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Structural analysis of the phytophagous insect guilds associated with the roots of *Centaurea maculosa* Lam. *C. diffusa* Lam., and *C. vallesiaca* Jordan in Europe:

1. Field observations

Heinz Müller*
CAB International Institute of Biological Control, Delémont, Switzerland

Summary. During extensive field surveys in central and eastern Europe, 21 herbivorous root insect species were found on *Centaurea maculosa* ssp. *rhenana* Boreau, 12 species on *C. diffusa* Lam. and 11 species on *C. vallesiaca* Jordan, representing 12 families in 4 orders. The large geographic distribution (species-area function), the high number of *Centaurea* spp. present (host speciation rate), and the high apparency of the rosettes and the rich food resources offered by the roots during winter, together with their poor accessibility, correlate with the high number of specialist feeders associated with the roots of *C. maculosa* and *C. diffusa*. The members of the taxonomically diverse root entomofauna exploit specific structures of the tap root (food niches). Interspecific competition among members of food niches, as well as species-specific responses to different phenological stages (for oviposition) and tissues (for larval development) are thought to be responsible for the high predictability in guild structure. The relatively low levels of host plant attack (two thirds of the roots were unattacked) and the fact that food niches remained unoccupied in most of the regions suggest, however, that the majority of the studied guilds do not represent equilibrium assemblages. Ecological (different habitats), climatic (transitional zone) and historical (ancient pre-Pleistocene communities) factors could account for the highest values of species diversity, infestation levels, species packing and food niche utilization, which are found on *C. maculosa* in E. Austria/NW. Hungary, compared to other regions. A positive correlation between species packing (number of root-feeding species per population) and infestation rates (percent of roots attacked) was only found for the more stable, semi-natural habitats. A comparative analysis of the regional root insect guilds of *C. maculosa* with corresponding data for the phytophagous insects associated with the flower heads revealed distinct taxonomical differences, but a high degree of numerical and structural similarity. The different geographical regions are similarly ranked for host plant attack, herbivore pressure, average species packing and level of food niche utilization.

Key words: Root – *Centaurea* – Herbivorous insects – Guild structure – Weed control

The analysis of factors determining the number and types of species that make up a community is central to an understanding of ecological systems. To assess the interactions that exist between member species it is helpful to analyse guilds, because interactions are expected to be most pronounced in a group of animal species which feed on the same plant species or exploit similar plant tissues.

Species richness of herbivorous insects was shown to be mainly influenced by habitat heterogeneity, plant distribution and abundance, plant architecture, taxonomic isolation and the host plant's life history (annuals versus perennials) (for reviews see Crawley 1983; Zwölfer 1987).

In addition, known determinants for the subset of insects found on a plant population (= species packing) include plant texture (Kareiva 1986), habitat topography (Strong et al. 1984), degree of interspecific competition (Zwölfer 1980), dispersal power of the insects (Price 1983) and natural enemies (Lawton 1984).

In a recent review of insects associated with Cardueae flower heads, Zwölfer (1987) found the number of regions sampled and species packing to be the most important factors determining species richness. The host plant speciation rate (inverse of taxonomic isolation) and host plant type were most important in predicting average species packing.

In this study, field observations on the insect guilds associated with the roots of three *Centaurea* species in Europe are described. Flower heads and root of Cardueae show similar ecological features. Both represent closed and limited units, which are structured into several distinct tissues. Herbivores which exploit the flower heads or roots show similar feeding strategies, since they are concealed within the plant and are relatively immobile. The structural diversity and species interactions of the flower head and root-feeding guilds are, therefore, expected to be similar.

Following the predictions of plant apparency theory (Feeny 1976; Rhoades and Cates 1976), and assuming an even distribution of grazing pressure among herbivore species, Lawton and Schroeder (1977, 1978) formulated the hypothesis that generalist species should be more abundant on rare and annual plants than on common and perennial species. In this study certain characteristics of the three knapweed species render them rather "unapparent" and "unpredictable" as hosts according to the general terminology of plant apparency theory. This includes being small, short lived, early successional colonizers, with patchy distri-

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* *Present address and address for offprint requests:* Zoologisches Institut der Universität, Rheinsprung 9, CH-4051 Basel, Switzerland

butions (Schroeder 1985), which is especially true for the western distribution of spotted knapweed (Müller 1984). We might expect, therefore, a predominance of generalist feeders to be associated with the roots of these knapweeds.

The relationship between species packing (number of species per population) and infestation rates (percent of roots attacked, a crude measure of resource utilization, cf. Zwölfer 1985) is of interest in ecological theory as well as for biological weed control. The predictability and the factors influencing the level of resource utilization by herbivores, however, are only poorly understood (Crawley 1983). The isolated position of the root as the only subterranean plant part and the associated species-rich herbivore complex makes this system a suitable object to study these questions.

The present study was carried out between 1979–1984 as part of a faunistic survey initiated by the Commonwealth Institute of Biological Control (CIBC) in 1977. The objectives were to investigate the insect species associated with the roots of spotted and diffuse knapweed, *Centaurea maculosa* Lam. and *Centaurea diffusa* Lam. and the closely related *C. vallesiaca* Jordan in their native range in Europe in order to assess their suitability as potential biological control agents for *C. maculosa* and *C. diffusa* 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 northwestern United States (Harris and Myers 1984). As a result of this survey and of host specificity studies and experiments to assess the efficiency of selected species, three moths (*Agapeta zoegana* (L), *Pelochrista medullana* Stgr. and *Pterolonche inspersa* Stgr.) and a weevil (*Cyphocleonus achates* Faber) were recommended for introduction into North America (Gassmann et al. 1982; Müller et al. 1988a; Müller et al. 1988b; Stinson 1987).

This paper presents and discusses field observations on 1) the species composition, dispersion, species associations and attack levels of the root entomofauna associated with the three knapweeds in Europe, 2) geographic variation in guild structure, and 3) it compares the root feeding insect guilds of *C. maculosa* with data given on the flower head infesting insects by Zwölfer (1977). Experiments to test the presented hypotheses on species interactions presented above, and to study the impact of herbivors on resource allocation and population biology of these knapweeds are being carried out and will be reported in a subsequent paper.

Natural history

Centaurea maculosa is a biennial or a short lived perennial, comprising several subspecies ranging from western Asia to western Europa (Dostal 1976). This study treats only the widely distributed, diploid ($2n=18$) populations of *C. maculosa* ssp. *rhenena* Boreau, typical of plant associations of continental dry habitats (Oberdorfer 1962). In the text below, the name *C. maculosa* will be used for this plant.

