

### **Vegetational complexity – the influence of plant diversity, chemical diversity and vegetation structure on herbivores and their natural enemies**

**Abstract.** When characterising vegetational complexity and its influence on herbivore-carnivore interactions, two main components are distinguishable: plant species diversity on the one hand and vegetation structure on the other. This review surveys (a) how plant species diversity affects herbivores and higher trophic levels, particularly with regard to the implications of plant species composition on olfactory orientation of arthropods. Further, it is highlighted (b) how vegetation structure *per se* can influence herbivores and their natural enemies. Finally, the (c) available information on plant species/chemical diversity and structural complexity is condensed to provide new impulses on the relationship between vegetational complexity and arthropod orientation, which take into account that volatile chemical diversity might change with both plant species composition and structural complexity. Since vegetation structure can influence access or exposure to chemical cues, this interference could have an effect on the perception of chemical diversity by herbivores and higher trophic levels.

**Key words:** arthropods · carnivore · habitat complexity · herbivore · plant species composition · plant structures · odour blends · orientation · vegetation

## Introduction

An important question in ecological research to date is how the species composition and the vegetation structure of habitats based on vascular plants influence the response of individuals and populations of arthropods. The plant species diversity and the associated diversity of plant secondary compounds as well as the structural complexity of plants contribute to the vegetational complexity of habitats. Understanding the effects of vegetational complexity on plant-arthropod interactions could be fundamental to manipulate environmental spatial heterogeneity and modify managed habitats to maintain ecosystem functioning and stability (Bukovinszky 2004, Butler *et al.* 2007, Tylianakis *et al.* 2007). A wide range of studies investigated the impact of heterogeneous plant communities on arthropod orientation and performance (for reviews see Kagata and Ohgushi 2006, Agrawal *et al.* 2006). Substantial knowledge was gathered from agroecosystems, wherein crop diversification is used as a tool to suppress herbivorous pest insects or enhance effectiveness of their antagonists (for reviews see Andow 1991, Tonhasca and Byrne 1994, Stamps and Linit 1998, Landis *et al.* 2000, Sunderland and Samu 2000, Hooks and Johnson 2003, Norris and Kogan 2005). So far, experimental studies produced contradicting results regarding the effect of plant diversity on arthropod individuals and populations. Various investigations provided insight into the relationship between olfactory orientation of arthropods and plant species identity and composition. Plant odours significantly influence the location of host plants by herbivores and the location of hosts and prey by carnivores (e.g. reviewed in Dethier 1982, Visser 1986, Vet and Dicke 1992, Steidle and van Loon 2003, Bruce *et al.* 2005, Hilker and Meiners 2006). However, volatiles emitted by non-host plants can alter the olfactory orientation of arthropods towards a target plant (e.g. Uvah and Cooker 1984, Gohole *et al.* 2003a, b). Research in this area focused largely on phytophagous insects or hymenopteran parasitoids, whereas studies on predator species are widely lacking.

In contrast to plant species diversity, less attention has been paid to the question how physical vegetation structure affects individuals and populations of arthropods (but see Kareiva 1983, Lawton 1983, Langellotto and Denno 2004). A number of studies revealed that structural features of the vegetation are an important part of arthropod habitats and can be crucial for reproduction and survival (Wiklund 1984, Bernays and Chapman 1994, Dennis 2004b, Meiners and Obermaier 2004, Tschanz *et*

*al.* 2005, Maes *et al.* 2006). On the other hand, neighbouring plants might physically impair the orientation towards host plants and plants with prey (Finch and Collier 2000). Further, the physical structures of non-host plants can indirectly affect herbivores *via* natural enemies (reviewed in Langellotto and Denno 2004, Shaw 2006). Therefore, in this review more emphasis is placed on studies dealing with the relationship of vegetation structure and arthropod orientation and performance.

Different studies addressed the chemical, optical and other physical properties of plants and several central hypotheses have been developed to give a mechanistic explanation for the responses of arthropods to complex vegetation. The associational-resistance hypothesis (Tahvanainen and Root 1972) and the thereof deduced resource-concentration hypothesis (Root 1973) both predict that plants in high diversity communities should experience less herbivore infestations than plants in low diversity communities. In this context, the enemies hypothesis proposes a greater abundance and diversity of natural enemies in more diverse plant communities (Root 1973). More recently, the disruptive crop hypothesis and the trap crop hypothesis (Vandermeer 1989) were proposed to explain results found in agricultural field studies. Both assumptions imply primarily chemical properties of plants to repel or attract herbivorous pests. In contrast, Finch and Collier (2000) put forward the appropriate-inappropriate landings hypothesis. This hypothesis relies mainly on the physical presence of different plant species within the habitat and emphasises the importance of visual stimuli during host plant selection of insects. Evidence has been gathered for each of the proposed theories, nevertheless they are still under heavy debate. When considering the available knowledge on the impact of vegetational complexity on arthropods, it appears that some possible interactions have been neglected so far.

At present, we are not aware of any hypothesis that deals with the relationship between plant species diversity and chemical diversity of the vegetation odour. How plant species diversity influences the composition of volatile blends and with it the chemical environment of arthropod habitats is largely unknown to date. Within a habitat the composition and chemical diversity of the volatile bouquet might change with plant species composition (Hadacek 2002, Dudareva *et al.* 2006). In highly diverse habitats host plant and prey location might require higher sensory perceptive power or better sensory integrative abilities for herbivores and carnivores due to the presence of various unspecific plant cues (Bernays 2001, Hadacek 2002). Furthermore, a possible interaction between vegetation structure and volatile chemical diversity has

not been addressed in this context so far. In addition to plant diversity, the structural complexity of the vegetation might influence the emission of plant volatiles, since vegetation structures might change the microclimatic conditions within habitats. Moreover, plant structures can alter odour plume characteristics (for reviews see Murlis *et al.* 1992, Vickers 2006). Thus, plant structure could interfere with the ability to locate host plants or plants with prey of herbivores and carnivores that try to follow a specific odour plume to its source. This might be especially relevant for biological control strategies to manage pest organisms in cropping systems. Therefore, the aim of this review is to elucidate how plant diversity, volatile chemical diversity and vegetation structure may act ‘in concert’, and how these interactions in turn affect herbivores and higher trophic levels.

When addressing in this review the major issues mentioned above, emphasis is placed on representative examples of research papers mainly from the last decade. Included are field and laboratory studies ranging from natural to intensively managed ecosystems. To keep measures on habitat characteristics qualitatively comparable, only studies are considered that measure vegetational complexity on a within-habitat or a smaller spatial scale. The focus is on the orientation of arthropods towards hosts, prey and mates in terrestrial above-ground interactions. In general, the consequences of the interaction of arthropods with vegetational complexity regarding movement, reproduction, abundance, herbivory and arthropod species diversity is highlighted. The review is divided into three main sections. Initially, an overview is given on the effects and mechanisms, which (a) plant diversity and (b) vegetation structure exert on individual performance, population dynamics and community structure of arthropods. Finally, we draw attention to (c) the interplay between plant diversity, volatile chemical diversity and structural complexity, i.e. the composition of odour blends and the shape of odour plumes. On the basis of the current knowledge the aim is to integrate the impact of plant diversity and vegetation structure on chemical diversity into new hypotheses.

## **Plant diversity**

### **Effects of plant species diversity on herbivores**

Plant species diversity can affect colonisation, abundance and reproduction of herbivorous insects. As a consequence, it also influences the level of herbivory or plant damage. In natural or manipulated plant communities both negative and positive effects of plant species diversity on herbivorous insects have been observed (Table 1). For instance, in natural habitats with higher plant diversity the colonisation rate and abundance of a specialist chrysomelid beetle was reduced (Bach 1984, 1993b). Likewise, higher plant species diversity decreased the infestation rate of host plants by a sap-feeding herbivore (Wilsey and Polley 2002) or the herbivore load (Otway *et al.* 2005) in experimental plant communities with native plant species. Similar outcomes of plant diversity on herbivore abundance have been reported for managed systems, which mostly comprise crop plant communities. However, Garcia and Altieri (1992) and Andow (1990) detected a negative influence of crop polyculture on the population densities of herbivores that occurred as pests on broccoli or bean cultivars. The abundance of several pest species on *Brassica* crops was reduced in field and laboratory cage experiments when crop plants were undersown with clover (Finch and Kienegger 1997). In managed home and municipal landscapes the abundance of an herbivorous bug was diminished in high plant diversity (Shrewsbury and Raupp 2000). In contrast, companion aromatic herbaceous plants or dried plant material did not affect or even augmented the abundance of the Japanese beetle, *Popillia japonica*, on cultivated roses (Held *et al.* 2003). Plant diversity enhanced the herbivore species richness of thistle communities in arable wheat fields within intensively managed landscapes (Clough *et al.* 2007). In this investigation high weed cover in organic managed fields represented high plant diversity, which also increased the likelihood of host plant colonisation. In natural habitats the abundance of galls and the species richness of gall-forming insects, determined on various occurring host plants, correlated negatively with plant diversity (Cuevas-Reyes *et al.* 2003).

**Table 1.** Effects of enhanced plant species diversity on different herbivore species or herbivore communities in natural and managed systems. The direction of significant effects (+/positive, -/negative) is given, brackets indicate a tendency; open circles (o) indicate that no significant effect was found.

