

# Herbivory and plant resource competition: a review of two interacting interactions

Peter A. Hambäck and Andrew P. Beckerman

Hambäck, P. A. and Beckerman, A. P. 2003. Herbivory and plant resource competition: a review of two interacting interactions. – *Oikos* 101: 26–37.

This review discusses the prevalence and potential for interactive effects between herbivory and competition on plant growth and biomass, and it is apparent that such effects typically arise when there is a mismatch between the spatial scale of herbivore behaviour (food or patch choice) and the spatial heterogeneity of the plant community. Historically, such interactive effects have been examined using two approaches. Studies using the first approach have excluded plant neighbors and herbivores in a factorial experiment, and scored effects on plant biomass. Studies using the second approach have observed herbivore abundance or herbivory on plants with or without plant neighbors, and have identified a large number of mechanisms underlying such interactive effects. The two types of studies have produced somewhat conflicting results, where interactive effects have been commonly observed in studies using the second approach and only rarely in studies using the first approach. This is most likely a consequence of a biased choice of study systems, where studies using the first approach have primarily studied mammalian herbivory while studies using the second approach have been more focussed on insect herbivory. Moreover, studies using the first approach have typically been very small-scale manipulations and this probably precludes most possible interactive effects in systems with mammalian herbivory. This points to the fact that studies examining interactive effects of herbivory and plant competition should more carefully consider the behaviour and life history of herbivores included in the study prior to the design of removal experiments.

*P. A. Hambäck, School of Forestry and Environmental Studies, 370 Prospect Street, Yale Univ., New Haven, CT 06511, USA. Present address: Dept of Ecology and Crop Production Science, SLU, P.O. Box 7043, SE-750 07 Uppsala, Sweden (peter.hamback@evp.slu.se). – A. P. Beckerman, School of Forestry and Environmental Studies, 370 Prospect Street, Yale Univ., New Haven, CT 06511, USA. Present address: Inst. of Biological Sciences, Univ. of Stirling, Stirling, Scotland FK9 4LA.*

Competition from plant neighbors and herbivory are two factors that determine the growth, survival and reproduction of plant individuals, and subsequently the abundance of plant populations (Harper 1977, Crawley 1983, Sheppard 1996, Gurevitch et al. 2000). Field observations further suggest that manipulation of plant neighbor and herbivore densities frequently have synergistic or substitutive effects on plant performance, e.g. when the removal of plant neighbors relax or intensify herbivory. The interactive effect of herbivory and plant competition may arise through two major routes. First,

rates of herbivory may increase or decrease when the abundance of plant neighbors, or some factor correlated with plant abundance, is altered (Root 1973, Holt 1977, Lubchenco 1978, Louda et al. 1990, Andow 1991, Trenbath 1993, Holt and Lawton 1994). Second, herbivory may increase or decrease the competitive effect of one plant on another through competitive effects on plant regrowth ability (Whitham et al. 1991).

This paper will focus on the empirical and theoretical background for such interactive effects. Each major route underlying interactive effects of herbivory and

Accepted 11 October 2002

Copyright © OIKOS 2003  
ISSN 0030-1299

plant competition on plant performance have been studied in many systems, and these studies have identified several potential mechanisms. However, few studies have evaluated the relative importance of different mechanisms, even for a single system. This is unfortunate as our ability to infer landscape patterns from small-scale experiments might vary with the specific mechanism. For instance, a small-scale observation of herbivores responding to shade-induced changes in plant quality could be easier to scale to larger spatial scales than a small-scale observation of herbivores affected by odor masking. A shade-induced change in plant quality can be expected to be consistent across small and large plots, whereas the odor signal from host-plants most likely increases non-linearly with plot size.

Most research to date on the interaction between plant competition and herbivory has employed one of two approaches to assess interactive effects. For simplicity, we will call the two approaches plant-based and herbivore-based, respectively. Studies using the plant-based approach identify the presence of interactive effects through an experimental design that manipulates neighboring plant and herbivore densities in a factorial experiment. The experimentalist then evaluates the null hypothesis of no process interaction by examining target plant performance. However, the specific herbivore responses to manipulations in these experiments are in most cases unknown. Studies using the herbivore-based approach identify the presence of interactive effects by comparing herbivory rates, or herbivore abundance, on focal plants in the presence or absence of plant neighbors of other species. While these herbivore-based studies provide important details about mechanisms underlying interactive effects, they provide little indication about consequences for plant biomass or fitness. Beside these methodological differences, the two approaches have reached somewhat conflicting conclusions: interactive effects have been more commonly observed in studies using the herbivore-based approach. We will argue that these differences arise because of systematic differences in the choice of study system between studies using the two approaches.

In this paper, we review studies using each approach and discuss possibilities to bridge the gap. First, we review all published plant-based studies. For these studies, we highlight the null-model choice and spatial scale and how these relate to the design and analysis of herbivore and plant neighbor exclusion experiments. Second, we provide an overview of herbivore-based studies. The aim of this section is different from the previous section as the focus is on identifying relevant mechanisms underlying the interactive effects of herbivory and plant competition on plant performance and how these depend on the spatial scale. Finally, we discuss how framing the question of interactive effects in a context defined by the scale that herbivores and

plants interact can be used to improve the design and interpretation of field experiments.

## A general model for investigating short-term interactive effects

The most general model describing effects of plant growth and herbivore consumption on plant biomass is (Rees and Brown 1992)

$$\frac{dB}{dt} = B(r(t) - n(t) - m(t)) \quad (1)$$

where  $B$  is the biomass of the target plant,  $r(t)$  is the relative growth rate of plants when alone,  $n(t)$  is the decrease in relative growth rate due to the presence of plant neighbors and  $m(t)$  is the relative loss rate of plant biomass caused by herbivory. Both  $r(t)$ ,  $n(t)$  and  $m(t)$  may vary over time and may be reclassified to account for any measure of plant fitness. In order to arrive at a useful null-model for the analysis of field experiments, it is necessary to express the change in plant biomass over time. For eq. (1), this is achieved by first integrating,

$$B_t = B_0 e^{\int_0^t r(u)du} e^{-\int_0^t n(u)du} e^{-\int_0^t m(u)du} \quad (2)$$

and then taking natural logarithms of both sides, i.e.

$$\ln(B_t) = \ln(B_0) + \int_0^t r(u)du - \int_0^t n(u)du - \int_0^t m(u)du \quad (3)$$

In the absence of interactive effects (the null hypothesis), the removal of plant neighbors affects only  $n(t)$  and the removal of herbivores affects only  $m(t)$ . Because effects of herbivore and plant neighbor removal on focal plant biomass in eq. (3) are additive, it is possible to analyse the presence of an interactive effect with a linear model. If the analysis indicate that herbivory and plant neighbor removal interact to affect plant biomass, i.e. the null-model is rejected, eq. (1) is no longer appropriate and the development of a more complex hypothesis explaining the interaction, and experiments testing this hypothesis, is called for.

