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Insects and Thistle Heads: Resource Utilization and Guild Structure

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Abstract

The relationship between resource utilization (percent of flower heads attacked) and 'species packing' (number of phytophagous species within a flower head sample) is investigated for 11 European Cynareae species. The correlation between these parameters depends on the trophic strategies realized within a phytophagous guild. The two most important trophic alternatives are: (1) formation of structural or physiological galls combined with an aggregated early attack; and (2) feeding on achene and receptacle tissues. Phytophagous species of type (1) can reach high levels of resource exploitation in autochthonous insect-Cynareae complexes and have been successful in biological control projects. In guilds where species of this type occupy a dominant position, an increase in species packing only weakly augments the level of resource utilization. In guilds without dominant phytophagous species the correlation between resource utilization and species packing can be high. The possible reasons for these differences and the implications for biological weed control are discussed.

Les Insectes et les Capitules de Chardons: Utilisation des Ressources et Structure des Communautés

Les complexes d'insectes phytophages et entomophages associés aux capitules des espèces de Cynareae forment des systèmes écologiques où le flux énergétique et les interactions entre des éléments simples peuvent être étudiés de façon approfondie. Par conséquent, ces complexes constituent des modèles appropriés pour l'analyse des interactions entre la diversité et la stabilité écologiques. L'auteur fournit et analyse des données sur les taux moyens d'utilisation des ressources par les insectes de Cynareae, sur la stabilité des systèmes insectes-Cynareae et sur la structure des communautés d'espèces phytophages. Le 'tassement' des espèces est, dans un grande mesure, fonction de l'évolution et des antécédents biologiques du système insect–plante, tandis que le degré d'utilisation des ressources dépend de la stabilité de l'habitat, de l'abondance et des possibilités de prévision des populations de plantes hôtes et du degré de prédation et de parasitisme. Les corrélations qui existent entre le 'tassement' des espèces et les niveaux moyens de consommation des ressources varient grandement. Des systèmes simples qui se sont établis au cours des projets de lutte biologique contre les plantes nuisibles (par example, *Rhinocyllus conicus* — *Carduus nutans*, *Urophora affinis*, et *U. quadrifasciata* — *Centaurea diffusa*) mettent en évidence des flux énergétiques plus importants et des effets plus notables des phytophages sur les populations de plantes hôtes que dans les systèmes autochtones présentant de vastes communautés d'insectes et des chaînes alimentaires complexes. Dans tous les systèmes insect-chardon qui ont fait l'objet d'études, l'élément 'contrôle des donneurs' (selon PIMM) est dominant, c'est-à-dire que les modèles de répartition spatiale, les modèles saisonniers de floraison et les réactions physiologiques des populations de plantes hôtes ont une fonction de contrôle par rapport à la dynamique des populations des insectes phytophages. Dans les complexes autochtones insectes-Cynareae, la compétition interspécifique pour la nourriture et l'espace nécessaire aux larves constituent un facteur dominant. Sur le plan de l'évolution, cette competition est à l'origine d'une structure caractéristique des communautés dans la grande majorité des complexes insectes-Cynareae. Chaque communauté possède des espèces qui disposent d'une 'stratégie d'attaque multiple au début de la floraison', ce qui favorise le transport des assimilés dans les capitules infestés; en outre, il existe des insectes granivores solitaires qui se sont souvent dispersés outre mesure et, finalement, un groupe d'insectes pouvant opérer à plusieurs niveaux trophiques.

Introduction

The relationships between the average resource utilization by a guild of phytophagous insects and the size and structure of this guild are of interest for the biocontrol of weeds as well as for the community ecologist. Flower heads of thistles and knapweeds (i.e. members of the tribe Cynareae of the Astereae) are suitable objects for a study of such relationships. Together with their complexes of phytophagous and entomophagous insects they form 'miniature ecosystems' where the energy flow and the interactions between single components can be investigated in detail. Moreover, the taxonomic and ecological diversity of thistles and knapweeds yields possibilities for a comparative approach.

In this contribution the following three questions will be discussed for European insect-thistle head systems: (1) How predictable is the degree of resource utilization by phytophagous insects for a given Cynareae species? (2) Which factors influence the level of utilization? (3) Which relationships exist between the level of resource utilization and the composition of the guilds of phytophagous insects associated with a population of thistle heads?