Herbivore species/guild	Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Chrysomelid beetle	Diversity of plant functional groups	Natural sand dune plant community	Habitat	Colonisation	-	Bach 1993b
Chrysomelid beetle	Low-diversity open patches and high-diversity forest patches	Natural tropical rain forest	Habitat	Colonisation Abundance	- -	Bach 1984
Tingid bug	Variable vegetation texture	Home and municipal managed habitats	Habitat	Abundance	-	Shrewsbury and Raupp 2000
Scarabid beetle	Aromatic companion plants, dried plant material	Mixed horticultural plantings	Habitat	Abundance	+ / o	Held <i>et al.</i> 2003
Clastopterid bug	Variable evenness of grass and forb species	Experimental plant communities	Habitat	Abundance	-	Wilsey and Polley 2002
Chrysomelid beetle	Monocropped and mixed broccoli stands	Crop plant communities	Habitat	Density	-	Garcia and Altieri 1992
Coccinellid beetle	Monocropped and mixed bean stands	Crop plant communities infested/uninfested with weeds	Habitat	Density	-	Andow 1990
Formicid herbivore	Coffee monocultures or polycultures with variable shade tree species	Coffee agroforestry systems	Habitat	Herbivory	-	Varón <i>et al.</i> 2007
Thripid herbivore	Chrysanthemum undersown with subterranean clover	Mixed horticultural plantings	Greenhouse	Herbivory	+	Den Belder <i>et al.</i> 1999

Eight herbivore species	<i>Brassica</i> plants undersown with clover	Crop plant communities	Field/lab cages	Abundance	-	Finch and Kienegger 1997
Nine specialist insect herbivores	Variable levels of plant species/functional group richness	Experimental native plant communities	Habitat	Herbivore load	-	Otway <i>et al.</i> 2005
Gall-forming insect community	Sites differing in biotope type/topography	Natural tropical rain forest	Habitat	Gall abundance Species richness	- -	Cuevas-Reyes <i>et al.</i> 2003
Herbivore community	Single/mixed species plots with tree seedlings	Natural tropical rain forest	Habitat	Herbivory	-	Massey <i>et al.</i> 2006
Herbivore community	Artificial host plant plots in arable fields	Organic and conventional wheat fields	Habitat	Colonisation Species richness	+ +	Clough <i>et al.</i> 2007
Herbivore community	Gradient of plant species diversity	Extensively managed hay meadows	Habitat	Herbivory Abundance	- (+)	Unsicker <i>et al.</i> 2006
Herbivore community	Variable species richness of three functional groups	Experimental plant communities	Habitat	Herbivory	+	Mulder <i>et al.</i> 1999
Herbivore community	Variable levels of species/functional group richness and functional group composition	Experimental plant communities	Habitat	Herbivory	+	Prieur-Richard <i>et al.</i> 2002
Herbivore community	Variable levels of species richness of four functional groups	Experimental native plant communities	Habitat	Herbivory	(+)	Scherber <i>et al.</i> 2006
Herbivore community	Monocultures or paired mixtures of birch with pine or spruce	Managed boreal forest	Habitat	Abundance Herbivory	- -	Vehviläinen <i>et al.</i> 2006

The relationship between plant species diversity and the level of herbivory was studied in detail within experimentally established plant communities varying in their degree of diversity. These investigations commonly revealed an increase in herbivory with increasing plant species diversity (Mulder *et al.* 1999, Prieur-Richard *et al.* 2002, Scherber *et al.* 2006). Although Scherber *et al.* (2006) detected a weak enhancing effect of plant species richness on herbivore damage, plant functional group such as growth form, life-history traits or the capacity for nitrogen-fixation by legumes turned out to be the best predictor for the extent of herbivory. The presence of legumes strongly decreased, whereas presence of grasses increased herbivory at the community level in this experimental investigation. In a greenhouse study, intercropping of ornamental host plants with non-host plants resulted in an elevated damage of host plants caused by thrips (den Belder *et al.* 1999). On the contrary, Unsicker *et al.* (2006) found a negative correlation of herbivory with plant species richness. However, in this study the abundance of insect herbivores tended to increase with increasing plant species richness within a successional gradient of semi-natural grasslands. Likewise, the herbivory of a focal tree species was diminished within diverse stands of different native tree seedling species in a tropical rainforest (Massey *et al.* 2006). Varón *et al.* (2007) investigated the degree of herbivory caused by the leaf-cutting ant, *Atta cephalotes*, in coffee plantations with differential shade tree species diversity. The study revealed that the herbivory of coffee leaves decreases with increasing diversity of shade trees within the plantations. In Scandinavian forest plantations the abundance of herbivores infesting birch trees and the intensity of herbivory were decreased in stands mixed with other tree species compared to birch monocultures (Vehviläinen *et al.* 2006). The effects of variable tree species diversity on herbivorous arthropods in forests have recently been summarised and evaluated with meta-analysis in a number of reviews (Koricheva *et al.* 2006, Jactel and Brockerhoff 2007, Vehviläinen *et al.* 2007). Consistently, it is reported that diverse tree stands reduce the damage caused by different herbivore species. Nevertheless, the outcome of a specific investigation may vary according the dietary specificity of the investigated species or the type of feeding guild and may further be determined by host tree species. Therefore, forest diversity may not generally and uniformly reduce insect herbivory (Koricheva *et al.* 2006, Vehviläinen *et al.* 2007).



### **Effects of plant species diversity on carnivores and their interaction with herbivores**

Plant diversity can exert direct or indirect influences on natural enemies and their interactions with prey or hosts. Recent investigations revealed mixed results regarding the impact of plant diversity on predators or parasitoid performance and abundance (Table 2). A number of studies dealt with the abundance of parasitoid individuals, the percentage of parasitism and the diversity of parasitoid assemblages in differently diverse plant communities. For example, interplanting cabbage with other crop plant species enhanced the percentage of parasitism caused by the larval parasitoid *Cotesia plutellae* and reduced larval densities of its host *Plutella xylostella* (Bach and Tabashnik 1990). In contrast, Langer (1996) showed that the risk of parasitism caused by different parasitoid species for cabbage root fly, *Delia radicum*, was reduced in diverse crop plant communities. In grazed semi-natural woodland sites increasing plant species richness correlated positively with parasitoid density and parasitism rate (Vanbergen *et al.* 2006). Research work in an Amazonian rain-forest mosaic elucidated that the number of plant species contributes positively to the number of parasitoid wasp species for two chosen ecologically defined parasitoid groups (Sääksjärvi *et al.* 2006). In addition, increasing tree species diversity is often associated with increased parasitoid abundance and diversity, as it was shown in for farm woodland habitats or cacao agroforestry systems (Sperber *et al.* 2004, Fraser *et al.* 2007).

Investigations on predatory arthropods generally analysed the abundance of occurring predator species or their foraging success, expressed in the number of prey consumed. In forest polycultures of Mediterranean pine stands, the abundance of a native predatory bug was positively affected, whereas the abundance of its prey, the pine bast scale bug, was negatively affected by tree species diversity (Jactel *et al.* 2006). In Finnish forests the survival of autumnal moth, a severe pest on birch trees, and the abundance of arthropod predators was investigated in experimental plots, where birch was grown in either monoculture or in varying dicultures together with pine, spruce or alder (Riihimäki *et al.* 2005). The birch-pine mixture contributed to a weak reduction in survival of moth larvae and an increase in ant abundance. In spite of that, the study did not detect an influence of tree species composition or diversity on the occurrence of spiders and parasitoids. Similarly, natural enemies of soybean

**Table 2.** Effects of enhanced plant species diversity on different carnivore species and their herbivorous prey/hosts or carnivore communities in natural and managed systems. The direction of significant effects (+/positive, -/negative) is given, brackets indicate a tendency; open circles (o) indicate that no significant effect was found.

Carnivore/Herbivore species/guild	Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Braconid parasitoid Plutellid moth	Monocropped cabbage or interplanted with tomato	Crop plant communities	Habitat	Parasitism rate Herbivore density	+ -	Bach and Tabashnik 1990
Pteromalid parasitoid Tephritid fly	Sites grazed or ungrazed by livestock	Artificial host plant plots in woodlands	Habitat	Parasitism rate Herbivore abundance	- +	Vanbergen <i>et al.</i> 2006
Anthocorid bug Margarodid bast scale	Variable composition of three pine species	Mediterranean pine forest	Habitat	Predator abundance Herbivore abundance	+ -	Jactel <i>et al.</i> 2006
Wood ants and spiders Geometrid moth	Variable tree species composition	Conifer-dominated boreal forest	Habitat	Ant abundance Spider abundance Herbivore survival	+ o (-)	Riihimäki <i>et al.</i> 2005
Staphylinid/Cynipid parasitoid	Monocropped cabbage or undersown with clover	Crop plant communities	Habitat	Parasitism rate	-	Langer <i>et al.</i> 1996
Three coccinellid and heteropteran predators	Mono/polycultures with three host plants	Laboratory microcosm	Microhabitat	Predation rate	-	Aquilino <i>et al.</i> 2005
Various egg predators	Monocropped and mixed squash stands	Crop plant communities	Habitat	Predation rate	-	Harmon <i>et al.</i> 2003
Foliage inhabiting natural enemies	Mono/polycultures of corn and soybean	Crop plant communities	Habitat	Carnivore abundance	+	Tonhasca 1993
Hymenopteran parasitoid community	Heterogeneous habitat patches	Natural tropical rain forest	Habitat	Species composition Species richness	+ +	Sääksjärvi <i>et al.</i> 2006
Ichneumonid parasitoid community	Variable tree species diversity	Farm woodland	Habitat	Abundance Diversity	+ +	Fraser <i>et al.</i> 2007
Hymenopteran and chrysoidea parasitoid community	Variable tree and herbaceous plant species richness	Cacao agroforestry system	Habitat	Diversity	+	Sperber <i>et al.</i> 2004

herbivores, such as predaceous bugs, beetles, spiders and parasitoid wasps, sampled in the foliage were enhanced in a more diverse plant assemblage consisting of soybean-corn intercropping (Tonhasca 1993). On the contrary, Harmon *et al.* (2003) detected that the predation rate of squash bugs was lower in diverse stands, because the herbivores' eggs were aggregated and much more unevenly distributed within polycultures of squash, bean and corn. On a smaller spatial scale in a greenhouse study three natural enemies of the pea aphid were negatively affected by an increase in plant diversity in microcosm experiments with three different host plant species (Aquilino *et al.* 2005).

### **Effects of plant species diversity on herbivore-carnivore communities**

In general, the data of recent studies, which are summarised here, revealed positive effects of high plant diversity on abundance and species richness in arthropod communities consisting of herbivores, carnivores and detritivores (Table 3). The positive effects of vegetational diversification seem to be independent of the habitat type wherein the surveys were performed. Investigations conducted in natural and semi-natural as well as in agricultural habitats support this tendency. Jonas *et al.* (2002) found that high plant species diversity results in high diversity and species richness of macroinvertebrate communities occurring in the plant canopy of natural or semi-natural grasslands. In this study, a further analysis of two focal insect groups showed that for coleopteran insects plant species composition was highly relevant whereas for orthopteran species mechanical disturbance seemed to be more critical. In a similar study, the diversity of herbivores and predators in unmanaged grassland, but not in managed pastures, increased with increasing plant species diversity (Pearson and Dyer 2006). In line with these findings, Siemann *et al.* (1999) detected a positive correlation of plant diversity with species richness of herbivores and parasites, but not with predators and detritivores, in different successional stages of abandoned agricultural fields. However, plant species diversity did not affect the overall arthropod abundance in this study. Moreover, other investigations performed in semi-natural grasslands revealed that a diverse plant species assemblage has a negative influence on arthropod abundance (Rambo and Faeth 1999, Perner *et al.* 2005). In contrast, diverse experimental plant communities assembled from native species were shown to have a positive effect on the abundance of herbivores, such as leafhoppers and aphids, but a

**Table 3.** Effects of enhanced plant species diversity on arthropod communities including both herbivorous and carnivorous species in natural and managed systems. The direction of significant effects (+/positive, –/negative) is given; open circles (o) indicate that no significant effect was found.

Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Different types of montane hay meadows	Semi-natural grassland	Habitat	Arthropod abundance	–	Perner <i>et al.</i> 2005
Different types of land use	Semi-natural grassland	Habitat	Arthropod diversity/ Species richness	+ +	Jonas <i>et al.</i> 2002
Grazed and ungrazed meadows	Semi-natural grassland	Habitat	Insect abundance/ Species richness	– ○	Rambo and Faeth 1999
Sites grazed or ungrazed by cattle	Semi-natural grassland	Habitat	Diversity of Herbivores Predators	+ +	Pearson and Dyer 2006
Variable plant species richness with three functional groups	Experimental native plant communities	Habitat	Abundance of Herbivores Predators Parasitoids	+ – ○	Koricheva <i>et al.</i> 2000
Variable plant species richness with four functional groups	Experimental native plant communities	Habitat	Arthropod abundance/ Species richness	○ +	Siemann <i>et al.</i> 1998
Variable grassland species richness with five functional groups	Experimental native plant communities	Habitat	Insect abundance/ Species richness	+ +	Haddad <i>et al.</i> 2001

Variable grassland species richness	Experimental native plant communities	Habitat	Abundance/Species richness of Herbivores Carnivores	+ / + ○ / +	Knops <i>et al.</i> 1999
Wildflower areas with mixed species composition and variable age	Field margin strips	Habitat	Bug abundance/ Species richness	+ +	Frank and Künzle 2006
Variable plant species composition	Field margin strips	Habitat	Arthropod abundance/ Species richness	+ +	Asteraki <i>et al.</i> 2004
Varying age of grassland field sites	Abandoned agricultural fields	Habitat	Arthropod abundance/ Species richness	○ +	Siemann <i>et al.</i> 1999
Weedy and weed-free cotton plots	Crop plant communities	Habitat	Abundance/Diversity of Herbivores Predators	+ +	Showler and Greenberg 2003

negative effect on predator abundance (Koricheva *et al.* 2000). Parasitoids were not influenced by plant species diversity in this study. Similarly, Knops *et al.* (1999) detected an increase of herbivore abundance with increasing plant species diversity. However, the abundance of carnivores was not influenced by plant diversity, but herbivore and carnivore species richness was positively correlated with plant species diversity (Knops *et al.* 1999). In the same way, the overall abundance of arthropods was not affected by a diverse plant species assemblage, but arthropod species richness was positively correlated with plant diversity in an investigation using artificially established grassland habitats (Siemann *et al.* 1998). Another experimental field study detected a positive influence of plant diversity on both insect species richness and abundance in different grassland communities (Haddad *et al.* 2001). Equal relationships between plant species diversity and invertebrate abundance and species diversity respectively were found in agricultural ecosystems composed of mixed crop plant communities or semi-natural field margins (Frank and Künzle 2006, Asteraki *et al.* 2004, Showler and Greenberg 2003).

### **Mechanisms acting upon herbivores regarding plant species diversity**

The types of responses of phytophagous insects to plant species diversity vary widely, even though the here gathered information suggests that vegetational diversification mostly exerts a negative influence on herbivores. The mechanisms underlying the given effects are still under discussion and in order to explain the observed effects, several modalities have been detected or proposed (Tahvanainen and Root 1972, Root 1973, Vandermeer 1989, Finch and Collier 2000) which are covered in the following section. The possibly involved mechanisms address olfactory and visual abilities of arthropods that influence their orientation behaviour when confronted with vegetational diversity (Table 4). Since volatile plant cues play a major role in host plant location of herbivores (for reviews see Visser 1986, Zhang and Schlyter 2004, Bruce *et al.* 2005), especially in long-range searching behaviour, a lot of studies dealt with the impact of plant odours from different plant species on the orientation behaviour of herbivores towards host plants. Particularly, the influence of non-host plant odours during the host location process was examined, commonly in laboratory studies using different types of olfactometer devices. The volatile constituents of plants other than host plants can interfere with the olfactory orientation of phytophagous

**Table 4.** Behavioural responses of herbivores to olfactory or visual cues derived from enhanced plant species diversity and underlying mechanisms. The direction of significant responses (+/positive, -/negative) are given, brackets indicate a tendency; open circles (o) indicate that no significant response was detected.

Herbivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Chrysomelid beetle	Mixed odour blends of potato (host plant) and tomato (non-host plant)	Laboratory, locomotion compensator, whole plant odour source	Olfactory	-	Odour masking	Thiery and Visser 1986, 1987
Three aphidid herbivores	Mixed odour blends of different host and non-host plants	Laboratory, y-tube olfactometer, plant leaves	Olfactory	-	Odour masking/ Repellency	Nottingham <i>et al.</i> 1991
Aphidid herbivore	Host plant odours mixed with single synthetic non-host plant compounds	Laboratory, linear-track olfactometer, plant leaves	Olfactory	-	Odour masking/ Repellency	Hardie <i>et al.</i> 1994
Aphidid herbivore	Mixed odour blends of sweet pepper (host plant) and chives (non-host plant) or leek plant extracts	Laboratory, two-way olfactometer, whole plant odour source, plant extracts	Olfactory	-	Odour masking/ Repellency	Amarawardana <i>et al.</i> 2007
Nitidulid beetle	Host plant flowers treated with non-host plant essential oils	Laboratory, olfactometer	Olfactory	-	Odour masking/ Repellency	Mauchline <i>et al.</i> 2005
Scarabid beetle	Dry plant material of non-host aromatic plants or companion planting	Field (intercropping) experiments	Olfactory	+	Attraction	Held <i>et al.</i> 2003

Table 4. (continued)

Herbivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Plutellid moth	Cabbage (host plant) monocrop or mixed with lettuce (non-host plant)	Laboratory minicrop design, y-tube olfactometer, wind tunnel	Olfactory/Visual	○ / (–)	No olfactory interference, slight visual interference	Couty <i>et al.</i> 1997
Two anthomyiid flies	<i>Brassica</i> or <i>Allium</i> host plants surrounded by four aromatic non-host plants	Field and laboratory intercropping experiments	Olfactory/Visual	–	Visual interference	Finch <i>et al.</i> 2003
Anthomyiid fly	Cabbage (host plant) surrounded by clover (non-host plant)	Laboratory, real plants and artificial plant models	Olfactory/Visual	–	Visual interference	Morley <i>et al.</i> 2005
Anthomyiid fly	<i>Brassica</i> host plants grown in diverse backgrounds	Laboratory, real plants and artificial plant models	Olfactory/Visual	–	Visual interference	Kostal and Finch 1994



insects in several ways. Tahvanainen and Root (1972) for example proposed in the ‘associational resistance’ hypothesis that non-host plant odours might exert a negative influence on herbivore response.

*The role of olfactory stimuli regarding herbivore orientation*

The presence of non-host plant odours may mask the odours of the host plant in a way that a generally positive response to the host plant is neutralised. This phenomenon was first described in the Colorado potato beetle, *Leptinotarsa decemlineata*. Thiery and Visser (1986, 1987) demonstrated that mixing the odours of the host plant with the odours of a non-host plant significantly altered the beetle’s anemotactic response to host plant volatiles tested on a locomotion compensator. The usually highly attractive volatile blend of potato plants (*Solanum tuberosum*) was no longer attractive after mixing the odours of potato with odours from tomato plants (*Lycopersicon hirsutum*) in a wind tunnel. Testing the odours of the non-host plant alone confirmed that the volatile bouquet of tomato was neither attractive nor repellent to potato beetles. Studies on other insect species such as aphids document similar results (Nottingham *et al.* 1991, Amarawardana *et al.* 2007). In contrast to the investigations on the Colorado potato beetle, the experiments with aphids showed that even a normally repellent non-host plant odour can result in a neutral response when offered in combination with an attractive host plant odour. The bean aphid, *Aphis fabae*, is repelled by the volatile blend of savory (*Satureja hortensis*) which is not a host plant of this herbivore species (Nottingham *et al.* 1991). Despite this finding, the odours of savory leaves masked the odours of bean leaves, when they were offered simultaneously to bean aphids in equal amounts, since the tested individuals were not attracted to the mixed volatile bouquet anymore.

Besides neutralising the response of herbivores towards the odours from their host plants, non-host plant odours may repel herbivores and thus, can impair host plant finding. Laboratory studies with different aphid species and the pollen beetle demonstrated that adding non-host plant volatiles to the odour blend of the host plant changes the orientation behaviour of phytophagous insects to the host plants and elicits avoidance behaviour in the observed animals (Nottingham *et al.* 1991, Hardie *et al.* 1994, Mauchline *et al.* 2005, Amarawardana *et al.* 2007). The study from Nottingham and colleagues further made evident, that the ratios of the offered amount of plant material play a considerable role for the observed olfactory response of the herbivores

towards the mixed volatile bouquets. The odours of several non-host aromatic plants of the cabbage aphid, *Brevicoryne brassicae*, were tested either alone or in combination with leaves of Brussels sprouts (*Brassica oleracea*), a preferred host plant of this herbivore. Non-host plant material was added in varying amounts to the host plant material offered to the aphids in y-tube olfactometer tests. The cabbage aphids showed avoidance behaviour when the odours of tansy leaves (*Tanacetum vulgare*) were offered alone or in a 1:1 mixture with leaves of Brussels sprouts. However, cabbage aphids were not repelled by a ratio of 1:4; in this case the tansy odours rather masked the host plant odours. In contrast, savory odours did not elicit any response in cabbage aphids, but mixing the volatile blend of savory with that of Brussels sprouts resulted in a repellent response in the observed aphids. Olfactometer tests and electrophysiological experiments elucidated that already single compounds which are emitted by non-host plants, for example glucosinolates or methyl salicylate, may cause the repellent effect (Nottingham *et al.* 1991, Hardie *et al.* 1994).

Contrary to repellent effects, volatiles derived from non-host plants might also attract herbivores. Held *et al.* (2003) described that odours emitted from dry plant material of aromatic plants significantly attracted a higher number of Japanese beetles, *Popillia japonica*, to ornamental host plants, such as rose bushes, in field experiments in comparison with control plots. Mesh bags containing leaves of aromatic herbs or other sources of putatively repellent non-host volatiles, e.g. crushed spearmint or pepper, fennel seeds and cedar shavings, were placed around the rose bushes to test their potentially protective properties. In the apple fruit moth, *Argyresthia conjugella*, it was discovered that male and female moths are attracted by odours of cultivated apple varieties, which are not suitable for larval survival and are therefore considered as non-host plants. Bengtsson *et al.* (2006) demonstrated that the odour bouquet of apple (*Malus domestica*) lacks some of the attractive compounds in comparison to the odour bouquet of the host plant rowan (*Sorbus aucuparia*). But the remaining compounds that are present in both of the volatile blends of the host plant and non-host plant proved to be sufficient for attracting the apple fruit moth to the non-host plant.