This model requires log-transformed data. If residual distributions with log-transformed data invalidates the use of ANOVA, one could use a generalized linear model to retain the log-transformation. It is not advisable to use a different transformation to fulfil the residual assumptions of the ANOVA, as this becomes a test of an alternative model which may at best be uninteresting and at worst misleading. For the present example, using untransformed data (eq. (2)) may have

two unwanted consequences; interactive effects may appear significant even when they are not and the model may predict negative plant biomass (Wootton 1994). If the underlying model is unknown, the best advice is to log-transform the data as this transformation is connected to the most simple time dependent null-model.

The null-model described in eq. (3) is appropriate whether the response variable is individual plant biomass or plant biomass per unit area: the latter tests for a wider range of potential mechanisms that could cause interactive effects, e.g. density compensation. When testing for effects on reproductive output it is first necessary to establish the relation between plant growth and reproductive output before deciding whether the present null-model is appropriate. However, as there often is a strong allometric relation between size and reproductive output (Niklas 1994), eq. (3) should be useful in many cases.

### **Plant-based experimental studies: tests of the null-model**

To identify the majority of studies that manipulated neighboring plant and herbivore densities in a factorial experiment, we searched Biosis for combinations of “herbivor\$”, “plant competit\$”, and “removal”. We also located a few additional papers in the reference lists of previously found papers. Finally, we searched Science Citation Index for papers that cited previously found papers. This process generated 16 papers (for a combined total of 30 plant-herbivore systems) that involved a manipulation of neighboring plant and herbivore densities in a factorial experiment, and that reported either data for all treatments or relevant statistics (Table 1). In a few cases, several papers involved the same study objects and we then only included one paper. In other cases, the same paper reported repeated experiments on the same species and we then included the experiment with the intermediate effect size. The effect sizes were similar between experiments within a study, even though the study by Bonser and Reader (1995) suggest systematic changes along a plant biomass gradient.

The papers fall into two broad categories; 10 studies were manipulated field densities of plants and herbivores and 6 studies were constructed plant communities with fixed initial herbivore densities. The studies that used fixed initial herbivore densities by design exclude the possibility of several important interactive effects, i.e. numerical responses by herbivores to plant density, and are therefore not pertinent to evaluate the relative importance of different mechanisms. Finally, most if not all studies included in this review are exploratory and are not designed to test a specific theory.

### **Data transformation, underlying models and plot sizes**

In the review, we only include variables related to absolute plant size, as the model choice for other variables, e.g. biomass allocation, is less clear. In only two of ten studies, data transformation were based on an underlying model (Rees and Brown 1992, Willis et al. 1998); the other eight studies log-transformed their data on statistical considerations, and by default rather than design tested the model in eq. (3). It is notable that in a few cases, different transformations were used for different plant variables within the same study. As discussed in the section ‘a general model for investigating interactive effect’, observed interactive effects in studies using transformations other than logarithms are hard to interpret in the context of plant-herbivore theory.

Plot sizes in studies varied from 0.1 to 20 m<sup>2</sup>. The choice of plot size seemed arbitrary in all cases except one, the study by Taylor et al. (1997), that selected plot size based on an eye-ball assessment of plant variability. The choice of plot size is important as manipulations at different spatial scales affect behavioural and population processes differently. This is particularly important when testing a specific theory, where underlying assumptions defines the domain of the model (Englund 1997), but no study included in this review was designed for this purpose. However, an examination of animals studied and associated plot sizes (Table 1) suggests that the research this far has focused on mechanisms based on small-scale herbivore foraging decisions, as opposed to larger habitat or patch selection decisions and the possibility for numerical responses. The only exceptions may be Willis et al. (1998), that studied mites using a plot size of 1 m<sup>2</sup>, and Sork (1987), that studied mammal removals using a plot size of 20 m<sup>2</sup>. These plot sizes might be sufficient to affect habitat selection, growth or reproduction of the herbivore.

Another important attribute is the inter-plot distance affecting the independence of replicates. The significance of this to plant competition studies is discussed by Fortin and Gurevitch (1993, see also Freckleton and Watkinson 2000), but the attribute is even more important for studies with mobile herbivores (Clarke et al. 1995a, b). The results of a study could be confounded by interplot distance if the herbivore density in a plot depends on the proximity to a neighbouring plot, with another treatment, or if herbivores respond to the collection of plots and not only to single plots. The latter could be the case if study plots cover large parts of a field, and the matrix for one experimental plot is the other plots. Unfortunately, the inter-plot distances is only given for the study by Bonser and Reader (1995), and even then it is not possible to judge from the presented information if inter-plot distances are far

Table 1. List of studies examining interactive effects of plant neighbor and herbivore removals, and log response ratios calculated from each study (only studies measuring plant weight are included). The log response ratio for the interaction is positive when one factor tends to substitute the effect of the other, i.e. when the plant size is larger in the interactive treatment than expected from each treatment alone, and it is negative when the two factors act in synergy.