Centaurea diffusa is a biennial or triennial, East-Mediterranean plant occurring in western Asia, and from southern Russian to western Germany. It is a typical plant of the continental steppe and silvo-steppe vegetation in the eastern part of its geographical distribution.

In their western distribution area both knapweed species are mainly found in sites disturbed by human activities, such as areas along roadsides or in abandoned or overgrazed natural pastures. At such sites both species occur locally but often in quite dense stands.

Centaurea vallesiaca is taxonomically closely related to *C. maculosa* (Dostal 1976; Hess et al. 1972) and probably

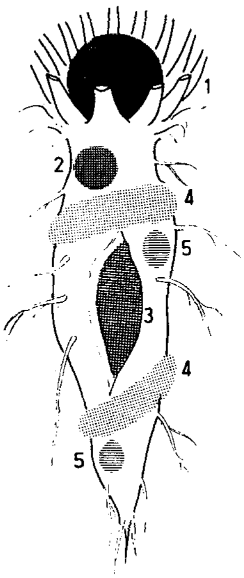
Root structures infested by phytophagous insect species	**Centaurea** **mac.**	**diff.**	**vall.**	**Feeding niches**
1. Central meristem of rosette				
Stenodes straminea Haw.	+	+	+	
Pegohylemyia centaureae Hennig	+	+	+	
2. Root collar				
Apion penetrans Germer	+	+	-	
Apion onopordi Kirby	+	+	+	
Apion orientale Gerst.	+	-	-	
Apion alliariae Herbst	+	-	-	
Cheilosia sp.	+	+	-	
3. Central vascular tissue				
Cyphocleonus achates Faber	+	+	-	
Cleonus piger Scop.	+	+	-	
Sphenoptera jugoslavica Ob.	+	+	-	
Pterolonche inspersa Stg.	+	+	-	
4. Root cortex				
Agapeta zoegana L.	+	-	-	
Pelochrista medullana Stgr.	+	+	-	
5. External on root				
Trama centaureae CB	?	+	?	
Sminthurodes betae Westw.	?	+	?	

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

occurs only in the Western Alps. It is mainly restricted to south facing, dry an stony slopes in the foothill zone (Hess et al. 1972).

The members of the phytophagous insect guilds associated with these host plants exploit different root structures. Figure 1 lists the more common insect species feeding in or on the roots of the three knapweed species and shows their larval food niches. Five food niches, each utilized by different insect species, can be distinguished.

1. Central meristem of rosettes: overwintering larvae of *Stenodes straminea* Haw. (Lep.: Cochylidae) and *Pegohylemyia centaureae* Hennig (Dip.: Anthomydae) feed in the center of the rosette, mine the bases of the rosette leaves, and often injure the apical meristem of the shoot. These larvae were never found in the actual tissue of the root (Müller 1983).
2. Root collar: small larvae of *Apion* spp. (Col.: Curculionidae) and of the syrphid fly, *Cheilosia proxima* Zett. feed externally on the root collar.
3. Central vascular tissue: this part of the root is attacked by the gallforming weevils *Cleonus piger* Scop. and *Cyphocleonus achates,* the gall-forming buprestid beetle *Sphenoptera jugoslavica*, and the pterolonchid moth *Pterolonche inspersa.* All hibernate as larvae within the tap root, except *C. piger,* which passes the winter as an adult in the soil.
4. Root cortex: *Agapeta zoegana* (Lep.: Cochylidae) and *Pelochrista medullana* (Lep.: Torticidae) develop in the root cortex, where the larvae feed beneath a silken web, but mine inside small roots or near the tip of larger tap roots. Both hibernate as larvae within their mines.
5. External on roots: Aphids and scavengers (5 Diptera spp., 1 Coleoptera sp, cf. Müller 1984) occur in this situation but were not investigated.

Material, methods and definitions

The survey of *C. maculosa* comprised a total of 110 samples taken at four sites in France, two in Germany, 15 in Austria and seven in Hungary. 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 two sites in Italy (Müller et al. 1988b). Most of the samples were collected in May and June and additional samples were taken at different time of the year. Each sample contained 50 to 100 randomly selected plants (see Whaba 1970). The roots with 5 cm of shoot were transported between slightly moistened layers of cellulose and packed in styropor boxes. Dissections and rearings were later made in the laboratory to assess to root feeding entomofauna. The term 'root' is used here to refer to the tap root including the root collar and the central meristem of the rosette.

Data were collected on plant associations, plant cover, soil type, host-plant phenology, and their density and vigour. A root sample formed the unit for our analyses and was assumed to represent a root population. In addition, 20–1000 attacked roots (depending on insect density and host plant availability) were collected for screening of host plant specificity and, later, for shipments to Canada. These roots were kept in cages between layers of moist sheets of cellulose at 23–25° C and 80–90% RH and checked daily for emergence of adult insects. Host records of the parasitoids were obtained from individually reared host larvae as well as from mass rearings.

Herbivore load is expressed as the average number of larvae per root, and is also referred to as level of attack. Species richness is defined as the total number of species associated with a host plant (i.e. total of all populations studied), and species packing describes the number of insect species per root population (sample). Guild structure is described by the degree of species packing, frequency of niche utilization and the level of species interactions. In addition, species diversity and frequency distribution of larvae and insect species are used to discuss concordance in guild structure between insects associated with the roots and the flower heads of *C. maculosa.* Frequency distributions of larvae and insect species were compared with Poisson series to assess possible deviations from a random distribution. Intraspecific aggregation of larvae on host plants is described by the simple variance/mean ratio ($s^2/\bar{x}$) (cf. Myers 1978 for discussion of aggregation coefficients). To assess this statistic, unattacked roots were counted as well. Interspecific association between species pairs was based on all sites at which both species occurred. Presence or absence data for each insect species in individual roots were obtained from dissections. A 2×2 contingency table and the corrected X^2 statistic were calculated (Southwood 1978).

The Shannon-Wiener diversity index (H_s) and the evenness (E) are used to describe alpha- and gamma-diversities. Since H_s is sensitive to species number (S) an the underlying model (Southwood 1978) the Berger-Parker dominance index (d), i.e., the highest relative species abundance is also used. Comparison of the diversity of insect species between geographical regions (*β*-diversities) is described by the quantitative Sorensen's coefficient (I_W) (Southwood 1978). Since species with extremely high relative abundances (which strongly influence I_W), were not present in the survey, I_W is a good description of the similarities between the regional root insect guilds. I_W was used to cluster populations based on their faunal composition, using the unweighted pair group method (UPGMA, Sneath and Sokal 1973).