#### *The role of visual stimuli regarding herbivore orientation*

On the other hand, visual attributes of plants such as colour may affect herbivores when orienting towards their host plants. Similar to olfactory cues, visual signals can disrupt the host location process of phytophagous insects. Already Prokopy and Owens

(1983) suggested that non-host vegetation might be attractive or disruptive through spectral characteristics such as colour and could interfere with the visual apparency of host plants. For arthropods it might be difficult to discriminate host plants growing in diverse stands from the surrounding non-host plants, because the colour contrast is reduced and the hue and saturation of leaf colours might be quite similar, even so plant species can differ in their spectral properties. Finch and Collier (2000) developed the ‘appropriate/inappropriate landings’ theory, which states that most herbivorous insects are eager to land on any green object, rather than on bare soil. In more diverse vegetation a greater number of landings are supposed to be ‘inappropriate’, because they occur on non-host plants and thus, non-host plants might disrupt host plant finding. A study with the cabbage root fly, *Delia radicum*, and the onion fly, *Delia antiqua*, revealed that a variety of companion aromatic plant species, tested as potential disruptive agents, did not interfere with host plant finding because of volatile emission, but rather by their green leaves (Finch *et al.* 2003). The flies stayed longer on leaves of non-host plants than on leaves of host plants (Finch *et al.* 2003, Morley *et al.* 2005). However, physical plant attributes, such as leaf area or height, contributed partly to the disruptive effect of the companion plants. In a study conducted by Kostal and Finch (1994) olfactory cues were excluded by using artificial green plants, which made evident that visual characteristics of plants may have the potential to disrupt host plant finding. However, whether the ‘appropriate/inappropriate landings’ hypothesis is applicable seems to depend on the nature of investigate herbivore species. Couty *et al.* (2006) revealed in a combination of experiments using an olfactometer, a wind tunnel and a semi-field setup with mixed crops that host plant location of the diamondback moth, *Plutella xylostella*, is predominantly guided by olfaction and only marginally by vision. Especially, by performing a part of the experiments under red light conditions Couty and colleagues confirmed that female moths display directed flights towards host plants in a mixture of host and non-host plant species.

### **Mechanisms acting upon carnivores regarding plant species diversity**

Olfactory orientation during host or prey search is of comparable relevance for natural enemies as it is for herbivores during host plant location. Plants with hosts or prey emit valuable volatile cues, which guide predators and parasitoids to their victims (e.g. reviewed in Vet and Dicke 1992, Dicke and van Loon 2000, Steidle and van Loon

2003, Hilker and Meiners 2006). However, in diverse plant vegetation the host location process guided by chemical host plant signals can be impaired by the odours of non-host plants present in the surroundings. Similar to the identified mechanisms underlying herbivore responses to mixed odour bouquets, analogue modalities were detected or proposed for natural enemies (Table 5). Here again, laboratory or semi-field experiments analysing the olfactory response of carnivorous arthropods helped to elucidate the operating mechanisms. However, the performed investigations concentrated largely on the behaviour of parasitoid species compared predator species. Furthermore, the role of different visual cues present in diverse habitats has been almost omitted so far regarding carnivore behaviour.

The phenomenon of odour-masking, which was described several times for herbivores, has rarely been investigated in carnivorous arthropods. An early study in 1960 conducted by Monteith detected that mixing an attractive host plant odour blend with non-host plant odours, which were neither attractive nor repellent on their own, inhibited the response of parasitic tachinid flies towards host plants both in the laboratory and in the field (Monteith 1960). Another example was given for a hymenopteran parasitoid species parasitising the eggs of a leaf beetle (Randlkofer *et al.* 2007, see chapter 2). The attraction to the host plant yarrow (*Achillea millefolium*) was masked by adding the odours of the non-host plant thyme (*Thymus vulgaris*) to the offered odour blend in a laboratory olfactometer test. In contrast to these examples Dicke *et al.* (2003) did not discover an overall effect of mixing the blends of different plant species on the host location behaviour of the predatory mite, *Phytoseiulus persimilis*. In olfactometer and semi-field experiments the odours of prey-infested lima bean plants (*Phaseolus lunatus*) and the odours of Brussels sprouts plants infested with a non-prey species did not camouflage the attractive odours of the plant harbouring prey. Measurements of the volatile profiles revealed that the two plant species possess a very distinct compound pattern and show no overlap in those compounds, which are attractive for the predatory mite.

Other studies provided evidence that non-host plant volatiles can have a repellent effect on parasitoids (Gohole *et al.* 2003b, Wäckers 2004, Sanon *et al.* 2006). Gohole *et al.* (2003b) tested the response of an ichneumonid parasitoid, *Dentichasmias busseolae*, which attacks a cereal stem borer, *Chilo partellus*, on maize or sorghum. When the odour of molasses grass, a non-host plant, was added to the odour bouquet of maize or sorghum respectively the odour mixture repelled the parasitoids.

**Table 5.** Behavioural responses of carnivores to olfactory or visual cues derived from enhanced plant species diversity and underlying mechanisms. The direction of significant responses (+/positive, -/negative, ±/positive and negative) is given; open circles (o) indicate that no significant response was detected.

Carnivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Phytoseiid mite	Mixed odour blends of host infested lima bean plants and non-host infested Brussels sprouts plants	Laboratory, y-tube olfactometer, whole plant odour source	Olfactory	○	No interference	Dicke <i>et al.</i> 2003
Two tachinid parasitoid flies	Mixed odour blends of host and non-host plants	Laboratory, y-tube olfactometer, plant foliage	Olfactory	-	Odour masking	Monteith 1960
Pteromalid parasitoid	Infested cowpea seeds mixed with non-host plant leaves or essential oil	Laboratory, y-tube olfactometer	Olfactory	-	Repellency	Sanon <i>et al.</i> 2006
Ichneumonid parasitoid	Mixed odour blends of infested/uninfested host plants and non-host plants	Laboratory, y-tube olfactometer, whole plant odour source	Olfactory	-	Repellency	Gohole <i>et al.</i> 2003b
Braconid parasitoid	Mixed odour blends of infested/uninfested host plants and non-host plants	Laboratory, y-tube olfactometer, whole plant odour source	Olfactory	+	Attraction	Gohole <i>et al.</i> 2003a
Braconid/Ichneumonid parasitoid	Mixed odour blends of infested/uninfested host plants and non-host plants	Laboratory semi-field setup, wind tunnel, whole plant odour source	Olfactory/Visual	○	No interference with close-range searching behaviour	Gohole <i>et al.</i> 2005

Table 5. (continued)

Carnivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Two braconid parasitoids	Host-infested plants arranged in monoculture or in diculture with non-host plants	Laboratory semi-field setup, wind tunnel, whole plant odour source	Olfactory/Visual	+ / ○	Attraction, no interference	Perfecto and Vet 2003
Ichneumonid parasitoid	Host-infested plants interspersed with uninfested host plants or non-host plants	Laboratory semi-field setup, whole plant odour source	Olfactory/Visual	±	Attraction or visual interference	Bukovinszky <i>et al.</i> 2007

Interestingly, when almost identical experiments were performed with another parasitoid species from the braconid family, *Cotesia sesamiae*, the volatiles emitted by molasses grass had an attractant effect on the tested wasps (Gohole *et al.* 2003a). A subsequent investigation analysed the close-range foraging behaviour of *D. busseolae* in the presence of non-host plant volatiles from molasses grass (Gohole *et al.* 2005). These experiments showed that once a wasp had landed on a host plant the presence of non-host plants nearby did not change the foraging behaviour of the parasitoid. Wäckers (2004) investigated the behavioural response of three different hymenopteran parasitoid species towards the flower odours of eleven plant species naturally occurring in meadows. The study aimed at evaluating, which plant species might effectively enhance parasitoid performance under natural conditions, for example when employing diverse flower strips at field edges for pest control reasons. The olfactometer tests revealed that some of the flower blends were repellent, some were attractive and others again were unattractive to the parasitoids. Therefore, when attempting to augment biological control agents through habitat management plant species composition should be considered (Lavandero *et al.* 2006).

Attractive effects of non-host plant volatiles have been verified in a number of studies investigating the olfactory response of parasitoids to non-host plant species (Takabayashi *et al.* 1991, Gohole *et al.* 2003a, Perfecto and Vet 2003, Bukovinszky *et al.* 2005, 2007). Perfecto and Vet (2003) detected that the generalist hymenopteran parasitoid, *Cotesia glomerata*, is less effective to locate its host, *Pieris rapae*, in dicultures of Brussels sprouts mixed with potato plants than in monocultures of Brussels sprouts. Aim of this study was to evaluate a potential masking effect caused by blending the odours from non-host plants (potato) with those of the host plant species (Brussels sprouts). However, the interference with host location behaviour was due to an attraction of the parasitoids towards the non-host plants. The potato plants had been damaged by feeding of Colorado potato beetle larvae to increase the emission of volatiles. The authors suggest that the parasitoids were attracted to the released general green leaf volatiles. Since the wasps were released downwind of the plants within the utilised wind tunnel setup, aside from olfactory information also visual cues might have played a role. In contrast, the host searching efficiency of the specialist parasitoid, *Cotesia rubecula*, was not reduced in the diculture setup. Bukovinszky *et al.* (2005) elucidated that *Diadegma semiclausum*, a specialist parasitoid of diamondback moth, is attracted by the odours of three *Brassica* host plants and a non-

host plant species when offered against bare soil in a y-tube olfactometer. In spite of that, the parasitoids always preferred the odour bouquet of the *Brassica* host plant species when tested against the odours of barley (*Hordeum vulgare*), which was employed as non-host plant species. In subsequent experiments the searching behaviour of *D. semiclausum* was examined in laboratory semi-field setups, wherein host-infested *Brassica oleracea* plants were interspersed either with white mustard (*Sinapis alba*) or barley (Bukovinszky *et al.* 2007). This investigation revealed that the initial host encounter rate of the parasitoid is reduced in both diculture setups. The odours of uninfested white mustard plants seemed to be more attractive than the odours of host-infested *B. oleracea* plants and hence, white mustard plants devoid of hosts were preferentially searched by the parasitoids. In contrast, the interference of barley with host searching behaviour of *D. semiclausum* was likely due to plant structural properties, since the odour blend of barley differs significantly from *Brassica* host plants (Bukovinszky *et al.* 2005). However, disruption caused by barley odours could not be completely excluded because of the test conditions.