Materials, Methods and Definitions

Most of the data presented here have been collected from 1962–72 when I was in charge of the 'weed section' of the European Station (Delemont, Switzerland) of the Commonwealth Institute of Biological Control. Sponsored by the Canadian Department of Agriculture and other institutions an extensive inventory of European Cynareae insects (Zwölfer 1965) was carried out. It included about 60 Cynareae species belonging to the subtribes Carduinae, Centaureinae, Carlininae and Echinopinae. Data were obtained by field observations, large-scale rearings of flower heads, and dissections of flower heads under a binocular microscope. Since 1981 much additional material became available by an interdepartmental research project of the University of Bayreuth, W. Germany (SFB 137 'Gesetzmäβigkeiten und Steuermechanismen des Stoffumsatzes in ökologischen Systemen', Projektbereich A: 'Die Steuerung des Energieflusses und Wettbewerbsstrategien in Nahrungsnetzen mit Primärund Sekundärkonsumenten').

Random samples containing from 50–200 mature flower heads collected at a given date at one locality form the units of our investigation. They are referred to as '*flower head populations*'. The degree of '*resource utilization*' is measured by the percent of flower heads of a sample containing phytophagous insects or showing signs of insect attack. This measure is less precise than the calculation of destroyed achenes or insect biomass/head. However, it is positively correlated with these parameters and it is meaningful for biological weed control. The term '*species packing*' represents the number of phytophagous insect species found in dissections or rearings from single flower head populations. Gall midges were not counted for the calculation of species packing, as in many samples the ubiquitous fungivorous *Clinodiplosis cilicrus* Kieff. (Diptera: Cecidomyiidae) was not assessed separately from phytophagous species such as *Dasyneura* sp. (Diptera: Cecidomyiidae). Species packing must not be confused with '*species richness*' which means the total number of species associated with a host plant and which is a function of the observation area and/or the intensity of sampling (Lawton and Schröder 1978).

Resource Utilization and Species Packing

If the relationship between resource utilization and species packing is analyzed by scatter diagrams (Fig. 1) or by calculating regression and correlation coefficients (Table

1), considerable differences are found between single Cynareae species. In the great majority of the investigated plant species there exists a statistically highly significant correlation between these variables, but in *Cirsium vulgare* (Savi) Ten. and in *C. oleraceum* (L.) Scop. the correlation can statistically not be proved. The correlation coefficients vary widely: in *Centaurea solstitialis* L. the degree of species packing explains almost 85% of the variation in resource utilization; in *Centaurea scabiosa* L. 55% can be explained. In the remaining species, however, these values are much lower (Table 1). The slopes of the regression lines are highest in *Centaurea scabiosa, Cirsium arvense* (L.) Scop., and *Carlina vulgaris* L., moderately high in *Centaurea jacea* L., *C. solstitialis,* *Carduus nutans* L., and *Cirsium heterophyllum* Hill, and low in the remaining Cynareae species. The most striking difference is found in the intercepts: in one group (*Cirsium vulgare, C. oleraceum, C. heterophyllum,* and *Carduus nutans*) their values are high; in another group (*Centaurea maculosa* Lam. and *C. jacea*) they are moderately high; and in a third group (*Carlina vulgaris, Cirsium arvense, Centaurea diffusa* Lam., *C. solstitialis* and *C. scabiosa*) they are low. Between the intercepts and the average levels of resource utilization exists a positive correlation ($r = 0.6780$, $p < 0.05$), whereas the correlation between intercepts and the correlation coefficients of the analysed Cynareae species is negative ($r = -0.8208$, $p < 0.01$). Also with increasing intercept values the slope values

