in North America). Therefore, by gradually filling the feeding niches on these knapweeds, an increasing herbivore load and resource utilization can be expected in the infested areas. Climatic, and especially microclimatic factors will be expected to play a major role in allowing species to coexist in the same locality. One should therefore attempt to introduce as many additional species as possible, as species interactions may not be predictable.

Recent studies on the population ecology of *C. diffusa* in British Columbia, Canada, suggest that agents attacking the rosette stage will be more effective in reducing knapweed densities than the seed feeding agents already present (J. M. MYERS, pers. communication). This is mainly because the effect of the flower head attacking insects is generally limited to seed reduction, whereas the root insects have the potential to 1. reduce the survivorship of seedlings and rosettes, 2. delay flowering and 3. reduce seed output (POWELL and MYERS 1988).

The high number of specialist feeders associated with the roots of these knapweeds in Europe, their observed and potential influence on knapweed population dynamics, especially on plant density, demonstrates the potential of these root feeders as biological control agents for spotted and diffuse knapweed. It is also hoped that this study will encourage workers to focus more attention to the importance of root herbivores as biological control agents, especially for biennial and perennial weeds.

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Zusammenfassung

Zur Entomofauna des Wurzelbereiches der Flockenblumen, *Centaurea maculosa* Lam., *C. diffusa* Lam. und *C. vallesiaca* Jordan in Europa. Räumliche und zeitliche Nischendifferenzierung

Phytophage Insekten aus 4 Ordnungen, 12 Familien und 22 Arten bilden die mit den Wurzeln von *Centaurea maculosa* Lam. (21 Insektenarten), *C. diffusa* Lam. (12 Insektenarten) und *C. vallesiaca*

Jordan (11 Insektenarten) assoziierte Insektenfauna. Zwischen 1979 und 1984 wurden insgesamt 192 Wurzelproben (110 Proben von *C. maculosa* und je 41 Proben von *C. diffusa* und *C. vallesiaca*) von 71 Lokalitäten aus 8 Ländern gesammelt und analysiert. Der relative Anteil bezüglich Insektenordnungen aller auf einer Pflanzenart gefundenen Insektenarten schwankte beträchtlich zwischen *C. maculosa*, *C. diffusa* und *C. vallesiaca*, zeigte jedoch eine übereinstimmende Reihenfolge für die Wurzelinsekten an *C. maculosa* und *C. diffusa*. Insgesamt wurden 30 Parasitoidenarten aus den gesammelten Wurzelphytophagen gezüchtet; der Parasitierungsgrad lag im allgemeinen unter 10 %, erreichte jedoch an 2 Lokalitäten 45 %.

Die Wurzelphytophagen (ohne Hemiptera) nutzen 4 unterschiedliche Wurzelstrukturteile (Gewebe) an *C. maculosa*, 3 an *C. diffusa* und nur 2 an *C. vallesiaca* (räumliche, innerpflanzliche Nischendifferenzierung). Der Nutzungsgrad dieser Fraßnischen schwankte beträchtlich zwischen den 3 Wirtspflanzen. Zeitliche Nischendifferenzierung scheint keinen wesentlichen Einfluß auf die Strukturierung dieser Wurzelinsektengilden zu haben. Eiablageplätze (Pflanzen mit grünen Blättern) sind über das ganze Jahr vorhanden, und der Larvenfraß fällt im allgemeinen mit hohem Wasser- (>60 %) und Stickstoffgehalt (>1,8 %) in den Wurzeln zusammen (Herbst und Frühling). Im Hinblick auf die Einfuhr von Arten zur biologischen Bekämpfung dieser Flockenblumen in Nordamerika schlagen wir daher vor, mindestens eine (wirtsspezifische) Art pro Wurzelstrukturteil auszuwählen. Mögliche Auswirkungen dieser Wurzelphytophagen auf das Wachstum der Flockenblumenpopulationen und deren Gleichgewichtsdichte werden kurz diskutiert.

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