The above-mentioned investigations proved that plant odours have a number of effects on the foraging behaviour of different species of natural enemies. At the same time, in view of these studies a major drawback becomes evident. The overwhelming majority of research has been conducted with hymenopteran parasitoid species, but almost no investigations have been performed with predatory species. Nevertheless, there is some knowledge available on the effect of induced plant volatiles of plants harbouring prey, which attract predators (Reddy 2002, de Boer and Dicke 2005, Mochizuki and Yano 2007), but the influence of non-host plants on the olfactory orientation of predatory arthropods has been almost completely ignored until now. Furthermore, the influence of visual cues on parasitoids and predators has not received much attention in investigations which sought after elucidating the mechanisms underlying the interactions between plant species diversity and carnivores. Both predators and parasitoids are known to use visual plant cues, additionally to olfactory signals, when searching for prey and hosts (Hatting and Samways 1995, Wäckers and Lewis 1999, Freund and Olmstead 2000, Hennemann *et al.* 2002, Fischer *et al.* 2004, Goyer *et al.* 2004). However, how non-host plants or neighbouring plants in the vicinity of the target plant affect the visual orientation of carnivores has not been taken into account to our knowledge so far.



## **Structural complexity**

### **Effects of structural complexity on herbivores**

The structural complexity of the vegetation, i.e. the three-dimensional spatial arrangement of plants or plant parts, has often been investigated in connection with the mobility of herbivores. These studies documented the effects of structural complexity on colonisation dynamics and abundances of phytophagous insects. Other investigations examined the impact of vegetation structure on oviposition site selection, herbivory or the diversity of herbivore assemblages. The information that is gathered here uncovers mixed effects of vegetation structure on herbivores (Table 6). No clear tendency emerges regarding abundance, reproduction and plant damage; however, herbivore movement tends to be influenced by plant structures usually in a negative way. Contrary to investigations on plant diversity, a considerable amount of surveys regarding structural complexity were conducted in varying natural or semi-natural systems and few in intensively managed cropping systems. These studies reveal that architectural traits of single plants or patches of plants are able to influence directly or indirectly the interaction between plants and herbivores. For example, the structural features of the non-host vegetation surrounding host plants may interact with the ability of herbivores to locate their host plants or may act upon microclimatic conditions on the host plant. Thereby non-host plants do not only represent a mediating factor in orientation and movement of arthropods, but their presence and structural features can constitute an essential component of herbivore habitats on its own.

### *Plant structures as resources for herbivores*

The value of so-called structural elements or utilities, that is vegetation or substrates other than foodplants, was particularly recognised in investigations on butterfly habitat requirements (Dennis 2004a, b). Dennis and Sparks (2006) for example could show that the relative abundance of a lycaenid butterfly depended directly on the occurrence of shrubs, which did not constitute host plants, in the surroundings. The butterflies used the non-host plant vegetation for resting, mate location and as shelter against adverse weather conditions. Petersson *et al.* (2006) investigated experimentally in the field how non-host vegetation surrounding conifer seedlings affects the damage caused by pine weevil (*Hylobius abietis*) feeding. The presence of neighbouring

**Table 6.** Effects of enhanced plant structural complexity on different herbivore species or herbivore communities in natural and managed systems. The direction of significant effects (+/positive, -/negative) is given, brackets indicate a tendency; open circles (o) indicate that no significant effect was found.

Herbivore species/guild	Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Lycaenid butterfly	Non-host vegetation structure	Semi-natural grassland	Habitat	Abundance	+	Dennis and Sparks 2006
Various butterfly species	Non-host vegetation structure	Habitat gradient (natural/ anthropogenic biotopes)	Habitat	Settling height	+	Hardy and Dennis 2007
Chrysomelid beetle	Shrub cover	Semi-natural grassland	Habitat	Oviposition	-	Meiners and Obermaier 2004
Coccinellid beetle	Tall corn intercrop	Crop plant community	Habitat	Density	-	Coll and Bottrell 1994
Two plutellid moths	Tall clover intercrop	Crop plant community	Habitat	Immigration/Oviposition	- / o	Åsman <i>et al.</i> 2001
Pyralid moth larvae	Presence of different intercrops	Crop plant community	Habitat	Larval dispersal success	-	Litsinger <i>et al.</i> 1991
Butterfly community	Vegetation height	Semi-natural grassland	Habitat	Species richness	+	Öckinger and Smith 2006

Chrysomelid beetle	Vegetation height and density	Semi-natural grassland	Microhabitat	Oviposition	+	Meiners and Obermaier 2004
Curculionid beetle	Vegetation surrounding host plants	Experimental field study, conifer planting	Microhabitat	Herbivory	+	Petersson <i>et al.</i> 2006
Chrysomelid beetle	Plant height	Semi-natural grassland	Plant	Oviposition	+	Obermaier <i>et al.</i> 2006
Tephritid fruit fly	Host plant height, number of leaves and branches	Natural/disturbed riparian vegetation	Plant	Abundance	+	Raghu <i>et al.</i> 2004
Lepidopteran leafyiting caterpillars	Number of touching leaves within host trees	Unmanaged secondary oak forest	Plant	Abundance/Plant damage	+ / +	Marquis <i>et al.</i> 2002
Noctuid moth larvae	Host plant branching order, stem length	Natural montane forest	Plant	Herbivory	-	Alonso and Herrera 1996
Herbivore community	Host plant height, branch length, leaf area	Natural coastal dune plant community, garden experiments	Plant	Herbivory	+	Rudgers and Whitney 2006

vegetation significantly increased pine weevil feeding for seedlings. The authors suggested that pine weevils perceive the vegetation as a shelter providing protection from predators or temperature extremes. The structural complexity of the vegetation proved to be important also for butterflies with respect to thermoregulation. Various butterfly species settle at specific plant structures, for example tall grasses or shrubs, to actively thermoregulate body temperature (Hardy and Dennis 2007). Thus, beyond the provision of nutritional resources habitats with enhanced structural complexity may considerably support the survival and performance of herbivorous insects. The importance of structural elements becomes even more apparent for a number of butterfly species, which use non-host plant structures as substrates for egg deposition (Wiklund 1984). Besides butterflies other herbivore species are also known to oviposit on non-food plants. For instance, the tansy leaf beetle, *Galeruca tanacetii*, generally deposits its egg clutches on dried up grass stems (Obermaier *et al.* 2006, see also chapter 4 and 5).

#### *Herbivore responses to vegetation structure*

Plants other than hostplants may not only provide valuable resources for herbivores, but non-host plant vegetation may interfere with the habitat and oviposition site selection process. Meiners and Obermaier (2004) analysed the influence of the shrub cover across habitats and the structural complexity within the microhabitat on oviposition site selection of the tansy leaf beetle, *Galeruca tanacetii*, in semi-natural grasslands. The shrub cover of different habitat patches showed a negative correlation with egg clutch occurrence, whereas the structural complexity on the microhabitat scale showed a positive correlation. Furthermore, a small-scale field survey on the oviposition site selection of *G. tanacetii* revealed that the maximum vegetation height at different grassland sites is positively related to oviposition height of the egg clutches on plants (Obermaier *et al.* 2006, see also chapter 3 and 4). Female leaf beetles seem to oviposit as high as possible within the vegetation and on the plants chosen for oviposition. This oviposition behaviour significantly reduces the probability of egg parasitism and thus, provides enemy-free space for the eggs. Findings in agricultural ecosystems confirm that the structural complexity of plant communities can affect egg deposition and density of herbivores. Åsman *et al.* (2001) investigated the effect of intercrop height on the oviposition and immigration of diamondback moth (*Plutella xylostella*) and leek moth (*Acrolepiopsis assectella*) in different crop plant

communities. A tall clover intercrop resulted in a decrease of diamondback moth immigration and egg deposition in *Brassica* host plant plots. In contrast, neither interplanting leek with tall or with short clover affected colonisation and reproduction of the leek moth in this investigation. Coll and Bottrell (1994) revealed that Mexican bean beetle (*Epilachna varivestis*) density is reduced by the presence of tall corn plants in a bean-corn intercrop. Short maize plants did not interfere with the immigration of adult beetles, demonstrating that plant species diversity *per se* had no influence on the population processes. Although adults have usually a greater mobility than larval stages, both can be affected by vegetation complexity. Hence, neighbouring vegetation may not only alter adult movement, but also larval movement. For example, the presence of varying companion plant species in maize polycultures diminished the dispersal success of silk-dispersing larvae of the oriental maize borer, *Ostrinia furnacalis* (Litsinger *et al.* 1991). Besides the influence of vegetation structure on individual behaviour or population dynamics it can also affect the species richness of herbivores. Öckinger and Smith (2006) investigated the butterfly species richness in grassland sites situated in an agricultural landscape. The species richness of the butterfly community correlated significantly positive with vegetation height measured at the study sites. An additional factor in this investigation was the abundance of flowers which further contributed to the positive relationship.

#### *Herbivore responses to plant architecture*

Aside from structural characteristics of plant assemblages the architecture of single plants impacts the colonisation, abundance and damage of host plants by herbivorous insects. Marquis *et al.* (2002) compared the abundance and amount of damage caused by leafy caterpillars for white oak trees varying in plant architectural traits. Augmenting the number of touching leaves artificially increased the abundance of caterpillars and the amount of plant damage in a natural secondary oak forest habitat. Also other host plant architectural characteristics such as plant height, number of branches and leaves were described to affect the oviposition behaviour of phytophagous insects. Host plant structure, for example, influences tephritid fruit flies, which can occur as horticultural pest organisms. In a survey on the *Solanum* fruit fly, *Bactrocera cacuminata*, the density of the host plant foliage enhanced the abundance of flies, especially of ovipositing females, on wild tobacco plants in natural riparian habitats (Raghu *et al.* 2004). Another factor investigated in this study were

microclimatic conditions prevailing within host plants, for example temperature and humidity, which correlated with plant architecture and affected only female flies. The influence of plant architecture on insect herbivory mainly caused by noctuid moth larvae was examined by Alonso and Herrera (1996) in a Mediterranean montane forest. Insect leaf consumption increased with the number of host plant leaf whorls, but decreased with stem diameter. A low branching order, short stems and a high number of leaves further enhanced the occurrence of larvae on host plants. Rudgers and Whitney (2006) studied the herbivore assemblage and folivory in two distinct architectural plant morphs of a perennial shrub in coastal dune communities. The prostrate plant morph supported significantly more midges, whereas the erect morph supported more moth species. As a consequence the erect morph suffered from higher levels of folivory and reduced reproductive output compared to the prostrate plants both in natural occurring plants and in a common garden experiment.