Results and discussion

Species composition and species associations of the root entomofauna

Species richness. A total of 57 and 42 oligophagous species (i.e. restricted to Compositae) associated with *C. maculosa* and *C. diffusa*, respectively, are reported in the literature (Schroeder 1985). Approximately one third of these species attack the roots. However, only 34 insect species were found during field surveys carried out by the CIBC (1969–1979) on both plant species, of which 15 and 13 were associated with the roots of *C. maculosa* and *C. diffusa*, respectively (Schroeder 1985).

In my survey a total of 21 phytophagous insect species were associated with the roots of *C. maculosa,* 12 species with *C. diffusa* and 11 species with *C. vallesiaca*, 4 orders, 12 families and 22 species being represented. Omitting rare species (less than 5 individuals found) there remain only 14, 10 and 3 insect species for *C. maculosa, C. diffusa* and *C. vallesiaca*, respectively. The complete species list and records of two previous surveys are given in Müller et al. (1988b).

In contrast to the number of insects recorded for other Cynareae species in western and central Europe (Zwölfer 1965; Lawton and Schroeder 1978), the relatively high number of insects associated with *C. maculosa* and *C. dif-*

Table 1. Frequency distribution of insect larvae on host plants

Host plant	Centaurea maculosa			Centaurea diffusa			Centaurea vallesiaca		
					Percentage of				
Number of larvae/root	roots $n=3071$	attacked roots	larvae $n=1894$	roots $n=550$	attacked roots	larvae $n=185$	roots $n=577$	attacked roots	larvae $n=299$
0	67.0			70.9			67.2		
1	16.5	49.9	26.6	25.8	86.8	76.8	21.7	66.1	41.6
2	6.9	20.9	22.5	2.2	7.5	13.0	5.9	16.8	22.7
3	5.4	16.4	17.6	0.9	3.1	8.1	3.4	10.6	20.1
4	2.2	6.8	14.6	0.2	0.6	2.1	0.9	2.6	6.7
5	1.3	3.8	10.3	–	–	–	0.7	2.1	6.7
6	0.4	1.2	3.8	–	–	–	0.2	0.6	2.0
7	0.3	0.4	1.5	–	–	–	–	–	–
8		0.2	0.8	–	–	–	–	–	–
9		0.2	1.0	–	–	–	–	–	–
10		0.1	0.5	–	–	–	–	–	–
11		0.1	0.6	–	–	–	–	–	–
Mean number of larvae	0.61	1.86		0.34	1.16		0.52	1.58	
X^2, df, P^a	3641, 5, $P<0.001$			9.31, 3, $P=0.03$			110, 4, $P<0.001$		

[a] Comparison of frequency distribution of insect larvae on host plants (including unattacked plants) with a Poisson distribution; $P<0.05$, the intensity of herbivore attack is not independantly (randomly) distributed over the plants

fusa is rather striking. The species-area function and the large number of European species of *Centaurea* are probably the main reasons for the high value of insect species richness (Zwölfer 1987). The genus *Centaurea* contains the highest number of congenerics in the Cynareae (Polunin 1969); they show frequent hybridization in all geographical regions (Hess et al. 1972; Dostal 1976) and occupy a wide range of habitats (Dostal 1976). This interpretation is supported by the low number of insects (excluding rare species) found in and on the roots (3 species) and flower heads (5 species, K. Marquardt, pers. communication) on the geographically restricted *C. vallesiaca* populations. The obvious rosettes and the rich food resource offered by the roots during autumn and winter provide additional possible explanations for the high species richness on roots of these three knapweeds.

Specialist-generalist ratio. In this study, herbivores have been separated according to their feeding behavior into host plant specialists (restricted at least to a plant tribe) and generalists. The root feeding guilds contained 20, 22 and 23% generalists on *C. vallesiaca, C. maculosa* and *C. diffusa* ($n=10$, 19, 13, respectively); these were rarely encountered (Müller 1984). Specialist herbivores dominated the root-feeding insect complexes of the three knapweeds.

An evaluation of results of survey data, screening tests and literature records reveal a generally low proportion of generalists associated with the genus *Centaurea* as a whole in Europe; 30% of a total of 103 phytophagous species are generalists (H. Müller, unpublished data). If records not confirmed by field data are omitted, the proportion of generalist feeders drops to 13%.

To test their hypothesis derived from 'plant apparency theory' (Feeny 1976; Rhoades and Cates 1976), which postulates a predominance of generalists on rare and annual plants, Lawton and Schroeder (1978) analysed Zwölfer's (1965) field data (predominantly flower head infesting insects) on European Cynareae, but found no differences in the proportion of polyphages among annual/biennial and perennial host plant species.

My results are similar and, thus, fail to support the hypothesis of Lawton and Schroeder (1977). Futuyma (1976), Scriber and Feeny (1979) and Slansky (1976) reported similar results and discuss possible explanations for the greater prevelance of specialized feeders on relatively "unpredictable" resources. The high proportion of specialists associated with the roots of the three knapweed species may have additional explanations. Firstly, the knapweed rosette has a well developed tap root which offers a predictive, nutrient rich resource. Consequently, specialist feeders can become established on these knapweeds. Secondly, root-feeding requires special adaptations. An analysis of the root-feeding guilds by feeding type shows that the majority of species and individuals are miners and gallformers. The narrower host ranges of these two feeding types, compared to those of chewers and sap-feeders has often been described (see references in Lawton and Schroeder 1978). The minor importance of occasional feeders and generalists is, therefore, not unexpected.