Reference	Source	Target <sup>a</sup>	Competitor	Herbivore <sup>b</sup>	Plot size (m <sup>2</sup> )	Log response ratios		
						C	H	H-by-C
Dormann et al. 2000	Fig. 1	<i>Artemisia maritima</i> <i>Atriplex portulacoides</i> <i>Plantago maritima</i>	Community	mammals	0.1	−2.34* −2.08* −2.41*	−0.89 <sup>ns</sup> −1.16* −1.85*	0.95 <sup>ns</sup> 0.98* 1.65 <sup>ns</sup>
Erneberg 1999	Fig. 2	<i>Anthemis cotula</i> (f)	Community	leaf-feeding insects (T+C)	0.1	−1.12*	−0.48*	0.05 <sup>ns</sup>
McEvoy et al. 1993	Fig. 6	<i>Senecio jacobaea</i> (f)	Community	leaf feeding moth (T)	0.25	−3.31*	0.16 <sup>ns</sup>	−3.64
				leaf/root-feeding beetle (T)		−3.31*	−1.86*	−1.70
				both		−3.31*	−4.92*	1.14
Parker and Salzman 1985	Tab. 4	<i>Gutierrezia microcephala</i> (s)	Community	leaf feeder (T)	0.2	−0.11*	−0.08*	−0.29 <sup>ns</sup>
Reader and Bonser 1998	Tab. 3	<i>Medicago lupulina</i> (f)	Community	leaf-feeding mammals and molluscs (T+C)	1.0	−1.52*	−0.60*	−0.08 <sup>ns</sup>
		<i>Hieracium floribundum</i> (f)				−1.54*	−0.73*	−0.66 <sup>ns</sup>
		<i>Poa pratensis</i> (g)				−2.27	−2.19*	0.89 <sup>ns</sup>
		<i>Bromus inermis</i> (g)				−2.85*	−1.51*	NC <sup>ns</sup>
		<i>Solidago canadensis</i> (f)				−2.64*	−1.99*	NC <sup>ns</sup>
		<i>Phalaris arundinacea</i> (g)				−3.42*	−1.07*	−0.06 <sup>ns</sup>
Sheppard et al. 2001	Fig. 2	<i>Echium plantagineum</i>	Community	root feeder (T)		−0.83*	−0.89*	0.26 <sup>ns</sup>
Sork 1987		<i>Gustavia superba</i> (t)	Community	mammals (T+C)	19.6	NA*	NA*	NA*
Taylor et al. 1997	Fig. 2	<i>Panicum virgatum</i> (g)	Grass	small mammals (T+C)	0.8	0.76 <sup>ns</sup>	−0.09 <sup>ns</sup>	−1.01
	Fig. 3	<i>Spartina patens</i> (g)	Grass			−0.78 <sup>ns</sup>	−0.11 <sup>ns</sup>	0.90
	Fig. 4	<i>S. alterniflora</i> (g)	Grass			−0.62 <sup>ns</sup>	−0.85 <sup>ns</sup>	0.19
Vilá and Lloret 1996	Fig. 2	<i>Erica multiflora</i> (s)	Community	mammals (T+C)	NA	−2.23 <sup>d</sup>	−0.92 <sup>d</sup>	1.76 <sup>d</sup>
Willis et al. 1998	Tab. 2	<i>Hypericum gramineum</i> (f)	Themeda triandra	leaf-feeding mites (T)	1.0	−0.92 <sup>d</sup>	−0.07 <sup>d</sup>	−0.01 <sup>d</sup>
		<i>H. perforatum</i> (f)						
Bentley and Whittaker 1979	Tab. 6	<i>Rumex crispus</i> (f)	<i>R. o.</i>	leaf-feeding beetle (T+C)	NA	0.35 <sup>d</sup>	−0.19 <sup>d</sup>	−0.09 <sup>d</sup>
		<i>R. obtusifolius</i> (f)	<i>R. c.</i>			−0.45 <sup>d</sup>	−0.06 <sup>d</sup>	−0.84 <sup>d</sup>
		<i>R. obtusifolius</i> (f)	Grass	leaf-feeding beetle (T)	NA	−1.42 <sup>d</sup>	0.04 <sup>d</sup>	−1.03 <sup>d</sup>
Cottam et al. 1986	Tab. 1							
Friedli and Bacher 2001	Tab. 3	<i>Cirsium arvense</i> (f)	Grass	shoot base feeder (T)	NA	−1.57*	0.02 <sup>ns</sup>	−1.01*
Kok et al. 1986	Tab. 1	<i>Carduus nutans</i> (f)	Grass	root & flower feeder (T)	NA	−1.75 <sup>d</sup>	0.36 <sup>d</sup>	−0.31 <sup>d</sup>
Nötzold et al. 1998	Fig. 2	<i>Lythrum salicaria</i> (f)	Grass	root-feeding weevil (T)	NA	−0.35 <sup>d</sup>	−1.53 <sup>d</sup>	−0.67 <sup>d</sup>
Steinger and Müller-Schärer 1992	Fig. 1	<i>Centaurea maculosa</i> (f)	Grass	root-feeding moth (T)	NA	−1.03*	−0.17 <sup>ns</sup>	0.07 <sup>ns</sup>
				weevil (T)		−1.03*	−0.99*	1.08 <sup>ns</sup>
				both		−1.03*	−1.03*	0.07 <sup>ns</sup>

<sup>a</sup> g = grass, f = forb, s = shrub, t = tree; <sup>b</sup> T = feeds on target plant, C = feeds on removed plants; <sup>c</sup> log-response ratios calculated in accordance to the multiplicative model in eq. (1), i.e.  $C = \ln(X_{c+h-}) - \ln(X_{c-h-})$ ,  $H = \ln(X_{c+h+}) - \ln(X_{c-h+})$ ,  $H\text{-by-}C = \ln(X_{c+h+}) - \ln(X_{c+h-}) - \ln(X_{c-h+}) + \ln(X_{c-h-})$ ; <sup>d</sup> statistics on data that was not ln-transformed; \*  $P < 0.05$ , <sup>ns</sup>  $P > 0.1$ ; NA = not available, NC = not possible to calculate.

enough apart to exclude the possibility that treatments in neighboring plots affect herbivore abundance.

Results show that only two appropriately analysed field studies actually detected a significant interactive effect from the removal of plant neighbors and herbivores on some plant variable (Table 1). The study by Dormann et al. (2000) reported a substitutive effect of plant competition and herbivory, i.e. plant size was larger in the plot with both treatments than predicted from plots with each treatment alone, for one of three investigated focal plants. This low incidence of interactive effects occurred despite that the removal of plant neighbors and herbivores, in almost all cases, caused significant direct effects on target plants. Thus there is weak evidence for interactive effects from plant based studies. While this may be a result of small sample sizes ( $N = 10$  studies), we will argue that it may also be a by-product of limited spatial scales involved in plant-based studies or a biased selection of study system.

### **Herbivore-based studies: theory and experiments**

We will now examine in more detail how manipulation of plant neighbors might alter rates of herbivory, patch residence time and herbivore population growth rates, moving our focus from the weak evidence for interaction in plant-based studies to herbivore-based studies. In particular, we will evaluate the mechanisms whereby plant neighbors affect herbivory on three spatial scales and describe theory that can describe these mechanisms. On a small scale, herbivores can respond to manipulations in the plant neighbor abundance by changing their foraging behaviour, which determines the immediate intake of resources in space and time. Alternatively, they can respond by adjusting their habitat choice, which affects the resource intake over a longer time period and a wider space. Both responses are behavioural and are assumed to have life history and population dynamic consequences. Finally, herbivores may respond numerically through effects on reproduction and mortality, which reflects the longest time period and the largest and most permanent change in abundance. These small, medium and large scale processes, which are subsets of each other, cover the breadth of reported experimental and theoretical responses by herbivores to plant density. They thus encompass the scales at which an interaction between herbivory and plant competition can occur, and we review these below.

### **Relatively small scale variations in plant abundance**

The decision to feed, or oviposit, on a plant is based on

the perception by herbivores of positive and negative feedbacks that arise from selecting that particular plant individual. The presence of plant neighbors may either decrease the perceived positive benefits (e.g. through masking) of selecting a plant individual or enhance the negative consequences (e.g. through repellency Kareiva 1983). Both processes may arise from interference of either olfactory or visual cues used by herbivores to locate food plants (Stanton 1983, Visser 1986).

*Masking:* Olfactory masking has been suggested to occur when insect herbivores use proportions of common leaf volatiles for host-plant detection rather than specific odor compounds. These host-plant specific proportions may be disrupted by the presence of non-hosts emitting other proportions of the same compounds (Stanton 1983, Visser 1986, Schlyter and Birgersson 1999, Zhang 2001). The generality of this masking mechanism is difficult to assess, but recent information on sensory perception indicate that such masking may be less important. First, neural receptors in many insect antennae are more specific than previously believed (Andersson et al. 1995, Hansson et al. 1999). Second, emitted odor molecules are transported through the air in stable filaments (Murlis et al. 1992), and are therefore likely to remain intact until intercepted by insect antennae. Not surprisingly, detailed experiments show a highly refined ability by insects to detect different compounds separated by very small distances (Liu and Haynes 1992, Rumbo et al. 1993, Lux et al. 1994, Potting et al. 1999).