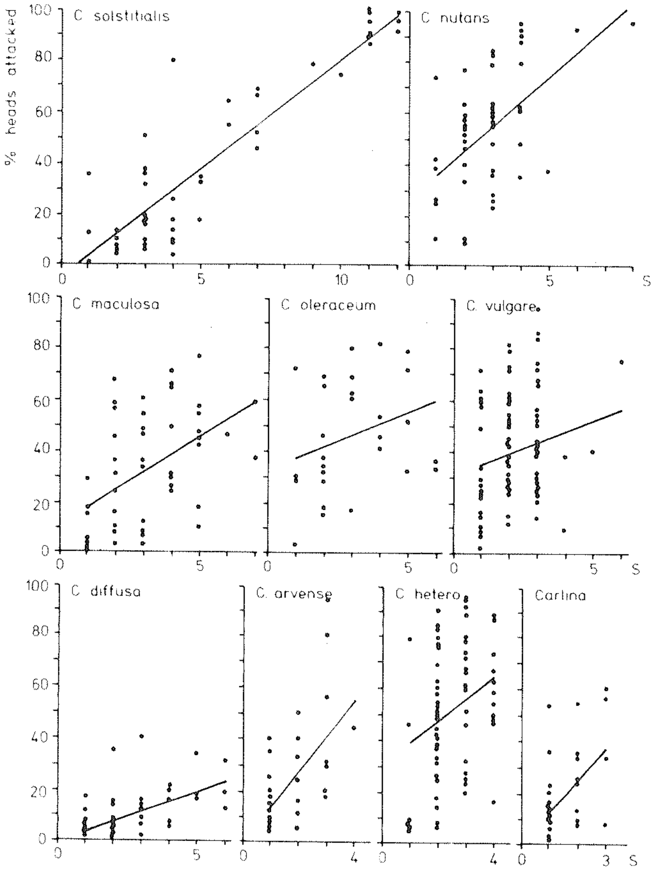

Fig. 1. Scatter diagrams of resource utilization plotted against species packing. S = species packing. Each dot represents a flower head population of 50–200 heads.

tend to decrease, but this relationship ($r = -0.5048$, $p < 0.1$) is statistically not significant.

These relationships can be interpreted in the following way: (1) In those insect–plant systems where one or two phytophagous species already reach a high average level of resource utilization (= systems with high intercepts), the effect of additional phytophagous species is relatively low (= systems with low slopes) and species numbers are a poor predictor of average resource utilization. (2) In insect–plant systems without clearly dominant phytophagous species (= low intercepts), the average level of resource exploitation increases with increasing values of species packing and the correlation between both parameters may be high; and (3) High values of resource utilization (attack of 90–100% of the flower head population) may be reached in systems with high species packing (*Centaurea solstitialis*) but also in systems with low species packing but highly dominant phytophagous insects (*Carduus nutans*, *Cirsium vulgare*, *C. heterophyllum*) (Fig. 1).

Table 1. Regressions of resource utilization on species packing (= S). n = number of flower head populations. Significance of the correlation coefficients: $^{+++} = P = 0.001$, $^{++} = P = 0.01$, $^{-} = P = 0.1$. A′ = resource utilization for S = 1. B = slope. $\bar{y}$ = average resource utilization. (Samples without phytophagous insects have not been included in the regression.)

System	n	r^2	A'	B	$\bar{y}$
Centaurea solstitialis L.	55	0.847^{+++}	4.5%	8.46	35.9%
C. scabiosa L.	60	0.562^{+++}	14.9%	13.81	32.0%
C. diffusa Lam.	63	0.387^{+++}	3.6%	3.94	8.6%
C. jacea L.	50	0.279^{+++}	16.3%	9.96	30.0%
C. maculosa Lam.	51	0.248^{+++}	17.8%	6.87	32.5%
Carduus nutans L.	48	0.311^{+++}	36.2%	9.46	54.6%
Carlina vulgaris L.	35	0.264^{++}	12.9%	12.11	18.7%
Cirsium arvense (L.) Scop.	36	0.334^{+++}	14.4%	13.60	24.3%
Cirsium heterophyllum (L.) Hill	74	0.092^{++}	39.4%	8.25	52.2%
C. oleraceum (L.) Scop.	30	0.087^{-}	37.8%	4.34	46.6%
C. vulgare (Savi) Ten.	94	0.178^{-}	35.6%	4.18	40.9%

Geographic Differences

In some insect–plant systems the prediction of the average resource utilization on the basis of species packing becomes more precise, if correlations are calculated separately for the main collection areas (Fig. 2). In *Centaurea solstitialis* the hypothesis that there is a common slope in the resource utilization–species packing regressions has to be rejected, but it cannot be rejected in the other species represented in Fig. 2. Statistically significant geographic differences in resource utilization levels occur in *Centaurea solstitialis*, *C. scabiosa*, *Cirsium arvense* and *Carduus nutans*, but not in *Centaurea diffusa* and *C. maculosa*.