Insect herbivore load and natural enemies. The frequency distribution of insect larvae within the roots is shown in Table 1. Approximately one third of the roots were attacked. Half of the *C. maculosa* roots, one third of the *C. vallesiaca* roots, and less than 10% of the *C. diffusa* roots contained more than 1 larva per attacked root. For all three plant species, the observed distribution of insect larvae on their host plants deviates significantly from a Poisson (random) distribution, with multiple attack overrepresented. Since the apparency and accessibility of individual plants to oviposition varies greatly, a true Poisson distribution can hardly be expected. Observed deviations may mainly be due to differences in plant size. The higher herbivore load (average number of larvae per root) in and on

Table 2. Frequency distribution of insect species

Host plant	C. maculosa	C. diffusa	C. vallesiaca
		Percentage of	
Number of insect species per root	roots $n=3071$	roots $n=550$	roots $n=577$
0	67.0	70.9	67.0
1	28.3	27.6	25.0
2	4.1	1.5	8.0
3	0.6	–	–
Mean number of insect species	0.39	0.29	0.41
X^2[a], df	11.18, 3	15.07, 2	7.07, 2
P	0.011	<0.001	0.029

[a] Comparison of the frequency distribution of insect species with a Poisson distribution

C. maculosa (100%) compared with *C. diffusa* (56%) and *C. vallesiaca* (85%), may simply reflect differences in the average root size. The average root diameters ($n=50$) for *C. maculosa, C. diffusa* and *C. vallesiaca* were 7.9 mm (SD 2.70), 5.7 mm (2.01) and 6.9 mm (2.34), respectively. Interference by a variety of other factors makes it extremely difficult to test this hypothesis under natural conditions. A positive correlation between root size and number of eggs laid by *S. straminea* was found for *C. vallesiaca* in the Swiss Valais (Müller, unpubl. data). However, 91% of potted plants containing more than three larvae in the autumn died during the winter, compared with no plant mortality at lower infestation levels (Müller 1983). Hence, field data collected in late spring before the emergence of overwintered species have to be interpreted with caution.

The frequency distribution of phytophagous species is shown in Table 2. The observed distributions depart significantly from a Poisson distribution. For *C. maculosa* and *C. diffusa,* observed values for multi species attack were slightly underrepresented, but attack by two species simultaneously was more common than expected on *C. vallesiaca.* 32% of attacked root of *C. vallesiaca* contained more than one insect species; the comparable figures for *C. maculosa* and *C. diffusa* are 14% and 5%. However, only 4.7%, 1.5% and 8% of the total roots of *C. maculosa, C. diffusa,* and *C. vallesiaca,* respectively, were occupied by more than one phytophagous species (Table 2).

At no site were more than 50% of the host plants attacked. Overall, less than one third of the roots examined were attacked, less than 17% contained more than two larvae and less than 8% contained more than one insect species. Possible causes of such apparently vacant niches will be discussed later.

Nine parasitoid species (mostly Ichneumonoidea spp.) were reared from *A. zoegana,* three species from *P. medullana* and four species from *S. straminea* (Müller et al. 1988b). No parasitoid species was found at more than six sites and in general parasitization of an individual species did not reach more than 15%. However, in one site in Hungary 45% of *A. zoegana* larvae were parasitized by *Chelonus intermedius* (Hym. Braconidae), an internal egg-larval parasitoid, and parasitism by ichneumonoid wasps reached up to 45% in some populations of the weevils *Cyphocleonous achates* and *Cleonus piger.*

As parasitization and predation was studied only in late larvae and pupae, their role in structuring the studied root insect guild remains unknown. As root feeders are difficult to locate, they generally have few parasitoids (Hawkins and Lawton 1987). This study shows however that egg-larval parasitoids may reach high numbers, at least locally.

Intra- and interspecific insect associations. Table 1 and 2 show that 73% of the larvae lived together with another competing individual on roots of *C. maculosa,* 58% on *C. vallesiaca* and 23% on *C. diffusa,* but that multi-species attack is a relatively rare event. An overview of the spatial distribution pattern of the more common species is given in Table 3. Interpretation of these data is difficult, because important factors such as oviposition patterns, natural enemies, competition and the impact of insect attack on host plant survival are little known.

The three coleopterans *Cleonus piger, Cyphocleonus*

Table 3. Attack levels and dispersion for the more common root feeders on *Centaurea maculosa C. diffusa* and *C. vallesiaca*[a]

	max *n* larvae/root	mean level of root attack (%) (min-max)	*n* larvae/attacked root $\bar{x}$(SD)	dispersion[c] $s^2/\bar{x}$; $\bar{x}$(SD)	distribution (with increasing insect density)
Agapeta zoegana	11	25.1 (7–40)	1.97 (0.29)	1.76 (0.73)	slightly clumped
Stenodes straminea	5	21.5 (7–33)	1.63 (0.59)	1.93 (0.23)	slightly clumped
Stenodes straminea[b]	17	46.7 (10–56)	2.56 (0.27)	3.02 (0.55)	
Pelochrista medullana	3	15.9 (4–41)	1.10 (0.07)	0.98 (0.04)	random-regular
Pterolonche inspersa	4	28.8 (1–45)	1.32 (0.08)	1.13 (0.16)	random
Apion spp.	25	26.7 (3–48)	3.12 (1.89)	6.13 (1.5)	clumped
Cleonus piger	3	12.5 (2–32)	1.08 (0.11)	0.91 (0.05)	random-regular
Cyphocleonus achates	4	11.0 (7–14)	1.10 (0.21)	1.19 (0.07)	random-regular
Sphenoptera jugoslavica	2	9.8 (1–25)	1.02 (0.02)	0.84 (0.08)	random-regular
Pegohylemyia centaureae	3	8.08 (2–25)	1.08 (0.12)	1.06 (0.11)	random
Cheilosia proxima	7	3.7 (2–4)	3.5 (2.08)	4.23 (2.71)	clumped

[a] all sites with the studied species present were pooled, data are from overwintered roots collected in June

[b] data from roots collected in october

[c] unattacked plants are included

Table 4. Joint occurrence (site) and interspecific association (root) of the studied insect species

A	B									
	PM	AZ	SS	PI	CP	CA	AP	SJ	PC	CH
Pelochrista medullana	—	0.17[a] *[b]	0.18 obs.	0.33 obs.	0.63 obs.	0.28 obs.	0.30 *	0.33 *	0.08 ∅	0.50 obs.
Agapeta zoegana	0.18 *	—	0.29 *	0.22 +	0.38 *	0.14 +	0.39 *	0.17 obs.	0.08 obs.	0.50 obs.
Stenodes straminea	0.18 obs.	0.42 *	–	0.33 obs.	0.13 obs.	0.0	0.39 *	0.17 ∅	0.83 *	0.25 ∅
Pterolonche inspersa	0.27 obs.	0.17 +	0.18 obs.	—	0.38 obs.	0.28 obs.	0.26 *	0.50 —	0.25 obs.	0.50 obs.
Cleonus piger	0.55 obs.	0.25 *	0.06 obs.	0.33 obs.	—	0.0	0.30 *	0.50 ∅	0.08 ∅	0.50 obs.
Cyphocleonus achates	0.27 obs.	0.17 +	0.0	0.22 obs.	0.0	—	0.13 *	0.33 ∅	0.0	0.25 ∅
Apion spp.	0.64 *	0.75 *	0.53 *	0.66 *	0.68 *	0.57 *	—	0.67 *	0.58 *	0.50 obs.
Spenoptera jugoslavica	0.27 *	0.08 obs.	0.06 ∅	0.33 —	0.38 ∅	0.28 ∅	0.17 *	—	0.0	0.25 ∅
Pegohylemyia centaureae	0.18 ∅	0.08 obs.	0.59 *	0.22 ∅	0.13 ∅	0.0	0.30 *	0.0	-	0.25 ∅
Cheilosia proxima	0.18 obs.	0.17 obs.	0.06 ∅	0.33 ∅	0.25 obs.	0.14 ∅	0.09 obs.	0.17 ∅	0.08 ∅	—
Sites ($n=37$)	11	12	17	9	8	7	23	6	12	4