A corresponding visual masking mechanism suggests that plant stature, leaf shape and spectral quality may visually impair the search ability of herbivores (Rausher 1978, Prokopy and Owens 1983, Stanton 1983, Mackay and Jones 1989, Bazely and Ensor 1989, Harris et al. 1993). The presence of non-host plants may either hide the plant rendering the host plant cue invisible, or distort the cue thereby reducing the likelihood that an insect will alight on the plant (Brown and Lawton 1991). For instance, confusion may arise because plant neighbors reduce the spectral contrast between host plants and matrix (Smith 1976, Dewar et al. 2000), or because of similarities in leaf shape among host and non-host species (Gilbert 1982). As in olfactory masking, the strength of visual masking depends on the visual acuity of the herbivore species relative to the back-ground against which they are searching. This far, little data exists to evaluate the generality of visual masking.

*Repellency:* Interference from neighboring non-host plants may also cause herbivores to actively avoid feeding on a host plant individual, commonly referred to as repellency. While masking and repellency historically have been used interchangeably, repellency should be reserved for those cases when herbivores actively avoid a non-host plant (for further discussion see Mitchell 1994). If the exact mechanism is unknown it might be better to describe the process as host-finding interference. Repellency through visual signals has mostly been docu-

mented for large herbivores, which may avoid grazing on even highly preferred plants when these grow inside thorny shrubs (McAuliffe 1984, 1986, Herrera 1991, Olff et al. 1999). Corresponding visual repellency mechanisms are probably less likely for smaller herbivores that can approach host plants without necessarily touching plant neighbors. Olfactory repellency by non-host plant neighbors and its effect on the distribution of herbivory on host-plants has not been supported experimentally (Finch and Collier 2000), even though repellency is often implied as an important mechanism for causing reduced herbivory in mixed crops (Atsatt and O'Dowd 1976).

*Plant neighbors as alternative food:* The idea that plant neighbors either increase negative or decrease positive feedbacks from the host plant is still valid for cases when the focal plant is surrounded by alternate edible plants, but now rates of herbivory on the focal plant may also increase in the presence of neighbors (Pfister and Hay 1988, Morrow et al. 1989, Hjältén et al. 1993, Edwards et al. 1994, Wahl and Hay 1995, WallisDeVries et al. 1999, White and Whitham 2000). Data suggest that less preferred plant neighbors reduce herbivory on a focal plant, similar to the case for non-edible plants, while more preferred plant neighbors rather increase herbivory on a focal plant (for a theoretical treatment see Holt 1984, Oksanen 1990). Unfortunately, a common oversight in many of these studies is that the experimental design did not include plant without plant neighbors (i.e. a substitutive rather than additive design). It is therefore not possible to evaluate if observed patterns are due to an increased positive signal by conspecifics, i.e. attraction by a larger food patch, or by a reduced positive signal caused by non-host plants.

*Summary:* It seems that the most likely mechanisms whereby non-host plant neighbors affect herbivory on a focal plant in small-scale experiments is visual or physical masking for insect herbivores and visual masking or repellency for large herbivores. In addition, the presence of alternative food might affect herbivory by polyphagous herbivores on a focal plant. These mechanisms suggest that interactive effects are likely to occur when there is mismatch between the spatial scale of the plant community structure and the perception/physiological constraints of the herbivore, e.g. when herbivores treat the resource population in a fine-grained way (sensu MacArthur and Wilson 1967). These mechanisms also suggest reasons why interactive effects were rare in the small-scaled plant-based studies (Table 1). Several of those studies involved polyphagous small mammals. It is possible that removed plants included species of higher and lower preference to mammalian herbivores, and these removals might have counteracted each other (Hambäck and Ekerholm 1997).

## Intermediate variation in plant abundance

At intermediate spatial scales, variations in herbivore density are mostly due to individual decisions to enter or to leave the patch. The presence of plant neighbors may affect these decisions through three principal pathways. First, non-host plants may affect herbivore decisions to enter the patch through the same mechanisms as described for small-scale mechanisms, by either masking food resources or by repelling herbivore individuals. For patch selection, these mechanisms are probably limited to herbivores that locate host plants or patches using long-distance cues (Schlyter and Birgerson 1999, Dicke 2000). Second, the presence of plant neighbors as alternative food may affect patch residence time and associated giving-up densities (Rosenzweig 1991). Third, plant neighbors may affect patch residence of herbivores through some factor other than food, such as perceived or real predation risk or the thermoregulatory environment. Finally, processes occurring at intermediate and small scales may interact to create more complex situations.

*Affecting residence time via food mechanisms:* The presence of non-host plants in a patch may create problems in the estimation of host plant density by herbivores. It is unclear whether such estimation problems cause herbivores to over- or underestimate host plant density as it depends on how the host plant density is estimated. If the propensity to stay in a patch is based both on the encounter rate with host (positively) and non-host plants (negatively), then the presence of non-host plants will always reduce patch residence times (see also Miller and Strickler 1984). This mechanism has been argued by Finch and Collier (2000) to be important for cabbage root flies (*Delia radicum*). In their model, herbivores approach host plants following rough olfactory and visual signals (as described above), but are unable to closely differentiate host and non-host species. If host and non-host plants are growing close together, herbivores face a certain probability of landing on non-host plant neighbors. Repeated landings on non-hosts may cause the insect to fly away while successive landings on host plants, verified by gustatory signals, induces egg-laying behaviour. Such herbivore response have been modelled through diffusion equation models that consistently show that these responses translate to differences in herbivore density between patches (Kareiva and Odell 1987, Turchin 1991, 1998). However, diffusion equation models seldom address the underlying mechanisms for specific movement behaviours (but see Kareiva and Odell 1987).

*Affecting residence times by non-food mechanisms:* The presence of non-host plant neighbors, and the distribution of host plants in general, may affect a large set of environmental factors, besides food quantity and quality. Two of the most commonly considered aspects,

affecting herbivore foraging decisions, are the role of non-host plants as shelter against a harsh environment or as cover against predation (Lima and Dill 1990). Interest in the influence of temperature, and other abiotic factors, on habitat selection has primarily centered on animal physiology and optimality models. For instance, moose activity budgets and patterns of habitat use conform quite well with predictions based on the use of habitats with varying plant composition in order to maintain thermal homeostasis (Belovsky 1981). Moreover, several small mammal species alter their patch use in response to variation in plant community structure in order to optimize the thermal environment (Bozinovic and Vásquez 1999), or to reduce predation risk (Callaway 1995, Brown 1999, Jacob and Brown 2000). Similarly, habitat selection in insect herbivores is governed by both temperature or humidity (Bach 1993, Willmer et al. 1996) and by predation risk (Rothley et al. 1997). As a consequence, one plant may experience increased herbivory when growing beneath another plant that creates a more favourable thermal environment for herbivores or reduce the predation risk (Hambäck et al. 1998, Brown 1999, Jacob and Brown 2000). These connections have been examined in modelling attempts, where the foraging efficiency (consumption and digestion rates) is emerging as a central physiological basis for behavioural changes in patch use response to predation risk and the thermal environment (Brown et al. 1999, Whelan et al. 2000).