Table 2 gives the coefficients of determination obtained in stepwise multiple regressions, where the variables ‘species packing’ and a geographic factor (‘region’) were used to explain the variations of the variable ‘resource utilization’. (The variable ‘region’ is the rank if regions are arranged according to increasing average resource utilization.) With the exception of *Centaurea diffusa* there is a statistically significant increase in the coefficient of determination if both variables are entered into the regression.

There are many possible causes for geographic differences in the levels of resource utilization by the phytophagous guilds of Cynareae flower heads. Differences in climates and habitats or in the stability and abundance of the host plant populations may be involved. In allochthonous insect-host systems; i.e. in situations where both the host plant and phytophagous species are introduced into another continent (e.g. in cases of successful biological control), absence of parasitoids and predators of the phytophagous species is certainly one of the reasons of an increased exploitation of the host plant. In autochthonous insect-host systems, both species packing and resource utilization can be a function of the evolutionary age (Price 1983) and of the biogeographic history of the insect–plant system. Sobhian and Zwölfer (1985) have shown this for *Centaurea solstitialis*, where the number of phytophagous species and the consumption rates of flower heads significantly increase from the western to the eastern Mediterranean.

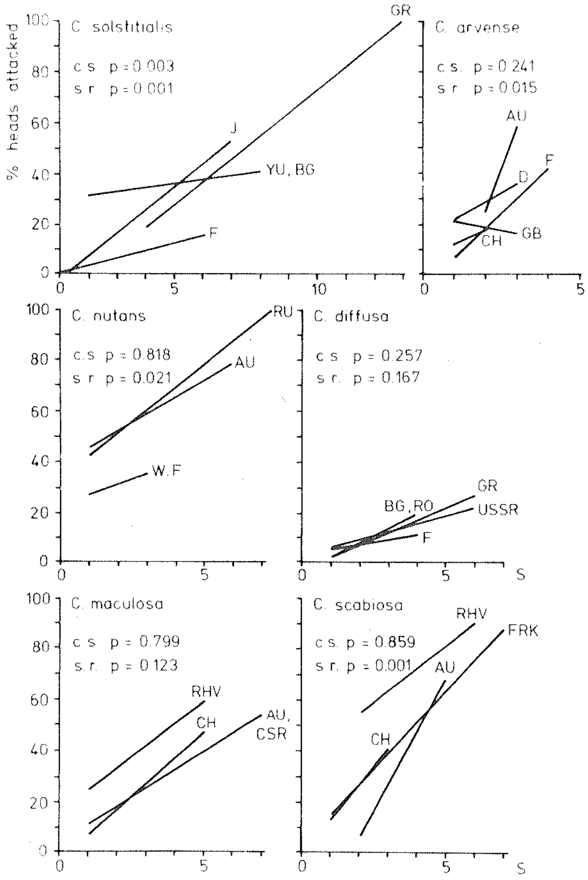

Fig. 2. Regressions of resource utilization on species packing calculated separately for geographic regions. c.s. = test for common slope (= O-hypothesis); s.r. = test for single regressions (O-hypothesis = no difference between regions); S = species packing; AU = eastern Austria; BG = Bulgaria; CH = Switzerland; CSR = western Slovakia; D = western Germany; F = France; FRK = Frankonia (w. Germany); GB = southern England; GR = Greece; I = southern Italy; RHV = Upper Rhine valley; RO = Rumania; USSR = Crimea, Caucasus; YU = Yugoslavia.