[a] A occurs at x % of all sites where B is present

[b] *interspecific association*: * random; — negative; + positive. Not enough data for statistical analysis: obs. observed; ∅ not observed

achates and *Sphenoptera jugoslavica*, which cause a gall-like enlargement of the roots (Shorthouse and Müller, in prep.), show a tendency towards a more regular distribution with increasing insect density (Table 3). The lack of plants with roots large enough to sustain more than one larva, cannibalistic behavior (frequently occurring in mining Coleoptera (Zwölfer 1976)) and the inability of young larvae to penetrate into the central cylinder as the gall tissue develops (eggs are laid singly) are probable explanations for this pattern. Up to 13 larvae of *P. inspersa* were found feeding in the central root cylinder, but without causing a gall. Its larvae were in general slightly clumped. Eggs of the three moths, *A. zoegana, S. straminea* and *P. medullana* are laid singly or in small batches on the rosette leaves. The larvae of both *S. straminea* and *A. zoegana* showed a slightly clumped distribution (Müller 1983, Müller et al. 1988a), whereas those of *P. medullana* were mostly found singly. In laboratory experiments older larvae injured smaller ones providing direct evidence for intraspecific competition between *P. medullana* larvae. The species attacking the root cortex, *Apion* spp. and *Cheilosia proxima* both showed a clumped distribution, most probably as a result of their oviposition behaviour.

The joint occurrence of two species at a site is shown in Table 4 (upper value in each cell). Only three of the 45 possible combinations were not observed. Two of these concern the rare species *P. centaureae*. The niche competitors *C. piger* and *C. achates* (Fig. 1) were never found at the same site, although they occur at ecologically similar localities in the same geographic region. No local differences in autecological requirements between these two closely related and similar weevil species could be determined. The same result was found during extended surveys carried out recently by the CIBC (Stinson 1987). Beside direct competition (interference or exploitation), competition for enemy-free space may also play a role in the observed habitat segregation between *C. achates* and *C. piger*, as they share two insect parasitoids, the ichneumonid wasp *Aritranis fuscicornis* Tschek. and the barconid wasp *Vipio tentator* Rossi, which locally parasitize up to 45% of larvae (Stinson 1987). If one species is already present, these parasitoids may prevent the colonization of a second species at a site.

Interspecific associations, i.e. the joint occurrence of a species pair on the same root, are also recorded in Table 4 (lower part in each cell). Most of the associations were random, but there were too few data available for statistical analysis. A positive interspecific association was found between *A. zoegana* and *C. achates* and between *A. zoegana* and *P. inspersa*; all three species hibernate as larvae within the tap root. The selection of larger rosettes for oviposition by *C. achates* (Stinson 1987) and the progressive dying during winter of the smaller plants attacked is a possible explanation for the observed pattern. No such positive association for *A. zoegana* was found with *C. piger*, which occupies the same feeding niche as *C. achates*, but overwinters as adult in the soil. The only negative association was found between the moth *P. inspersa* an the beetle *S. jugoslavica* on *C. diffusa* in Greece (G. Campobasso pers. communication).

Table 5. Relative species abundancies, attack levels of host plants and species diversities in various geographical areas

	Relative abundance of insect species[a] (attack rates of host plants in %)						
	Centaurea maculosa					C. diffusa	C. vallesiaca
	E-Rumania	C-Hungary	E-Austria NW-Hung.	C-Austria	Alsace (FRG, F)	E-Rumania	Swiss valais
Lepidoptera							
Agapeta zoegana		0.133 (4.0)	0.193 (12.0)	0.259 (8)	0.134 (2)		
Stenodes straminea		0.047 (1.7)	0.13 (1.0)		0.547 (10.0)		0.456 (34.0)
Stenodes meridiana	0.265 (11.5)						
Pelochrista medullana	0.179 (12.0)		0.045 (5.0)			0.392 (14.8)	
Pterolonche inspersa		0.233 (10.3)	0.003 (0.3)				
Coleoptera							
Cleonus piger	0.130 (1.0)	0.037 (2.2)	0.049 (6.0)			0.154 (6.3)	
Cyphocleonus achates	0.066 (5.0)	0.034 (2.0)		0.133 (8.0)		0.127 (5.2)	
Apion penetrans	0.381 (9.5)	0.226 (4.3)	0.241 (9.5)	0.149 (9.0)	0.104 (1.0)	0.202 (2.7)	
Apion onopordi		0.236 (4.5)	0.316 (12.5)	0.305 (6.0)	0.104 (1.0)	0.053 (0.7)	0.453 (17.5)
Apion orientale			0.025 (1.0)	0.154 (3.0)			
Sphenoptera jugoslavica	0.096 (7.0)					0.046 (1.8)	
Diptera							
Cheilosia proxima		0.030 (0.5)	0.113 (4.0)			0.026 (0.3)	
Pegohylemyia centaurea		0.024 (1.3)	0.004 (0.5)		0.111 (3.0)		0.089 (10.0)
sites (n)	2	6	4	2	8	7	4
samples (n)	5	10	10	5	10	18	16
roots dissected (n)	300	600	1200	600	750	1450	2400
roots infested (%)	20	30	31	22	14	27	23
Phyt. spp./site total	6	9	10	5	5	7	3
$\bar{x}$	2.6	3.4	4.1	3.0	2.5	2.1	1.8
min-max	2–4	2–5	1–9	2–5	2–4	1–4	1–3
No. of lavrae/100 roots	77.6	59.3	123.4	61.1	29.8	41.6	121
No. of larvae/infst. roots	2.6	2.6	3.5	1.9	2.0	1.4	3.7
Hs (species diversity)	1.49	1.86	1.75	1.55	1.31	1.63	0.93
E (evenness)	0.83	0.85	0.76	0.96	0.82	0.94	0.85