*Interactive effects across spatial scales:* Herbivores may naturally respond to processes at small and intermediate spatial scales simultaneously, and this creates problems in the interpretation of patterns. For instance, it has been proposed for agricultural situations that planting a more preferred plant species along the field edges may reduce attack rates on the crop (Vandermeer 1989). This method of 'pulling' insects away from the crop may seem to contradict the discussion in the section 'plant neighbors as alternative food', where the presence of a more preferred plant rather increased herbivory on a less preferred plant. However, the use of trap crops is aimed at manipulating the patch selection behaviour rather than food selection within patches. This distinction points to the importance of carefully considering the spatial scales involved in patch and food selection by herbivores when evaluating interactive effects of plant neighbors and herbivory, e.g. in the distribution of plots relative to each other. For reviewed plant-based studies (Table 1), the inter-plot distance was seldom reported. It is therefore not possible to evaluate if herbivores selected a given treatment in preference of an unmanipulated matrix or in preference of a matrix consisting of other treatments.

## Relatively large scale variation in plant abundance

On sufficiently large spatial scales, immigration and emigration from plants and patches are less important mechanisms compared with reproduction and mortality for explaining density variations between sites. This distinction is critical for experiments designed to examine interactions between herbivory and plant competition: when will patterns of resource and habitat use by herbivores and their connection to plant diversity reflect the processes governing population dynamic patterns? Host and patch finding mechanisms exhibited at small spatial scales may, or may not, be expressed as differences in population growth rates and ultimately as differences in population densities. For instance, it has been suggested that insect outbreaks may be less prevalent in mixed compared with large monospecific forest stands (Watt 1992), and through three small-scale mechanisms: increased predation, host-finding interference, or reduced larval growth (Tammaru et al. 1995, Floater and Zalucki 2000, Zhang 2001). The last mechanism applies to a situation when oviposition is unselective and when eggs deposited on non-host plants have reduced performance. The outcome of this unselective behaviour is reduced growth in mixed stands (cf. the 'fly-paper' effect in the pathogen literature, Trenbath 1993).

A problem when evaluating the importance of each hypothesis, from a plant perspective, is that they have seldom been evaluated in relation to the available plant biomass. It is therefore not possible to examine if herbivory is actually higher in monospecific than mixed forest stands. An even more general problem is that very few studies have experimentally examined if plant neighbor presence and herbivory at all have interactive effects on plant growth and abundance on the scale of population dynamics. The only study, to our knowledge, that examined interactive effects by plant neighbors and herbivores on a population scale is the study by Hambäck and Ekerholm (1997), but this study did not include resource competition. The lack of studies on this large spatial and temporal scale is perhaps not surprising as the manipulation would require removal of single plant species over very large areas.

The theoretical interest in the population level consequences caused by interactive effects of plant neighbors and herbivory has centered around negative effects by plant neighbors, mainly through apparent competition (sensu Holt 1977). Apparent competition, at this scale, can arise if herbivores respond numerically to changes in food abundance and at the same time are able to affect plant biomass (Holt 1977, Holt and Lawton 1994). The outcome is well known and depends on the relative growth rates of plant species and relative attack rates by herbivores on different plants (Armstrong 1979, Holt et al. 1994, Hambäck 1998), but is not always realized in strongly fluctuating systems (Ham-

bäck and Ekerholm 1997, Abrams et al. 1998). Fewer studies have addressed positive indirect interactions on a population scale, e.g. the consequences of non-host interference on the host-finding ability or directly on herbivore population growth rates have not been treated theoretically.

## Conclusions and perspectives

Information about interactive effects of plant neighbors and herbivory on plant growth and biomass is important for developing a more general theory on plant-herbivore interactions. Moreover, it is vital for understanding how plant and herbivore responses scale from the details of resource competition and herbivory to patterns of plant and herbivore distribution and abundance at the landscape level. To this end, examinations of interactive effects must involve not only measurements on the strength of the statistical interaction, but also an identification of underlying mechanisms giving rise to it. The key aspect of any study of interactive effects must therefore be the recognition that plant and herbivore responses alone are insufficient to establish the nature of the interaction. Unless plant community responses can be mapped to herbivore behavior, distribution and abundance and herbivore responses to plant community patterns linked to plant population dynamics, the nature of interactive effects will remain less understood.

We reviewed two approaches, where the first (plant-based) approach is centered on factorial experiments that manipulate plant neighbors and herbivores and score effects on plant growth or biomass, while the second (herbivore-based) approach focuses on experiments that manipulate plant neighbors and score herbivore attack rates (feeding, oviposition). Interestingly, the two approaches have arrived at somewhat contrasting conclusions concerning the prevalence of interactive effects of herbivory and competition. Interactive effects have only rarely been observed in studies using the plant-based approach (Table 1), but are common in studies using the herbivore-based approach (Andow 1991). This incongruity between the approaches may emanate from (A) measuring different entities (herbivory versus plant biomass), (B) biases in the choice of study system, or (C) systematic difference in the execution of experiments. The last problem is difficult to assess based on study descriptions and will not be discussed further.

The first problem, from measuring different entities, may arise because there is not always a close connection between observed rates of herbivory and reductions in plant biomass, due to compensatory plant growth. However, this explanation is less likely for the experiments included in this review as herbivore removals mostly had large effects on plant biomass (Table 1, Fig. 1). The bias problem is more difficult to evaluate, but it is clear that

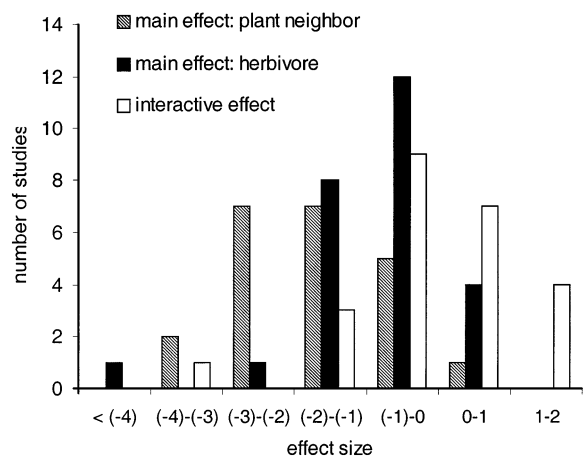


Fig. 1. Observed effect sizes in factorial experiments examining the effect of removing plant neighbors and herbivores on plant biomass (for definition of effect size see Table 1).

plant-based studies have mainly focussed on mammalian herbivory (5 of 10 studies, Table 1) while herbivore-based studies have mainly focussed on insect herbivory (Root 1973, Andow 1991, Tonhasca and Byrne 1994). It is possible that plant neighbor removals have larger effects on herbivory in insect- than in mammalian-dominated systems, due to differences in underlying mechanisms. Studies using the herbivore-based approach show that interactive effects in mammalian-dominated systems arise mainly for two reasons; from small mammals hiding under cover (Callaway 1995) or from attraction/repulsion by alternative food (Hjältén et al. 1993), while multiple mechanisms may cause interactive effects in insect-dominated systems. It is possible that plot sizes in most removal experiments were too small to affect the hiding behaviour by small mammals. The only plant-based study using a plot size larger than 1 m<sup>2</sup> also observed a significant interactive effect on plant biomass from removing plant neighbors and mammalian herbivores (Sork 1987). Similarly, the effect size and sign from removing plant neighbors on herbivory rates depend on herbivore selectivity (Wahl and Hay 1995), and since plant removals (in plant-based studies) may include species of both higher and lower preference, positive and negative effects of removing plant neighbors may have cancelled in studies with mammalian herbivores (see also Hambäck and Ekerholm 1997).