### **Effects of structural complexity on carnivores and their interaction with herbivores**

Often crop plants or ornamental plants have been employed to analyse the potential of carnivores to suppress arthropod pests in agroecosystems. In addition, most of the studies dealing with structural complexity and its influence on natural enemies were conducted on the plant level and only a few on habitat level. Furthermore, an unbalance in research effort concerning the types of natural enemies becomes evident, since the number of studies on hymenopteran parasitoids exceeds by far the number of studies that address predator species. These investigations quantified foraging efficiency of predators and parasitoids measured as number of prey consumed or hosts attacked and parasitised. Several examples illustrate that foraging success is linked to the movement ability of carnivores and that physical vegetation properties change the movement pattern of predators and parasitoids. Where the structural complexity of the vegetation interferes negatively with the foraging behaviour of natural enemies it can provide refuges for the prey and may release herbivores into enemy-free space. The studies referred to in this review elucidate that in most cases complex vegetation structure and plant architecture exerts a negative influence on the foraging efficiency of natural enemies (Table 7). However, data have been obtained to a large amount in

**Table 7.** Effects of enhanced plant structural complexity on different carnivore species and their herbivorous prey/hosts in natural and managed systems. The direction of significant effects (+/positive, -/negative) is given; open circles (o) indicate that no significant effect was found.

Carnivore/Herbivore species/guild	Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Hymenopteran predator Tetracampid parasitoid Chrysomelid herbivore	Natural and potted host plants in dense or sparse vegetation	Uncultivated meadows, wildflower field	Habitat	Predation rate Parasitism rate Herbivore oviposition	- o o	Tschanz <i>et al.</i> 2005
Eulophid parasitoid	Shrub cover	Semi-natural grassland	Habitat	Parasitism rate	-	Meiners and Obermaier 2004
Trichogrammatid parasitoid	Plant leaf area and height	Crop plant communities	Habitat	Parasitism rate	-	Wang <i>et al.</i> 1997
Eulophid parasitoid	Vegetation height of bean-tall maize intercrop	Crop plant communities	Habitat	Parasitoid immigration	-	Coll and Bottrell 1996
Ichneumonid parasitoid	Mono-/polyculture grouping of host and non-host plants	Greenhouse, semi-field setup	Microhabitat	Foraging efficiency	-	Gols <i>et al.</i> 2005
Eulophid parasitoid	Vegetation height and density	Semi-natural grassland	Microhabitat	Parasitism rate	-	Obermaier <i>et al.</i> in press
Eulophid parasitoid	Height of plant with egg clutch	Semi-natural grassland	Plant	Parasitism rate	-	Obermaier <i>et al.</i> 2006
Aphidiid parasitoid	Structurally manipulated/unmanipulated host plants	Individual infested host plants, laboratory	Plant	Oviposition rate	+	Weisser 1995
Encyrtid parasitoid	Host plant architecture	Greenhouse	Plant	Attack rate	-	Cloyd and Sadof 2000
Two trichogrammatid parasitoids	Three <i>Brassica</i> host plants species varying in age	Individual host plants, greenhouse	Plant	Parasitism rate	-	Gingras <i>et al.</i> 2003

Table 7. (continued)

Carnivore/Herbivore species/guild	Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Trichogrammatid parasitoid	Structural complexity	Artificial plant models, laboratory	Plant	Parasitism rate	-	Gingras and Boivin 2002
Trichogrammatid parasitoid	Structural complexity of plant models and three <i>Brassica</i> host plants	Artificial plant models: laboratory, individual host plants: greenhouse	Plant	Parasitism rate	-	Gingras <i>et al.</i> 2002
Trichogrammatid parasitoid	Structural complexity	Plant paper models	Plant	Parasitism rate	-	Andow and Prokrym 1990
Trichogrammatid parasitoid	Structural complexity	Plant paper models, plant foliage	Plant	Searching success	-	Lukianchuk and Smith 1997
Coccinellid predator	Host plant architectural complexity	Greenhouse	Plant	Number of prey consumed	-	Legrand and Barbosa 2003
Three coccinellid predators Aphidid herbivore	Host plant architectural complexity	Laboratory, crop field	Plant	Predation efficiency Herbivore population growth	- +	Kareiva and Sahakian 1990
Coccinellid predator	Host plant morphological structure	Individual host plants, laboratory	Plant	Foraging behaviour	+	Vohland 1996
Wood ants and spiders/ Geometrid moth	Tree architectural complexity of natural and manipulated birch trees	Boreal conifer-dominated forest	Plant	Density of Spiders/Ants Parasitism rate Herbivore survival	- 0 +	Riihimäki <i>et al.</i> 2006
Chrysopid predator	Two grasses with divergent leaf architecture	Individual host plants, laboratory	Plant	Prey capture rate	-	Clark and Messina 1998a
Coccinellid predator	Two grasses with divergent leaf architecture	Individual host plants, laboratory	Plant	Prey capture rate	-	Clark and Messina 1998b



laboratory studies and in many cases it still needs to be clarified whether the laboratory findings are transferable to the prevailing natural conditions in the field.

#### *Carnivore responses to vegetation structure*

Studies that examined the foraging success of carnivores on the habitat level comprise semi-natural grasslands and intensively managed crop plant communities. Meiners and Obermaier (2004) showed that at semi-natural grassland sites the cover of shrubs correlates negatively with the parasitism rate of a eulophid parasitoid wasp. On a microhabitat scale the complexity of the vegetation reduced significantly the parasitism success of the parasitoid, as dense and tall vegetation diminished the probability of host eggs being parasitised (Obermaier *et al.* 2006, Obermaier *et al.* in press, see also chapter 3 and 4). Tschanz *et al.* (2005) investigated the predation rate of paper wasps (*Polistes dominulus*) preying on *Cassida rubiginosa* shield beetle larvae in extensively managed meadows. They detected that neighbouring vegetation, which hid the host plants, reduced the predation success of the wasps compared to host plants which were not surrounded by vegetation. However, in this study the neighbouring vegetation did not affect the parasitism probability of the beetle larvae, since there was no difference in parasitism rate between larvae on exposed or hidden host plants. Coll and Bottrell (1996) investigated in an intercropping experiment the impact of vegetation height on the immigration of parasitoids into host patches. The immigration rate of wasps parasitising the Mexican bean beetle was diminished in bean plots interplanted with tall corn plants. The diversity of plant species in the intercrop plots had no effect on the parasitoids. In an experimental greenhouse study the foraging efficiency of the ichneumonid parasitoid, *Diadegma semiclausum*, a specialist on diamondback moth, was examined in the presence of different intercrops (Gols *et al.* 2005). In a semi-field setup cabbage was arranged in monoculture or in polycultures either with mustard or barley. Differential effects of polycultures and height of companion plants on the foraging behaviour of the wasp were detected, among other effects it was revealed that tall intercrops interfere with host finding and slow down immigration into mixed patches with host and non-host plants.

#### *Carnivore responses to plant architecture*

Investigations addressing parasitoid foraging efficiency on the plant level have been frequently performed in the laboratory to analyse the foraging behaviour of the natural

enemies on different crop plant species varying in plant architecture. Gingras and colleagues conducted a series of studies in which they combined the usage of artificial plant models and real plants to elucidate the effects of plant architectural complexity and the host finding success of *Trichogramma* parasitoids. Artificial plant models have the advantage that the influence of chemical plant properties on animal behaviour is excluded. In a laboratory study Gingras and Boivin (2002) used plastic plant models with simple, intermediate and complex plant architecture. The parasitism rate of *Trichogramma evanescens* females was significantly reduced with increasing complexity of the structure. A successive investigation with plant models and three different *Brassica* species confirmed these results and demonstrated that the laboratory findings gained from artificial plant models are transferable to the natural situation with living plants (Gingras *et al.* 2002, 2003). In maize fields infested with the European corn borer (*Ostrinia nubilalis*) it was demonstrated that the percentage of parasitism caused by *Trichogramma* wasps correlated negatively with the amount of plant leaf area (Wang *et al.* 1997). Additionally, parasitism rate was reduced, when host eggs were located in the upper third of the maize plants, which makes evident that plant height can have considerable influence on foraging efficiency of parasitoids. Andow and Prokrym (1990) investigated the parasitism efficiency of *Trichogramma* wasps on paper models mimicking differential complex plant foliage. Foraging success of the wasps was significantly negatively affected by increasing structural complexity of the surfaces. Lukianchuk and Smith (1997) obtained comparable results when analysing the searching success of *Trichogramma minutum* on paper models and modified foliage of trembling aspen and balsam fir. On structural very complex surfaces the foraging success of the wasps was significantly diminished. Architectural plant characteristics did also affect the attack rate of a parasitoid wasp parasitising citrus mealybug on an ornamental plant species (Cloyd and Sadof 2000). All measured characteristics such as plant height, number of leaves, leaf surface area or number of branches were negatively correlated with the attack rate of the parasitoid. In contrast to the aforementioned studies, Weisser (1995) found positive effects of complex plant architecture on the foraging behaviour of the aphid parasitoid *Aphidius funebris*. In this investigation *Centaurea jacea* plants were either intact or manipulated in a way that all leaves adjacent to aphid colonies were removed. The wasps significantly benefited from a structural more complex plant architecture of intact host plants regarding their oviposition rate, which was increased on intact plants.

Investigations dealing with the impact of plant architecture on the efficiency of predator species reported on here, have been conducted on herbaceous plants or trees. Legrand and Barbosa (2003) examined the foraging efficiency of a coccinellid predator (*Coccinella septempunctata*) in cage experiments in the greenhouse on garden pea varieties. The morphological complexity, ranging from low to high, of three near-isogenic garden pea lines differing in leaf form, i.e. the number of leaflets and stipules, substantially influenced foraging efficiency of the predator. An increased complexity, represented by an increasing leaf edge to leaf area ratio and the number of junctions, revealed negative effects and reduced the maximum number of consumed aphids. Similar effects of leaf shape were detected by Kareiva and Sahakian (1990) when investigating the foraging behaviour of three ladybird species on a normal and leafless variety of the common garden pea. Ladybirds showed a higher efficiency on the leafless compared to the normal variety. Aphid population growth was significantly reduced on the leafless pea variety in greenhouse experiments and in field trials. In contrast to these results the foraging behaviour of a ladybeetle preying on the pine needle aphid was positively affected by more complex plant morphology, at least for adult beetles (Vohland 1996). Nevertheless, all developmental stages of the predator remained significantly longer in the upper and outer parts with high needle density and high prey abundance of potted pine plants. The architecture of birch trees infested by the autumnal moth in Finnish mixed forests influenced larval survival and carnivore abundance in different ways. In field experiments varying degrees of structural complexity of natural occurring or manipulated trees were examined (Riihimäki *et al.* 2006). In trees with high architectural complexity larval survival was enhanced, whereas parasitism rate and the density of spiders was decreased. The density of ants was not affected by canopy structure in the investigated birch trees. Plant architecture can also exert indirect influences on the foraging efficiency of predators. Clark and Messina (1998a, b) performed experiments on Indian ricegrass and wheatgrass with two different predator species of the wheat aphid. For lacewing larvae and ladybird beetle adults or larvae prey accessibility was modified by plant morphology. Because wheatgrass offered concealed locations to the aphids prey capture rate of both predators was reduced on wheat compared to ricegrass.