[a] The Berger-Parker Dominance Index (d) for regional insect abundance is underlined

Geographic variations in guild structure: species diversities, species packing and infestation rates

Regional importance of the root insect species. The two small weevils *A. penetrans* and *A. onopordi* were numerically the most important species on *C. maculosa* (Table 5). The moths *P. medullana* and *S. straminea* dominated the root insect guilds on *C. diffusa* and *C. vallesiaca*, and on *C. maculosa* in Alsace. Moths represent in four regions the most common species and in the remaining four areas they were the second most common species after the pooled *Apion* species. Thus, all local guilds are dominated by specialists and most of these species are found on both *C. maculosa* and *C. diffusa*, and often in several isolated regions. According to Fox and Morrow (1981) it is likely that local specialization is a common property of more generalized (oligophagous) herbivores. It would be worthwhile to study the possibility of different ecotypes (host races, geographic races) with regard to the introduction of the most suitable for biological control (Müller 1988a). For example in E. Romania, where this moth is trivoltine, *A. zoegana* was found only on isolated stands of *C. arenaria* growing on sand dunes, and never on *C. maculosa* and *C. diffusa*. However, *A. zoegana* is an important feeder on *C. maculosa* in Hungary, where it is bivoltine, in Austria, where it is partially bivoltine, and in Alsace, where it is monovoltine (Müller et al. 1988a).

Regional species diversities and their similarities. The number of insect species, species composition and infestation levels varied greatly between the different geographic areas investigated. Values for species diversities and evenness, however, document a relatively even distribution of the insect species within each region (Table 5). The fact that 45% (25–76%) of the total individuals were Lepidoptera species and 40% (21–61%) *Apion* spp. is the reason for the moderate dominance values (d: 0.31–0.55).

Beta-diversities between host plants and between geographical regions (Sorensen's similarity coefficients I_S, I_W) were computed and a dendrogram, based on a cluster analysis (UPGMA) of I_W is presented in Fig. 2. Corresponding guild parameters are given in Table 5. The dendrogram reveals four groups. 1) The Alsace region was characterized by generally low values for species packing, infestation levels and species diversity. 2) the *C. vallesiaca* root guild reached high incidence and level of attack despite its fewer

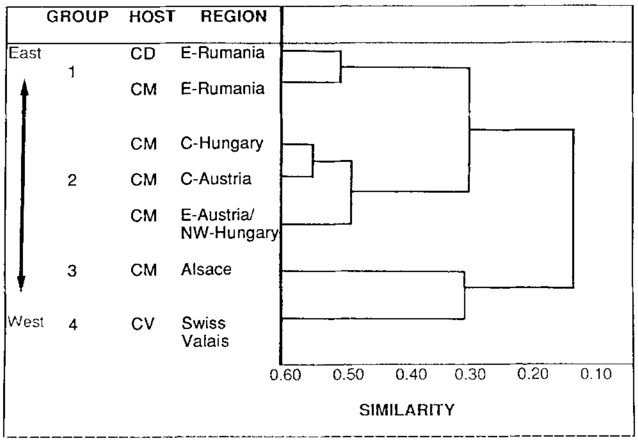


Fig. 2. Dendrogram based on the species composition of the root entomofauna on *Centaurea maculosa* (*CM*), *C. diffusa* (*CD*), and *C. vallesiaca* (*CV*) in different regions (β-diversities were determined with the qualitative Sorensen's coefficient for similarity and the populations clustered using UPGM)

component herbivore species and the fact that two food niches, the root cortex and root cylinder, remained unattacked (Table 5). The two isolated western areas are weakly related, but are distinctly separated from the other two groups. 3) The high similarity between the Romanian *C. maculosa* and *C. diffusa* root feeding complexes is the reason for the previously discussed similarity in species composition between these two plants. Both guilds showed intermediate values for structural and numerical parameters. 4) The central regions, especially E. Austria/NW. Hungary, showed the highest values for species packing, species diversities, food niche utilization, host plant attack and infestation levels for the *C. maculosa* populations studied. The central European position of these regions (combined in group 3) and the transitional, temperate continental climate facilitates the occurrence of east European species (*P. medullana*), along with south-east European ones (*P. inspersa, C. achates*), as well as the more western ones (*S. straminea*).

Biogeographical history may, however, also be partly responsible for the high species richness of specialized root feeders on *C. maculosa* in eastern Austria/north-western Hungary. During the Pleistocene glaciations, the vegetation from the east edge of the Alps to western Hungary was, according to Frenzel (1964, 1968), dominated by species rich herb-steppes. During this period, huge layers of loess were deposited in this region, causing a tree free zone. The Austrian loess steppe was characterized by species typical of dry grassland associations existing today (Frenzel 1964). This forest- and permafrost-free region is thought to have been one of the essential sites of retreat for Tertiary plant species during the last glaciation period.

Species packing and infestation rates. The data were arranged according to regions and habitat type. Habitats were separated into more natural and stable types, such as dry grassland and steppic vegetation and permanent sheep pastures, and disturbed, ephemeral and less predictable habitats such as roadsides, embankments and gravel pits.

No correlation between species packing and infestation rate was found for the *C. maculosa* sites in each of the different regions (Table 6). *C. vallesiaca* and *C. diffusa* were only sampled in one region where, in contrast to the *C. maculosa* regions, they occured predominantly in more stable habitats. A slightly positive correlation was also found for all *C. maculosa* sites combined, as well as for mean values of the five *C. maculosa* regions.