Taxonomic Isolation of the Host Plant

In contrast to Lawton and Schröder (1978), who could not show that 'taxonomic isolation' of Cynareae host species had a negative influence on insect species richness, Zwölfer (1982) demonstrated that there exists a statistically significant correlation between 'taxonomic isolation' (measured as the number of congeners of the Cynareae host) and 'species packing' (measured as the average number of phytophagous insects in a flower head population). Cynareae species in large genera tend to be exploited by more phytophagous species. The background of this phenomenon is discussed by Lawton and Price (1979). It can be explained by the fact that large Cynareae genera such as *Centaurea* or *Cirsium* have a broader pool of phytophages which facilitates host shifts and speciation. The level of 'species packing' obviously results from a stepwise recruitment of more or less specialized phytophagous insects, and this process requires both evolutionary time (Price 1983) and a reservoir of species predisposed to become associated with the plant. It is therefore plausible that species packing and usually also the level of resource exploitation is relatively low in Cynareae species belonging to small genera. As an example I have included *Carlina vulgaris* into my synopsis (Fig. 1). In Europe there exist only 12 species in this genus (as compared to 221 spp. in *Centaurea*, 60 spp. in *Cirsium*, 48 spp. in *Carduus*) (numbers from Tutin 1976). Cynareae species such as *Xeranthemum annuum* L. (3 spp. in the genus), *Echinops sphaerocephalus* L. (11 spp. in the genus), *Arctium lappa* L. (5 spp. in the genus), *Stachelina dubia* L. (5 spp. in the genus), *Galactites tomentosa* (L.) Moench (2 spp. in the genus), or *Silybum marianum* (L.) Gaertner (2 spp. in the genus) are other examples for low degrees of species packing in taxonomically isolated host plants (Zwölfer, unpubl. data).

Table 2. Coefficients of determination of regressions of resource utilization on the 'geographic factor' (= region), on species packing (= S) and on both 'region' and 'S' (= region + S). The 'geographic factor' represents the rank if observation regions are arranged according to increasing levels of resource utilization. (+) = Introducing the variable 'region' in addition to the variable S yields a statistically significant increase of the correlation coefficient.

System	r^2 (Region)	r^2 (S)	r^2 (Region + S)
Centaurea maculosa Lam.	0.083	0.248	0.339 (+)
C. diffusa Lam.	0.072	0.387	0.387 (−)
C. jacea L.	0.171	0.279	0.463 (+)
C. scabiosa L.	0.291	0.562	0.606 (+)
C. solstitialis L.	0.704	0.847	0.879 (+)
Cirsium arvense (L.) Scop.	0.289	0.334	0.423 (+)

Guild Structure and Resource Utilization

Wherever the insect complexes in Cynareae flower heads have been studied in detail (e.g. Varley 1947; Mellini 1951*a*, *b*; Zwölfer 1965, 1979; Redfern 1968; Eschenbacher 1982; Romstöck 1982; Angermann 1984; Michaelis 1984; Sobhian and Zwölfer 1985), it has been found that coexisting phytophagous species differ in parts of their ecological niches. If coexisting species belong to different families or orders (e.g. tephritids of the genus *Urophora* [Diptera: Tephritidae], gall wasps of the genus *Isocolus* [Hymenoptera: Cynipidae], and weevils of the genus *Larinus* [Coleoptera: Curculionidae]), they are exposed to different sets of parasitoids; i.e. to different mortality factors (Zwölfer 1975). Niche diversification is further increased by differences in: larval feeding habits (e.g. feeding in the receptacle, the ovarioles and maturing achenes); host ranges (stenophagous and euryphagous species); voltinism (univoltine and plurivoltine species); degree of larval aggregation (gregarious and solitary species); hibernation sites (within the flower head or outside); and so on. Thus, even if 12 phytophagous species coexist in a flower head population, as is the case with *Centaurea solstitialis* in Greece (Sobhian and Zwölfer 1985), the single members of the guild can be distinguished by traits of their life history, trophic strategies and mortality factors.

As concerns resource utilization, the most important niche difference is obviously that between gall-formers and species which feed without inducing gall formation. Gall-formers channel additional assimilates into the flower heads which they occupy, even if they do not cause a distinct structural gall as is the case with *Tephritis* spp. (Diptera: Tephritidae) in *Cirsium* heads (Romstöck 1982). As a rule, gall-formers are highly specialized in host selection: they oviposit early and, as there is only a short span during which oviposition is possible, they are dependent on strict synchronization with their host plants. As gall-formers can adjust the supply of assimilates of an individual flower head to the number of larvae occupying this head (Michaelis 1984; Romstöck 1982), they usually do not suffer from intraspecific competition. Therefore, they can afford to live gregariously within the flower heads of their hosts. Thus, the trophic strategy of the great majority of gall-formers associated with Cynareae heads is that of an 'early aggregated attack'.