**Effects of structural complexity on herbivore-carnivore communities**

Unlike to plant species diversity only a few investigations dealt with the relationship of vegetation structure and the assemblage of whole arthropod communities. Nevertheless, several studies demonstrate that the structural complexity of habitats does mediate general arthropod abundance and species richness. Most of the studies referred to in this review determined a positive influence of structural complexity on arthropod communities (Table 8). Variation in grazing intensity and differential vegetational complexity of semi-natural grassland sites was shown to have an effect on the spatial distribution of ground and rove beetles (Dennis *et al.* 2002). The distribution pattern between species differed significantly according to land use. Zurbrugg and Frank (2006) assessed the abundance and species diversity of a heteropteran bug community in managed and unmanaged grassland in relation to vegetation structure. In vegetational more complex habitats, such as wildflower areas and meadows, the number of individuals and the diversity of carnivorous and phytophagous bug species was increased in contrast to intensively managed pastures. Kruess and Tschamtkke (2002) evaluated the influence of vegetation complexity and grazing intensity of differentially managed grasslands on insect species richness. The richness and abundance of the assessed insect species belonging to several taxa, especially Auchenorrhyncha, Heteroptera, Coleoptera and Hymenoptera Parasitica, increased with increasing vegetation height. The plant species diversity did not affect the insect community. These results are in accordance with an investigation performed by Dennis *et al.* (1998) on the abundance and species richness of insects and spiders in native upland grassland sites with experimentally manipulated grazing intensity. More arthropod species and greater abundances were determined in patches with tall vegetation height formed by grass tussocks. The changing of plant structure and cover during the course of the successional development of a habitat can also exert an influence on insect communities (Martinko *et al.* 2006). Martinko *et al.* (2006) studied the succession of an old-field site over a time span of eight years. This study revealed that the added structural complexity of growing woody plants and forbs increased the species richness and trophic diversity of the occurring insect community. Likewise, Brose (2003) showed that the heterogeneity of vegetation structures in early successional wetland sites situated in an agricultural landscape had a positive impact on carabid beetle species richness. Plant diversity on the contrary had no effect on carabid beetle community. Woodcock *et al.* (2007) examined the influence of sward

**Table 8.** Effects of enhanced plant structural complexity on arthropod communities including both herbivorous and carnivorous species in natural and managed systems. The direction of significant effects (+/positive, -/negative) is given; open circles (o) indicate that no significant effect was found.

Plant/Vegetation parameter	Habitat type/ Test conditions	Scale	Response criterion	Direction of effect	Reference
Vegetation structure of managed and unmanaged sites	Three types of semi-natural habitat	Habitat	Heteropteran bug	+	Zurbrügg and Frank 2006
			Abundance	+	
			Species richness	+	
Structural complexity and plant cover of different successional stages/management regimes	Experimentally fragmented old-field site	Habitat	Insect		Martinko <i>et al.</i> 2006
			Abundance	+	
			Species richness	o	
Heterogeneity of vegetation structure	Early successional temporary wetlands	Habitat	Carabid beetle abundance	+	Brose 2003
Vegetation height	Grasslands with varying grazing intensity	Habitat	Insect		Kruess and Tschardtke 2002
			Abundance	+	
			Species richness	+	
Heterogeneity of vegetation structure	Semi-natural grasslands with varying grazing intensity	Habitat	Ground and rove beetle spatial distribution	+	Dennis <i>et al.</i> 2002
Sward architectural complexity	Field margin plots	Habitat	Arthropod species richness	+	Woodcock <i>et al.</i> 2007
Heterogeneity of vegetation structure	Native upland grassland with varying grazing intensity	Microhabitat	Arthropod		Dennis <i>et al.</i> 1998
			Abundance	+	
			Species richness	+	
Bare ground or covered with logging residue (slash)	Forest clear-cuts	Microhabitat	Abundance of ground-active		Nittérus and Gunnarsson 2006
			Carabid beetles	+	
			Spiders	o	

architectural complexity on the species richness of predatory and phytophagous arthropod functional groups, e.g. spiders, beetles and true bugs, in experimentally established field margin plots over 2 years. Sward architectural complexity was found to be an important determinant of species richness for all phytophagous and predatory functional groups in addition to plant community assemblage. The analysis of individual species responses revealed that 62.5% of the spider and beetle species and 50.0% of the true bugs responded to sward architectural complexity. The authors suggest that manipulating the sward architecture of habitats may increase the number of invertebrate species. Another experimental study investigated the impact of the residues of logging (slash) in forest clear cuts on the abundance of ground active spiders and lycosid spiders (Nittérus and Gunnarsson 2006). The structural complexity of the microhabitat increased beetle abundance, but had no effect on the number of spiders when slash covered patches were compared to uncovered bare ground.

### **Mechanisms acting upon herbivores regarding plant structural complexity**

Plant structures interfere with herbivore behaviour in a direct or an indirect way. The structural complexity of habitats and the architectural traits of single plants influence, for example, the movement ability of herbivores and the process of host plant finding (Table 9). Thus, structural features of the vegetation may affect the access to resources and with it the population dynamics of phytophagous arthropods. Vegetation structure further can modify the abiotic conditions prevailing in the environment and may therefore impact colonisation dynamics by affecting the abundance and the reproductive behaviour of herbivores, which can result in distinct distribution patterns of herbivore species within and between different types of habitats.

#### *The role of vegetation structure regarding herbivore movement*

Regarding the vegetation structure of habitats there exist a few studies that experimentally manipulated habitat structure or used a complete artificial setup to investigate the influence of structural complexity on the movement of herbivores on a microscale. In an abandoned farm field Goodwin and Fahrig (2002) constructed three different types of microlandscapes to analyse the small-scale movement of the chrysomelid beetle *Trirhabda borealis*. The field microlandscapes consisted of either natural vegetation or cut vegetation with and without camouflage netting mimicking

**Table 9.** Behavioural responses of herbivores to enhanced plant structural complexity and underlying mechanisms. The direction of significant responses (+/positive, -/negative, ±/ positive and negative) is given.

Herbivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Chrysomelid beetle	Three types of microlandscapes differing in structural complexity	Field experiments	Movement	-	Interference with direction and speed	Goodwin and Fahrig 2002
Mirid bug	Structures varying in the proportion of connecting/ non-connecting plant parts	Laboratory, artificial vegetation structures	Movement in vertical direction	+	Increased mobility	Hannunen 2002
Tenebrionid beetle	Varying density of randomly arranged tooth picks	Laboratory, artificial vegetation structures	Movement	-	Interference with direction and speed	Jopp 2006
Coccinellid beetle	Presence of tall corn intercrop	Field experiments	Movement	-	Interference with movement speed	Coll and Bottrell 1994
Pyralid moth larvae	Presence of different intercrops	Field experiments	Movement	-	Reduced mobility	Litsinger <i>et al.</i> 1991
Noctuid moth larvae	Host plants differing in architecture	Field survey	Movement	±	Structure determines movement path	Alonso and Herrera 1996
Tephritid fly	Structural complexity of apple tree canopies	Field experiments	Movement	±	Structure determines movement path	Casas and Aluja 1997
Papilionid butterfly	Isolated host plants or surrounded by non-host vegetation	Field experiments	Visual	-	Visual interference	Rausher 1981

Table 9. (continued)

Herbivore species/guild	Test conditions	Methods	Response criterion	Direction of response	Involved mechanism	Reference
Plutellid moth	Presence of tall clover intercrop	Field experiments	Visual	-	Visual interference	Åsman <i>et al.</i> 2001
Two chrysomelid beetles	Free-standing host plants or surrounded by non-host plants	Field experiments: real plants, artificial plant models, laboratory: two-arm olfactometer	Olfactory/Visual	-	Visual interference	Hambäck <i>et al.</i> 2003
Chrysomelid beetle	Dense host plant stands	Field survey	Abundance Herbivory	+ +	High relative humidity	Bach 1993a
Tephritid fly	Density of host plant foliage	Field survey	Oviposition	+	Low relative humidity and low light intensity	Raghu <i>et al.</i> 2004
Two lasiocampid moths	Tree canopy architecture	Field survey	Pupation site choice	±	Solar radiation	Veldtman <i>et al.</i> 2007
Curculionid beetle	Narrow cotton plantings	Field survey	Infestation Survival	+ +	Low temperature and high relative humidity	Pierce <i>et al.</i> 2001



natural vegetation. The differences in vegetation structure of the three patch types significantly affected the movement ability of the leaf beetles. The direction of the movement and the speed of the individually tracked beetles varied considerably between the three patch types. In laboratory studies, researchers employed fully artificial structures to simulate the variable structural complexity of habitats in order to investigate the movement patterns of arthropods in simple and complex vegetation. The behavioural observations are commonly combined with computer simulations to uncover underlying mechanisms that influence the distribution of arthropods within the vegetation structures. Hannunen (2002) aimed at identifying characteristic structural features of the vegetation, which might influence the movement of plant bug nymphs (*Lygus rugulipennis*) within the plant canopy. The proportion of connecting structures with no dead ends and the proportion of connecting structures leading in horizontal direction both enhanced the mobility of the plant bug nymphs within the artificial plant canopy. This example illustrates that a complex vegetation structure does not necessarily impair herbivore movement, but a high degree of connectivity between plant parts may also enhance the movement ability. Another laboratory study, which mimicked the small-scale vegetation density and heterogeneity of grasslands, analysed the influence of the potentially occurring spatial resistance the vegetation might exert on beetles moving on the ground (Jopp 2006). An increasing local spatial resistance, represented by a higher density of randomly arranged toothpicks in an arena, decreased significantly the covered distance and velocity of the observed beetles. Here, a more complex vegetation structure negatively affected movement ability. Physical impediment caused by neighbouring plants may result in diminished dispersal rates of herbivores (Perrin and Phillips 1978). Besides slowing down the movement speed of individuals walking on the ground in dense vegetation (see Jopp 2006), it also may hamper individuals that conduct flights in low altitude as proposed by Coll and Bottrell (1994). Particularly, when early larval instars of herbivores disperse by ballooning, a type of movement for which the young larvae use a strand of silk to be transported by the wind, vegetation structure may seriously disrupt the dispersal process (Zalucki *et al.* 2002). For example, Litsinger *et al.* (1991) gave evidence that the dispersal success of *Ostrinia furnacalis* larvae is considerably lowered by companion plants which acted as a barrier in intercropping experiments. As several species in lepidopteran families and other arthropods are known to use ballooning as dispersal strategy (Bell *et al.*

2005, Reynolds *et al.* 2006), this mechanism may apply to other herbivore lepidopteran species as well.