However, when the spotted and diffuse knapweed sites were grouped according to habitat type, a highly positive correlation was found between species packing and infesta-

Table 6. Correlations (r_S) between species packing (number of phytophagous root insects/sample) and infestation rates (% of attacked roots) and knapweed density, for regions and habitat types

Host plant[a]		*n*	spp. packing of insects	% plant attack	r_S[c] for r_S	*P*-value	plant density (plants/m^2)
Regions							
CM	Alsace	10	2.5 ab[d]	13.5 a	0.14	0.6736	0.82 a
CM	C-Austria	5	3.0 ab	22.0 ab	0.54	0.2795	0.14 b
CM	E-Aust/W-Hung.	10	4.1 b	30.7 b	0.21	0.1336	0.72 a
CM	C-Hungary	10	3.4 b	29.8 b	−0.04	0.9162	0.95 a
CM	E-Rumania	5	2.6 ab	19.6 ab	0.45	0.3711	0.94 a
CM	total, all samples	40	3.2	23.7	0.51	0.0015	0.71 –
CM	all regions	5			$r^2 = 0.78$	0.0302	
CV	total, Swiss Valais	16	1.8 a	23.4 ab	0.66	0.0106	0.45 –
CD	total, E-Rumania	18	2.1 ab	27.3 b	0.58	0.0167	0.54 –
Habitat type[b]							
CM	natural, stable	18	3.4 a	25.4 a	0.73	0.0026	0.20 a
CM	disturbed, ephem.	22	3.0 a	22.3 a	0.34	0.1193	1.13 b
CD	natural, stable	7	2.0 a	25.6 a	0.91	0.0265	0.20 a
CD	disturbed, ephem.	10	2.2 a	28.5 a	0.38	0.2257	0.89 b

[a] CM: Centaurea maculosa, CV: C. vallesiaca, CD: C. diffusa

[b] see text for details

[c] r_S = Spearman rank correlation coefficient

[d] Mann-Whitney test, corrected for number of tests; means followed by the same letter are not statistically different at the 5% level

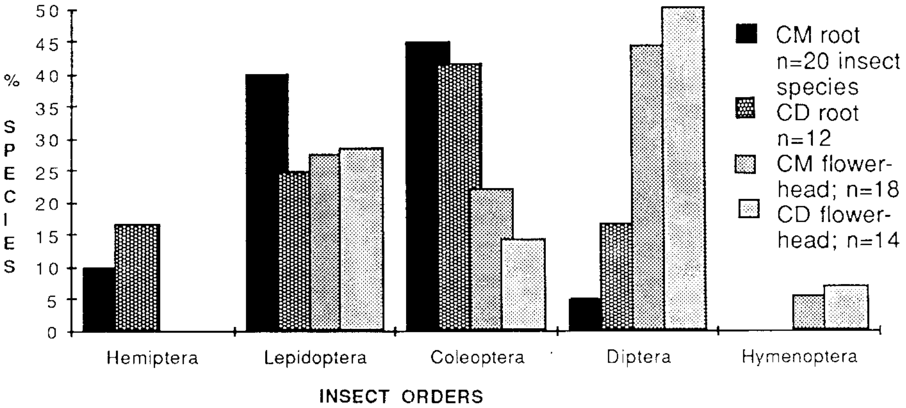


Fig. 3. Taxonomic composition of insect faunas on roots and flower heads of *Centaurea maculosa* (*CM*) and *C. diffusa* (*CD*) (Flower head data from Lawton and Schroeder (1978) who analysed Zwölfer's (1965) Cynareae data)

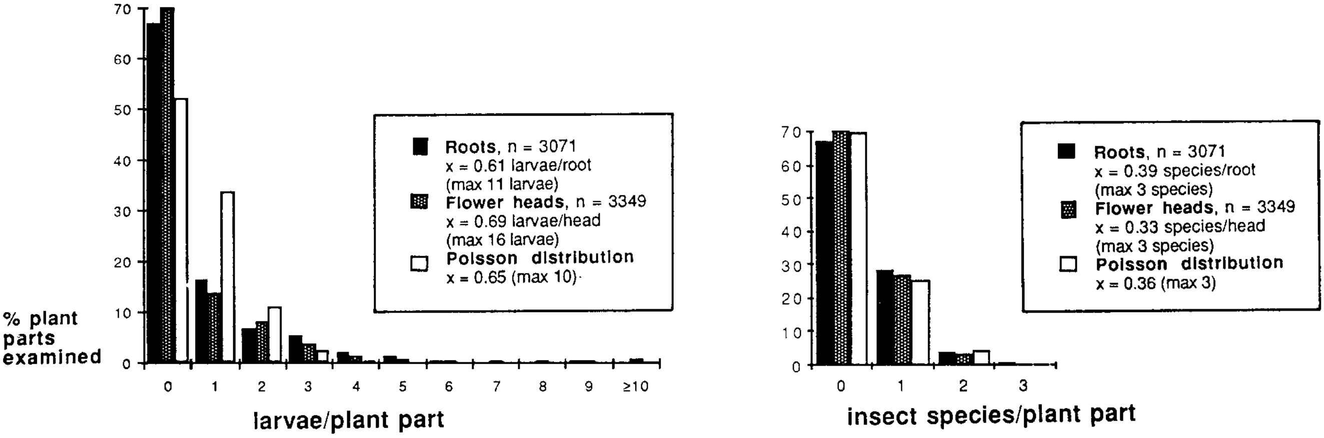


Fig. 4. Frequency distribution of larvae and insect species within roots and flower heads of *Centaurea maculosa* in Europe (Flower head data from Zwölfer (1977)

tion rate for the semi natural and more stable habitats, but no such relation was found for the ruderal sites (Table 6). From the point of view of biological control, multiple introductions into the dense and stable knapweed populations in North America should, therefore, lead to an increased herbivore pressure on these weeds. Values for species packing and incidence of attack did not differ between habitat types for either plant. Plant density was considerably lower in the more stable habitats (low density equilibrium) compared to the disturbed areas, where both knapweeds are early colonizing species and may occur at relatively high densities. In disturbed habitats, a high level of infestation was reached frequently by only a few insect species. Differences in the period of time available for species interactions (longer in stable habitats) and habitat specific prevalence of specialized natural enemies may partly explain these observations. Prasitization was distinctly higher in the more stable semi-natural (Müller 1984). Thus insects which colonize host plants in disturbed areas early may escape predation and temporarily build up higher populations.

Comparison of the regional root and flower head insect guild on Centaurea maculosa

Root insect data for *C. maculosa* were compared with corresponding results on flower head insects in order to test concordance in guild structure. Infestation data for flower head insects are taken from Zwölfer (1977), who made detailed studies between 1964 and 1973 in the areas studied during my survey.

Flower heads and root have several distinct tissues, which differ in structure, nutritional value and position (accessibility). Moreover, both structures are relatively closed systems for the immature stages of their exploiting herbivores. The role of temporal niches is in general less important for root herbivores than for flower head insects (Müller et al.1988b, Zwölfer 1988), as growth stages are morphologically and physiologically less distinct in roots than in flower heads. The rosette leaves are available for oviposition far longer than any developmental stage of the flower heads that may be required for successful oviposition. In addition, flower heads are more abundant and more apparent than roots, but the food resource available in a single flower head is smaller than in a root, although more easily accessible.