Studies on the energy flow in flower head systems of *Cirsium vulgare*, *C. heterophyllum*, *Centaurea scabiosa*, and *C. jacea* have shown that this 'early aggregated attack' by single gall-former species accounts for 76% of the energy removed by the phytophagous guild from the flower head systems and transformed into larval biomass. This figure rises to 95% if the joules invested in lignified gall tissues are also taken into consideration (Zwölfer 1985).

Gall-formers with 'early aggregated attack' are the dominant phytophagous species in *Carduus nutans* (*Urophora solstitialis* F., *Rhinocyllus conicus* Froel. [Coleoptera: Curculionidae]), *Cirsium oleracum* (*Tephritis conura* Loew, *C. heterophyllum* [*Tephritis* nr. *conura*]), and *C. vulgare* (*Urophora stylata* L.). These species are responsible for the fact that in the respective Cynareae hosts, high levels of resource utilization are already reached with low values of species packing (= high intercepts of regression lines in Fig. 1).

From Fig. 1 it is obvious that in guilds with a dominant gall-former with 'early aggregated attack' the efficiency of additional species — usually solitary seed- and receptacle-feeders — tends to be lower and that the size of the guild tends to be smaller than if there are no dominant phytophages. The question arises: Which is cause and which is the consequence? Do dominant phytophagous species prevent other phytophages from reaching a higher efficiency? Or does a high degree of species packing prevent phytophagous species from becoming dominant? A definite answer must await the results of further analyses. The data presented here suggest for two reasons that the occurrence of dominant species may be rather a function of low species packing than a factor influencing it: (1) the regression of resource utilization on species packing of *Centaurea solstitialis* in the northern Balkan Peninsula (Fig. 2, 'BG,RO') demonstrates that there is a dominant phytophage. This is the tephritid *Urophora sirunaseva* (Her.) with a density of 37.2 ± 3.0 (mean and s.e., respectively) larvae/100 heads. *U. sirunaseva* is a gall-former with early and often aggregated attack, being comparable to the dominant *U. stylata* in *Cirsium vulgare* heads. *U. sirunaseva* also occurs in the Greek populations of *Centaurea solstitialis* with their unusually high degree of species packing (Fig. 2, 'GR'), but here it loses its dominant position (density 9.5 ± 3.6 larvae/100 heads) (Sobhian and Zwölfer 1985); and (2) So far the well documented cases of dominant phytophagous species reaching a high level of resource utilization in Cynareae heads refer to insect–plant associations in habitats of a post-Pleistocene age. This is particularly the case with *Cirsium heterophyllum* (Romstöck 1982), *Cirsium oleraceum* (Eschenbacher 1982), *Cirsium vulgare* (Redfern 1968; Michaelis 1984) and *Carduus nutans* and it has also to be assumed for the *Centaurea solstitialis* population in the northern Balkans. A span of less than 10,000 yrs may be enough for adapted phytophages to increase their specialization (Seitz and Komma 1984), but it is not sufficient for the accumulation of a large guild of phytophagous insects as occurred in the Greek populations of *C. solstitialis* occupying their sites for a much longer period.

Discussion

With regard to resource utilization, the insect communities in Cynareae flower heads can be arranged in three groups:

Group 1. Here, resource utilization as well as species packing is low (Fig. 3, lower third of the diagonally crosshatched area). Into this group fall host species which are taxonomically isolated (e.g. *Carlina vulgaris*) or allochthonous, geographically isolated host populations (e.g. west-European populations of *Centaurea diffusa*). Taxonomically isolated hosts are not (or only slightly) attacked by generalists and the specialized phytophages which we have observed so far on this type of host are mostly not very efficient as concerns resource utilization. Allochthonous host species, on the other hand, may be exploited by certain generalists but usually do lack specialists.