## Suggestions for future work, and their synthesis

It is clear that much remains to be learned about interactive effects of herbivory and plant competition on plant growth and biomass. We are aware that a large number of mechanisms can give rise to these interactions, but there is still no comprehensive understanding



of both the prevalence of different mechanisms and their relative importance for explaining patterns of plant distribution in nature. We have identified examples of research at the three herbivory scales where effort could be made to achieve this understanding.

At small and intermediate scales, studies show that some herbivore species react stronger to non-host plants and herbivory by these species is consequently more strongly reduced in mixed compared with monospecific stands (Finch and Collier 2000). However, the mechanisms, and species characteristics, underlying these differences in herbivore responses to plant neighbors are less known. One could hypothesize that herbivore species that mainly use general plant characteristics, such as plant stature or color, in host-finding could be more easily confused by plant neighbors than species using specific characteristics, such as unique odor cues. Alternatively, monophagous herbivores, having experienced strong selection pressure for specific plants, could be better able to locate host-plants, and would consequently be less confused in mixed stands, than oligophagous species. This far, few empirical or theoretical studies have examined either hypothesis.

At medium, and perhaps large scales, reduced herbivory may be one reason for increased plant productivity in diverse plant communities, as suggested by recent ecosystem function experiments (Mulder et al. 1999, Hulot et al. 2000, Koricheva et al. 2000, Loreau et al. 2001), although it is unclear whether this is due to plant diversity per se or to specific plant functional groups. When investigating herbivore effects in these ecosystem function experiments, the approach is similar to the plant-based approach of investigating interactive effects of removing plant neighbors and herbivores. As suggested in the current paper, a complementary approach would be an analysis of actual mechanisms underlying herbivore responses and plant-plant interactions, which would be helpful in defining the role of biodiversity or functional groups.

On a more general level, integrating physiology in studies on plant competition and herbivory could be the most promising approach for developing a general framework for understanding the interaction between plants and herbivores across scales (Brown and West 2000). Physiological rules use metabolic based functions of plant and herbivore growth and development, as well as perceptual constraints by herbivores, to generate basic allometric scaling rules (a common feature in plants and animals) for life histories and community structure. If scaling rules can be combined to reflect plant-plant and herbivore-plant interactions, this may facilitate scale-independent insight into the interactive effects of herbivores and plant competition. This is exemplified by Ritchie and Olff (1999, see also Belovsky 1997) who showed that inclusion of habitat heterogeneity, and herbivore responses to this heterogeneity, in

simple competition models may provide a more general understanding of the connection between overall primary productivity and herbivore diversity.

In conclusion, it is worth revisiting our introduction of the simplest model for interactive effects of plant competition and herbivory. Eq. (3) is at its heart a statistical model of interactive effects and as such presents a straightforward null hypothesis about the existence of interactions among plant competition and herbivory. While this model certainly is an over-simplification of most plant-herbivore systems, we firmly believe that progress within plant-herbivore studies will only be achieved if we start from such simple relationships. Contrasting this model's generality and applicability to the few plant-based studies and the plethora of herbivore-based studies indicates the necessity of establishing statistical tests with a firm understanding of population models because testing ecological theory is more than fulfilling statistical assumptions. Otherwise, we will continue to produce special cases that only with difficulty can be connected to a general theory of plant-herbivore interactions.

**Acknowledgements** – This paper has benefited from comments by Jan Bengtsson, Christer Björkman, Jon Chase and Oswald Schmitz. We are also grateful to J. B. Grace and B. D. Marx for reanalysing their data. The study was made possible through a post-doctoral fellowship from the Swedish foundation for international cooperation in research and higher education (STINT, to PAH).

## References

- Abrams, P. A., Holt, R. D. and Roth, J. D. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. – *Ecology* 79: 201–212.
- Andersson, P., Hanson, B. S. and Löfqvist, J. 1995. Plant-odour-specific receptor neurons on the antennae of female and male *Spodoptera littoralis*. – *Physiol. Entomol.* 20: 189–198.
- Andow, D. A. 1991. Vegetational diversity and arthropod population response. – *Annu. Rev. Entomol.* 36: 561–586.
- Armstrong, R. A. 1979. Prey species replacements along a gradient of nutrient enrichment: a graphical approach. – *Ecology* 60: 76–84.
- Atsatt, P. R. and O'Dowd, D. J. 1976. Plant defense guilds. – *Science* 193: 24–29.
- Bach, C. E. 1993. Effects of microclimate and plant characteristics on the distribution of a willow flea beetle, *Altica subplicata*. – *Am. Midl. Nat.* 130: 193–208.
- Bazely, D. R. and Ensor, C. V. 1989. Discrimination learning in sheep with cues varying in brightness and hue. – *Appl. Anim. Behav. Sci.* 23: 293–300.
- Belovsky, G. E. 1981. Optimal activity budget and habitat choice of moose *Alces alces*. – *Oecologia* 48: 22–30.
- Belovsky, G. E. 1997. Optimal foraging and community structure: the allometry of herbivore food selection and competition. – *Evol. Ecol.* 11: 641–672.
- Bentley, S. and Whittaker, J. B. 1979. Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*, on competition between *Rumex obtusifolius* and *Rumex crispus*. – *J. Ecol.* 67: 79–90.
- Bonsler, S. P. and Reader, R. J. 1995. Plant competition and herbivory in relation to vegetation biomass. – *Ecology* 76: 2176–2183.