The taxonomic composition of root-feeding guilds of *C. maculosa* and *C. diffusa* is distinct from the flower head guilds (Fig. 3). The dispersal capacities of most of the root insects (six species of weevils), compared to flower head insects (eight tephritid species) are in general more restricted, as shown by results of releases of biological control agents in Canada (Harris and Myers 1984). Although both are taxonomically quite diverse, a high numerical and structural similarity between the root and flower head guilds was found; 80% of the flower head infesting larvae and 75% of the root-feeding larvae share their niches with at least one other competitor, and 14% of the infested roots and 11% of the infested flower heads contain more than one herbivore species. However, a simple pair-wise comparison using X^2 shows that the distribution of both larvae

Table 7. Numerical and structural parameters of regional insect guilds associated with the roots and the flower-heads of *Centaurea maculosa*

Region	Upper Rhine Valley	Swiss Rhone Valley	E-Austria[a] Hung/Slov[b]	E-Rumania[a] Bulgaria[b]
Number of samples	**10**[a]	**16**	**10**	**5**
	19[b]	13	19	2
% attack	**13.5**	**23.4**	**30.7**	**19.6**
(resource utilization)	47.1	20.1	31.6	10.0
No. of larvae	**29.8**	**121**	**123.4**	**77.6**
per 100 roots/fl. heads	80.9	25.2	89.8	14.9
n larvae	**2.0**	**3.7**	**3.5**	**2.6**
attacked root/fl. head	1.6	1.2	2.5	1.5
n species per site	**2.5**	**1.8**	**4.1**	**2.6**
(species packing)	2.7	2.6	3.9	3.5
n sub-niches $\sum = \mathbf{4}$	**3**	**2**	**4**	**3**
used $\sum = 6^{c}$	2	3	6	3
Total insect species in the region	**5 (5)**	**3 (3)**	**10 (8)**	**6 (6)**
(excluding rare[d] species)	7 (2)	9 (4)	10 (5)	4 (4)
H_S (species density)	**1.31**	**0.93**	**1.75**	**1.49**
	0.46	1.58	1.44	1.38
E (evenness)	**0.82**	**0.85**	**0.76**	**0.83**
	0.24	0.72	0.89	1.0

[a] root guild
[b] flowerhead guild; data from Zwölfer (1977)
[c] P. Harris and C. Stinson unpublished work
[d] species with less than 1% of individuals per regions

and insect species are significantly different between the roots and flower heads ($X^2 = 67.7$, df = 7 and $X^2 = 19.35$, df = 3, $p < 0.001$) and the observed distributions all depart significantly from a Poisson distribution (Fig. 4).

It is of interest to note, that values of average species packing, level of food niche utilization and regional infestation show a fairly similar ranking for both insect guilds, with the exception of the Upper Rhine Valley, where the fly *Urophora affinis* reached very high densities (Zwölfer 1977) (Table 7). In the flower head insect guild, the highest values for species packing and food niche utiliztion were also found in Eastern Austria/noth-western Hungary.

Conclusions

Root herbivory has been relatively ignored by ecologists, despite the accumulated literature in recent years on plant-herbivore interactions (Crawley 1983, Andersen 1987). No comparable data on root-herbivore guilds are, therefore, available.

The tap roots of the knapweeds studied constitute a relatively closed "arena", which can be divided into 5 structurally distinct food niches, each exploited by a sub-set of the root entomofauna. With regard to feeding type, three different types of interactions between species pairs can be distinguished: 1) Food niche competition and additional substrate modification via gall-formation by at least one of the competitors. This may result in habitat exclusion (*C. achates* - *C. piger*) or displacement (*S. jugoslavica* - *P. inspersa*), possible through (interference or exploitation) competition, or indirect competition for enemy free space. These species in general show a more regular distribution of larvae with increasing insect density. 2) Food niche competition without habitat deformation (*P. centaureae-S. straminea, C. piger-Apion* spp., *A. zoegana-P. medullana*) seems to be of minor importance (Müller et al. 1988a). These larvae generally occurred slightly clumped. 3) Species which develop in different tissues of the root coexisted randomly or showed positive associations (*A. zoegana-P. inspersa, A. zoegana-C. achates*). These were possibly the result of species-specific oviposition responses to larger rosettes. Hence, the high predictability in guild structure seems to be a result of a) food niche competition involving resource modification, b) resource segregation through larval associations to specific food niches and c) of probable species specific responses to rosette size for eviposition. When gall formation, similar phenotype preference for oviposition and food niche specificity all coincide for a species pair (which is the case for the two large weevils in the central part of the root), interspecific competition may well occur and explain the observed distribution pattern of these species. However, as only the effects of these interactions were studied, the mode of species interactions remains to be studied.

The taxonomic composition of the root feeders varied widely between sites, but climatic conditions, the time period of a species' presence in a region (distance from evolutionary center of origin or from a Pleistocene refuge (Goeden 1971, Wasphere 1974), and habitat type correlate well with the number of species (species packing) and the species diversity at a given site. The relatively low levels of host plant attack (two thirds of the roots were unattacked) and the fact that food niches remained unoccupied in most of the regions suggest, however, that the majority of the studied guilds do not represent equilibrium assemblages (Müller, in preparation). Even in some semi-natural habitats in Eastern Austria, where up to 9 species of root feeders coexisted and all food niches were occupied by at least two species, species numbers and abundances may not yet have attained a level to render interspecific competition of overall importantance. The low encounter rate for more than 2 species on a single root indicates that interspecific competition is generally low. Host plant characteristics, such as differences in morphology, phenology or chemistry, may in general be more important in determining species associations (Price 1983, 1984).

With regard to insect herbivores, flower heads and roots of *C. maculosa* have several ecologically relevant features in common. Althoug taxonomically quite diverse, the two guilds show much numerical and structural similarity, as well as a similar ranking of the geographic areas for some of the guild parameters assessed. Thus, this study provides evidence for a structural concordance of insect guilds associated with two different parts of the same plant species.

So far, five of the studied root feeders have been introduced into North America for the biological control of spotted and diffuse knapweed (Müller 1988a). Differences in the life cycle (Müller 1988b) and density (dense monocultures over large areas in North America) between spotted knapweed in Europe and the targed weed in North America, and the absence of specific enemies in the area of introduction should yield interesting, comparative data. These, together with the results of experiments on species interactions and their impact on plant performance, which are presently being carried out, should provide a better understanding of the mechanisms that affect the structure of these root guilds.

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