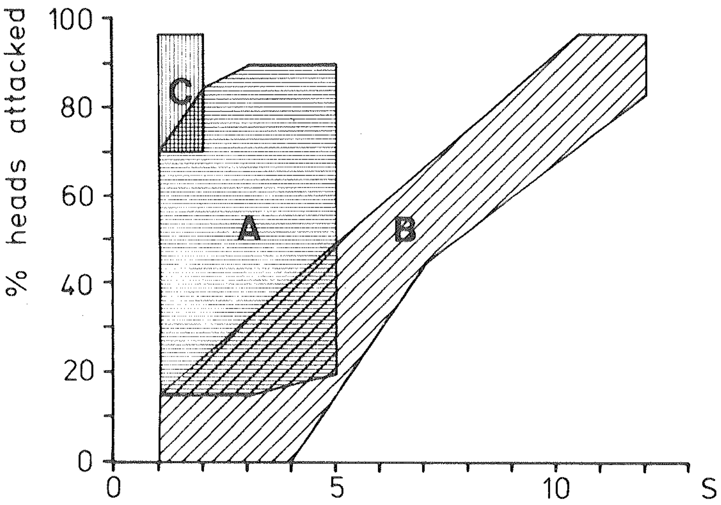

Fig. 3. Types of relationships between resource utilization and species packing (= S). A = Insect–plant systems with dominant phytophagous species. B = Insect–plant systems with correlations between resource utilization and species packing. C = Allochthonous insect–plant systems (successful biological control).

Group 2. In host species such as *Cirsium vulgare, C. oleraceum* or *C. heterophyllum*, resource utilization can be fairly high in spite of a low degree of species packing (Fig. 3, horizontally crosshatched area). The reason why these systems are undersaturated in species may be found in their post-Pleistocene origin; i.e. in an evolutionary relatively young age. The high level of resource utilization is mainly due to one or two phytophagous species belonging to a type which has also been successfully used in biological weed control. Such species form structural or physiological galls, attack the host in an early phase and usually exploit it gregariously.

Group 3. A high level of resource utilization has been reached in projects of biological weed control with one or two selected phytophagous species (Fig. 3, vertically crosshatched area). It also was found in the Greek populations of *Centaura solstitialis*; i.e. in an insect–plant system saturated in species (Fig. 3, upper third of the diagonally crosshatched area). In the case of biological control, well adapted phytophagous species can maximally exploit a host population, as they are not hindered by specialized natural enemies. In the case of east-Mediterranean *C. solstitialis* populations enough evolutionary time was available for the formation of a guild, the members of which fill almost all possible niches (Sobhian and Zwölfer 1985).

Efficient agents in the biological control of Cynareae (*R. conicus* against *Carduus nutans*, *U. stylata* against *Cirsium vulgare*, and *U. affinis* Frfld. against *Centaurea maculosa* and *C. diffusa*) commonly induce an additional supply of assimilates into the flower head and are fairly resistant against effects of interspecific competition. When used as biocontrol agents they may attack from 80–100% of the flower heads of a host population (Fig. 3). Harris (1980) and Myers and Harris (1980) have shown that in the case of *Centaurea maculosa* and *C. diffusa* heads, overall resource utilization is increased where two introduced species (*U. affinis* and *U. quadrifasciata* [Meig.]) exploit the same host population. This should encourage attempts in biocontrol projects to complement the effect of gall-formers of the type of 'early aggregated attack' by the introduction of selected seed feeders which exploit a later phase of the host and which are compatible with the gall-formers. Two problems are that such members of the phytophagous guilds of Cynareae heads are usually less specific, and that there are relatively few species suitable for biological control projects.

Our comparative study of insect complexes associated with European Cynareae hosts have shown that phytophages with 'early aggregated attack' only reach high levels of host utilization if they are genetically sufficiently adapted to a particular host species. In the weevil *R. conicus* this led to the evolution of host races (Zwölfer and Harris 1984) and in the tephritid *T. conura* to host races or sibling species (Seitz and Komma 1984). The geographic distribution patterns of these races and siblings suggest that this evolutionary process was slow and occurred only where abundant resources were available. Therefore the risk that introduced biocontrol agents would compromise the survival of endangered native North American *Cirsium* spp. seems negligible.

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