- Bozinovic, F. and Vásquez, R. A. 1999. Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. – *Funct. Ecol.* 13: 602–610.
- Brown, J. H. and West, G. B. 2000. *Scaling in biology*. – OUP, NY, USA.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. – *Evol. Ecol. Res.* 1: 49–71.
- Brown, J. S., Laundre, J. W. and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. – *J. Mammal.* 80: 385–399.
- Brown, V. K. and Lawton, J. H. 1991. Herbivory and the evolution of leaf size and shape. – *Philos. Trans. R. Soc. Lond. Biol.* 333: 265–272.
- Callaway, R. M. 1995. Positive interactions among plants. – *Bot. Rev.* 61: 306–349.
- Clarke, J. L., Welch, D. and Gordon, I. J. 1995a. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. II. The impact of heather. – *J. Appl. Ecol.* 32: 177–186.
- Clarke, J. L., Welch, D. and Gordon, I. J. 1995b. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. – *J. Appl. Ecol.* 32: 166–176.
- Cottam, D. A., Whittaker, J. B. and Malloch, A. J. C. 1986. The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. – *Oecologia* 70: 452–456.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. – Blackwell.
- Dewar, A. M., Haylock, L. A., Bean, K. M. et al. 2000. Delayed control of weeds in glyphosate-tolerant sugar beet and the consequences on aphid infestation and yield. – *Pest. Manag. Sci.* 56: 345–350.
- Dicke, M. 2000. Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. – *Biochem. Syst. Ecol.* 28: 601–617.
- Dormann, C. F., Van der Wal, R. and Bakker, J. P. 2000. Competition and herbivory during salt marsh succession: the importance of forb growth strategy. – *J. Ecol.* 88: 571–583.
- Edwards, G. R., Newman, J. A., Parsons, A. J. et al. 1994. Effects of scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep. – *J. Anim. Ecol.* 63: 816–826.
- Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. – *Ecology* 78: 2316–2325.
- Erneberg, M. 1999. Effects of herbivory and competition on an introduced plant in decline. – *Oecologia* 118: 203–209.
- Finch, S. and Collier, R. H. 2000. Host-plant selection by insects – a theory based on ‘appropriate/inappropriate landings’ by pest insects of cruciferous plants. – *Entomol. Exp. Appl.* 96: 91–102.
- Floater, G. J. and Zalucki, M. P. 2000. Habitat structure and egg distribution in the processionary caterpillar *Ochrogaster lunifer*: lessons for conservation and pest management. – *J. Appl. Ecol.* 37: 87–99.
- Fortin, M.-J. and Gurevitch, J. 1993. Mantel tests: Spatial structure in field experiments. – In: Scheiner, S. M. and Gurevitch, J. (eds), *Design and analysis of ecological experiments*. Chapman & Hall, pp. 342–359.
- Freckleton, R. P. and Watkinson, A. R. 2000. On detecting and measuring competition in spatially structured plant communities. – *Ecol. Lett.* 3: 423–432.
- Friedli, J. and Bacher, S. 2001. Direct and indirect effects of a shoot-base boring weevil and plant competition on the performance of creeping thistle, *Cirsium arvense*. – *Biol. Contr.* 22: 219–226.
- Gilbert, L. E. 1982. The coevolution of a butterfly and vine. – *Sci. Am.* 247: 102–107.
- Gurevitch, J., Morrison, J. A. and Hedges, L. V. 2000. The interaction between competition and predation: a meta-analysis of field experiments. – *Am. Nat.* 155: 435–453.
- Hambäck, P. A. 1998. Seasonality, optimal foraging, and prey coexistence. – *Am. Nat.* 152: 881–895.
- Hambäck, P. A. and Ekerholm, P. 1997. Mechanisms of apparent competition in seasonal environments: an example with vole herbivory. – *Oikos* 80: 276–288.
- Hambäck, P. A., Schneider, M. and Oksanen, T. 1998. Winter herbivory by voles during a population peak: the relative importance of local factors and landscape pattern. – *J. Anim. Ecol.* 67: 544–553.
- Hansson, B. S., Larsson, M. C. and Leal, W. S. 1999. Green leaf volatile-detecting olfactory receptor neurones display very high sensitivity and specificity in a scarab beetle. – *Physiol. Entomol.* 24: 121–126.
- Harper, J. L. 1977. *Population biology of plants*. – Academic Press.
- Harris, M. O., Rose, S. and Malsch, P. 1993. The role of vision in the host plant-finding behaviour of the Hessian fly. – *Physiol. Entomol.* 18: 31–42.
- Herrera, J. 1991. Herbivory, seed dispersal, and the distribution of a ruderal plant living in a natural habitat. – *Oikos* 62: 209–215.
- Hjältén, J., Danell, K. and Lundberg, P. 1993. Herbivore avoidance by association: vole and hare utilization of woody plants. – *Oikos* 68: 125–131.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – *Theor. Popul. Biol.* 12: 197–229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. – *Am. Nat.* 124: 377–406.
- Holt, R. D. and Lawton, J. H. 1994. The ecological consequences of shared natural enemies. – *Annu. Rev. Ecol. Syst.* 25: 495–520.
- Holt, R. D., Grover, J. and Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. – *Am. Nat.* 144: 741–771.
- Hulot, F. D., Lacroix, G., Lescher-Moutoué, F. et al. 2000. Functional diversity governs ecosystem response to nutrient enrichment. – *Nature* 405: 340–344.
- Jacob, J. and Brown, J. S. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. – *Oikos* 91: 131–138.
- Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: Resource concentration and herbivore movement. – In: Denno, R. F. and McClure, M. S. (eds), *Variable plants and herbivores in natural and managed systems*. Academic Press, pp. 259–290.
- Kareiva, P. and Odell, G. 1987. Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. – *Am. Nat.* 130: 233–270.
- Kok, L. T., McAvoy, T. J. and Mays, W. T. 1986. Impact of tall fescue grass and *Carduus* thistle weevils on the growth and development of musk thistle (*Carduus nutans*). – *Weed Sci.* 34: 966–971.
- Koricheva, J., Mulder, C. P. H., Schmid, B. et al. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. – *Oecologia* 125: 271–282.
- Lima, S. L. and Dill, L. M. 1990. Behavioural decision made under the risk of predation – a review and a prospectus. – *Can. J. Zool.* 68: 619–640.
- Liu, Y.-B. and Haynes, K. F. 1992. Filamentous nature of pheromone plumes protects the integrity of signal from background chemical noise in cabbage looper moth, *Trichoplusia ni*. – *J. Chem. Ecol.* 18: 299–307.
- Loreau, M., Naeem, S., Inchausti, P. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – *Science* 294: 804–808.
- Louda, S. M., Keeler, K. H. and Holt, R. D. 1990. Herbivore influences on plant performance and competitive interactions. – In: Grace, J. B. and Tilman, D. (eds), *Perspectives on plant competition*. Academic Press, pp. 413–444.

- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. – *Am. Nat.* 1978: 23–39.
- Lux, S. A., Hassanali, A., Lwande, W. et al. 1994. Proximity of release points of pheromone components as a factor confusing males of the spotted stem borer, *Chilo partellus*, approaching the trap. – *J. Chem. Ecol.* 20: 2065–2076.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.
- Mackay, D. A. and Jones, R. E. 1989. Leaf shape and the host-finding behaviour of two ovipositing monophagous butterfly species. – *Ecol. Entomol.* 14: 423–431.
- McAuliffe, J. R. 1984. Prey refugia and the distribution of two Sonoran Desert cacti. – *Oecologia* 65: 82–85.
- McAuliffe, J. R. 1986. Herbivore-limited establishment of a sonoran desert tree: *Cercidium microphyllum*. – *Ecology* 67: 276–280.
- McEvoy, P. B., Rudd, N. T., Cox, C. S. et al. 1993. Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. – *Ecol. Monogr.* 63: 55–75.
- Miller, J. R. and Strickler, K. L. 1984. Finding and accepting host plants. – In: Bell, W. J. and Cardé, R. T. (eds), *Chemical ecology of insects*. Chapman & Hall, pp. 127–158.
- Mitchell, B. K. 1994. The chemosensory basis of host-plant recognition in Chrysomelidae. – In: Jolivet, P. H., Cox, M. L. and Petitpierre, E. (eds), *Novel aspects of the biology of Chrysomelidae*. Kluwer Acad. Publ, pp. 141–151.
- Morrow, P. A., Tonkyn, P. W. and Goldberg, R. J. 1989. Patch colonization by *Trirhabda canadensis* (Coleoptera: Chrysomelidae): effects of plant species composition and wind. – *Oecologia* 81: 43–50.
- Mulder, C. P. H. et al. 1999. Insects affect relationships between plant species richness and ecosystem processes. – *Ecol. Lett.* 2: 237–246.
- Murlis, J., Elkinton, J. S. and Cardé, R. T. 1992. Odor plumes and how insects use them. – *Annu. Rev. Entomol.* 37: 505–532.
- Niklas, K. J. 1994. Plant allometry: The scaling of form and process. – Univ. of Chicago Press.
- Nötzold, R., Blossey, B. and Newton, E. 1998. The influence of below ground herbivory and plant competition on growth and biomass allocation of purple loosestrife. – *Oecologia* 113: 82–93.
- Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. – *Evol. Ecol.* 4: 220–234.
- Olf, H., Vera, F. W. M., Bokdam, J. et al. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. – *Plant Biol.* 1: 1–11.
- Parker, M. A. and Salzman, A. G. 1985. Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. – *J. Ecol.* 73: 903–913.
- Pfister, C. A. and Hay, M. E. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. – *Oecologia* 77: 118–129.
- Potting, R. P. J., Lösel, P. M. and Scherckenbeck, J. 1999. Spatial discrimination of pheromones and behavioural antagonists by the tortricid moths *Cydia pomonella* and *Adoxophyes orana*. – *J. Comp. Physiol. [A]* 185: 419–425.
- Prokopy, R. J. and Owens, E. D. 1983. Visual detection of plants by herbivorous insects. – *Annu. Rev. Entomol.* 28: 337–364.
- Rausher, M. D. 1978. Search image for leaf shape in a butterfly. – *Science* 200: 1071–1073.
- Reader, R. J. and Bonser, S. P. 1998. Predicting the combined effect of herbivory and competition on a plant's shoot mass. – *Can. J. Bot.* 76: 316–320.
- Rees, M. and Brown, V. K. 1992. Interactions between invertebrate herbivores and plant competition. – *J. Ecol.* 80: 353–360.
- Ritchie, M. E. and Olff, H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. – *Nature* 400: 557–560.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – *Ecol. Monogr.* 43: 95–124.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. – *Am. Nat.* 137: S5–S28.
- Rothley, K. D., Schmitz, O. J. and Cohon, J. L. 1997. Foraging to balance conflicting demands: novel insights from grasshoppers under predation risk. – *Behav. Ecol.* 5: 551–559.
- Rumbo, E. R., Deacon, S. M. and Regan, L. P. 1993. Spatial discrimination between sources of pheromone and an inhibitor by the light brown apple moth *Epiphyas postvittana* (Lepidoptera: Tortricidae). – *J. Chem. Ecol.* 19: 953–962.
- Schlyter, F. and Birgersson, G. 1999. Forest beetles. – In: Hardie, R. J. and Minks, A. K. (eds), *Pheromones of non-lepidopteran insects associated with agricultural plants*. CAB International, pp. 113–148.
- Sheppard, A. W. 1996. The interaction between natural enemies and interspecific plant competition in the control of invasive pasture weeds. – In: Moran, V. C. and Hoffmann, J. H. (eds), *Proc. IX Int. Symp. of biological control of weeds*. January 1996. Univ. of Cape Town, Stellenbosch, South Africa, pp. 47–53.
- Sheppard, A. W., Smyth, M. J. and Swirepik, A. 2001. The impact of a root-crown weevil and pasture competition on the winter annual *Echium plantagineum*. – *J. Appl. Ecol.* 38: 291–300.
- Smith, J. G. 1976. Influence of crop background on aphids and other phytophagous insects on Brussel sprouts. – *Ann. Appl. Biol.* 83: 1–13.
- Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. – *Ecology* 68: 1341–1350.
- Stanton, M. L. 1983. Spatial patterns in the plant community and their effects upon insect search. – In: Ahmad, S. (ed.), *Herbivorous insects, host-seeking behaviour and mechanisms*. Academic Press, pp. 125–157.
- Steinger, T. and Müller-Schärer, H. 1992. Physiological and growth responses of *Centaurea maculosa* (Asteraceae) to root herbivory under varying levels of interspecific plant competition and soil nitrogen availability. – *Oecologia* 91: 141–149.
- Tammaru, T., Kaitaniemi, P. and Ruohomäki, K. 1995. Oviposition choices of *Epirrita autumnata* (Lepidoptera: Geometridae) in relation to its eruptive population dynamics. – *Oikos* 74: 296–304.
- Taylor, K. L., Grace, J. B. and Marx, B. D. 1997. The effects of herbivory on neighbor interactions along a coastal marsh gradient. – *Am. J. Bot.* 84: 709–715.
- Tonhasca, A. and Byrne, D. N. 1994. The effects of crop diversification on herbivorous insects: a meta-analysis approach. – *Ecol. Entomol.* 19: 239–244.
- Trenbath, B. R. 1993. Intercropping for the management of pests and diseases. – *Field Crops Res.* 34: 381–405.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. – *Ecology* 72: 1253–1266.
- Turchin, P. 1998. Quantitative analysis of movement. – Sinauer Associates.
- Vandermeer, J. 1989. The ecology of intercropping. – CUP, Cambridge.
- Vilá, M. and Lloret, F. 1996. Herbivory and neighbour effects on the sprout demography of the Mediterranean shrub *Erica multiflora* (Ericaceae). – *Acta Oecol. Oecol. Plant.* 17: 127–138.
- Visser, J. H. 1986. Host odor perception in phytophagous insects. – *Annu. Rev. Entomol.* 13: 121–144.
- Wahl, M. and Hay, M. E. 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. – *Oecologia* 102: 329–340.

- WallisDeVries, M. F., Laca, E. A. and Demment, M. W. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. – *Oecologia* 121: 355–363.
- Watt, A. D. 1992. Insect pest population dynamics: effects of tree species diversity. – In: Cannell, M. G. R., Malcolm, D. C. and Robertson, P. A. (eds), *The ecology of mixed-species stands of trees*. Blackwell, pp. 267–275.
- Whelan, C. J., Brown, J. S., Schmidt, K. A. et al. 2000. Linking consumer-resource theory and digestive physiology: application to diet shifts. – *Evol. Ecol. Res.* 2: 911–934.
- White, J. A. and Whitham, T. G. 2000. Associational susceptibility of cottonwood to a box elder herbivore. – *Ecology* 81: 1795–1803.
- Whitham, T. G., Maschinski, J., Larson, K. C. et al. 1991. Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. – In: Price, P. W. et al. (eds), *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. J. Wiley & Sons, pp. 227–256.
- Willis, A. J., Groves, R. H. and Ash, J. E. 1998. Interactions between plant competition and herbivory on the growth of *Hypericum* species: a comparison of glasshouse and field results. – *Aust. J. Bot.* 46: 707–721.
- Willmer, P. G., Hughes, J. P., Woodford, J. A. T. et al. 1996. The effects of crop microclimate and associated physiological constraints on the seasonal and diurnal distribution patterns of raspberry beetle (*Byturus tomentosus*) on the host plant *Rubus idaeus*. – *Ecol. Entomol.* 21: 87–97.
- Wootton, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. – *Ecology* 75: 1544–1551.
- Zhang, Q. H. 2001. Olfactory recognition and behavioural avoidance of angiosperm non-host volatiles by conifer bark beetles. PhD thesis of the Swedish Univ. of Agricultural Sciences. – *Acta Universitatis Agriculturae Sueciae: Agraria* 264.