#### *The role of plant architecture regarding herbivore movement*

Two field studies addressed the impact of the architecture of individual plants on the movement pattern of phytophagous insects. Alonso and Herrera (1996) investigated the foraging behaviour of noctuid moth larvae on a shrub species and detected that within plants the larvae significantly preferred leaf whorls with lower branching orders and shorter supporting stems, leading to a non-random pattern of herbivory. It was assumed that specific plant architectural traits allow the moth larvae to forage selectively and reduce travel costs while moving within plants. In contrast, based on these data Neuvonen (1999) hypothesised that also random foraging behaviour could lead to the same non-random pattern of herbivory, because the foodplant's dichotomous branching order may have determined the probability of visiting specific leaf whorls within the plant by the caterpillars. In general, independent of the type of foraging behaviour, whether it is directed or random, walking herbivores are guided by plant architectural characteristics, and thus, plant architecture can determine the probability of visiting certain plant parts. Therefore, the risk of herbivory for specific plant components such as leaves, flowers or seeds may depend on their position within a plant. Comparable outcomes have been discovered in a study which analysed the foraging behaviour of the apple fruit fly, *Rhagoletis pomonella*, within the canopy of apple trees in an orchard (Casas and Aluja 1997). The authors observed the movement behaviour of single flies and developed simulation models that predicted the fly's movement in trees devoid of fruit. This approach made evident that canopy architecture has the potential to define the rules of movement, that is the direction of the movement, and the set of locations, which a foraging arthropod is likely to visit within a tree canopy.

#### *The role of vegetation structure regarding herbivore visual orientation*

Vegetation structure can also interfere with the visual orientation behaviour and the process of host plant finding of herbivores. The shape and spatial pattern of individual plants as well as the height and the density of patches of plants within habitats matter here (Prokopy and Owens 1983). The visual apparency of host plants growing in diverse stands, where various non-host plants surrounded them, might be reduced (see

Feeny 1976). Rausher (1981) detected that *Battus philenor* butterflies deposit a greater number of eggs on isolated host plants compared to host plants growing in dense vegetations. Female *B. philenor* are known to distinguish host plants from non-host plants by the specific shape of host plant leaves and the butterflies approach host plants generally by flight. However, when host plants are surrounded by dense vegetation this may complicate the discrimination. Perrin (1977) suggested that tall surrounding non-host plants might hide the target plant species from sight, especially when young seedlings are intercropped with larger plants (see also Sequeira and Moore 2003). In intercropping experiments Åsman *et al.* (2001) found hints that visual camouflage could have caused the reduced numbers of egg depositions by an herbivorous insect in a mixed crop plant community. Hambäck *et al.* (2003) conducted field and laboratory experiments to elucidate the role of surrounding non-host plant vegetation on host plant finding of two chrysomelid and one curculionid beetle species. In olfactometer tests it was confirmed the odours of the host plant, *Lythrum salicaria*, were only attractive for the curculionid beetle, *Nanophyes marmoratus*. Odours of the non-host plant, *Myrica gale*, were attractive for both tested chrysomelid beetle species, *Galerucella californiensis* and *Galerucella pusilla*, but not for the curculionid beetle. However, in the field both chrysomelid beetles were less abundant and deposited fewer eggs on *L. salicaria* host plants that were surrounded either by *M. gale* non-host plant thickets or artificial plant models. In contrast, the curculionid species, *N. marmoratus*, was not distracted by neighbouring non-host vegetation or structures. The authors conclude that the non-host plant vegetation had visually masked the host plants from the two chrysomelid beetles, which seemed not to use plant odours for host location, whereas the curculionid beetle was able to find the host plant within dense vegetation due to the use of olfactory host plant cues.

*The role of vegetation structure regarding suitable microclimatic conditions for herbivores within habitats*

The structural complexity of the vegetation may not only act directly upon movement and orientation of herbivores, but also indirectly by altering the abiotic conditions in the environment. A specific microclimate is often associated with specific structural characteristics of plants, for instance the foliage density of the canopy. The actual state of the abiotic environment in terms of temperature, relative humidity and light intensity can control the occurrence of insects within and between host and non-host

plants of habitats. Bach (1993a) examined the effects of microclimate and host plant architectural characteristics on the local distribution pattern of the flea beetle *Altica subplicata*. The beetles caused significantly more damage and were more abundant in areas with higher relative humidities and on taller host plants. Raghu *et al.* (2004) elucidated that microclimate influences the abundance and oviposition decision of female herbivores on host plants. There are further indications that microclimatic conditions influence the choice of the pupation site of lepidopteran caterpillars (Veldtman *et al.* 2007). Moreover, microclimatic conditions do influence the time needed for arthropod development, which can severely affect population dynamics of herbivorous insects. Pierce *et al.* (2001) investigated different management practices in cotton plantations and its influence on the infestation and survival of the cotton boll weevil *Anthonomus grandis*. Cotton plantings with narrow row widths showed higher survival of boll weevils, lower temperatures and higher relative humidity than plantings with broad row widths. Flower buds under the plant canopy had higher rates of adult emergence compared to flower bud close to the gap of bare soil between plant rows.

### **Mechanisms acting upon carnivores regarding plant structural complexity**

Comparable to investigations dealing with herbivore species, plant structures have been shown to interfere directly or indirectly with carnivore behaviour. The movement ability of parasitoids and predators can be impeded or facilitated *via* vegetation structure, plant architectural traits and surface characteristics of plants. In general, negative influences seem to outweigh positive influences exerted by vegetation structure (Table 10). Furthermore, the structural complexity of the vegetation affects the abiotic conditions and may therefore determine the carnivore's position within habitats.

#### *The role of vegetation structure regarding carnivore movement*

So far, little is known on the impact of complex plant canopies on the movement behaviour of carnivores. There appear to exist only two studies that analysed experimentally the influence of leaf overlap on the dispersal of predators such as mites or coccinellid beetles (Kareiva and Perry 1989, Skirvin and Fenlon 2003). In these experiments individual plants were arranged in a way that plant leaves between plants

**Table 10.** Behavioural responses of carnivores to enhanced plant structural complexity or plant surface texture and underlying mechanisms. The direction of significant responses (+/positive, -/negative, ±/positive and negative) is given.

<b>Carnivore species/guild</b>	<b>Test conditions</b>	<b>Methods</b>	<b>Response criterion</b>	<b>Direction of response</b>	<b>Involved mechanism</b>	<b>Reference</b>
Phytoseiid mite	Leaves of individual plants overlap and touch	Laboratory experiments	Movement	+	Bridges facilitate movement	Skirvin and Fenlon 2003
Coccinellid beetle	Leaves of individual plants taped together	Laboratory experiments	Movement	+	Bridges increase net displacement	Kareiva and Perry 1989
Three coccinellid beetles	Host plant architectural complexity	Laboratory, field experiments	Movement	-	Increased falling frequency	Kareiva and Sahakian 1990
Seven coccinellid beetles	Plant models varying in branching pattern and leaf arrangement	Laboratory, artificial plant models	Movement	±	Interference with searching time and method of leaving	Frazer and McGregor 1994
Four coccinellid beetle species	Four host plant species varying in architecture and surface texture	Laboratory experiments	Searching efficiency	±	Interference with mobility and falling frequency	Grevstad and Klepetka 1992
Trichogrammatid parasitoid	Structural complexity	Laboratory, plant paper models	Searching efficiency	-	Reduced searching time	Andow and Prokrym 1990
Braconid parasitoid	Structurally simple and complex host plants	Laboratory, individual intact or manipulated host plants	Searching efficiency	+	Increased activity and attack rate on complex plants	Weisser 1995
Pentatomid bug	Three host plant species varying in surface texture	Laboratory experiments	Movement	-	Reduced movement rate	Yang 2000

**Table 10.** (continued)

<b>Carnivore species/guild</b>	<b>Test conditions</b>	<b>Methods</b>	<b>Response criterion</b>	<b>Direction of response</b>	<b>Involved mechanism</b>	<b>Reference</b>
Trichogrammatid parasitoid	Leaf/non-leaf materials varying in surface texture	Laboratory experiments	Movement	-	Reduced walking speed	Olson and Andow 2006
Anthocorid bug	Leaves varying in surface texture	Laboratory, leaves of three different host plant species	Searching efficiency	-	Reduced walking speed	Coll <i>et al.</i> 1997
Trichogrammatid parasitoid	Plant parts varying in surface texture	Laboratory experiments	Foraging efficiency	-	Reduced walking speed	Romeis <i>et al.</i> 1998
Braconid parasitoid	Epicuticular wax of two cauliflower varieties	Laboratory experiments	Foraging efficiency	-	Reduced walking speed, increased falling frequency	Gentry and Barbosa 2006
Eulophid parasitoid	Microhabitat structural complexity	Field survey	Parasitism	+	Sunny microclimate	Meiners and Obermaier 2004
Ichneumonid parasitoid	Structural complexity of different habitat types	Field survey	Parasitism	+	Moderate microclimate	Dyer and Landis 1997

could touch and formed 'bridges'. Concordantly, these investigations report that bridges created by touching leaves facilitate predator movement within the plant canopy, allowing the predators to move more easily through the plant canopy and disperse faster. A recent simulation study investigated the impact of plant architecture and canopy connectedness on the movement of predators within a complex canopy. The simulation experiments revealed that randomly searching predators accomplish to search a greater proportion of the plant canopy within a simplified plant canopy, when the connectedness between plants increases. However, enhanced architectural complexity of individual plants affected the proportion of plant canopy searched negatively, with a lower proportion of the canopy visited on more complex plant architectures (Skirvin 2004). This finding is in line with the results obtained by a laboratory study on a hymenopteran parasitoid searching within differentially complex vegetation structures (Randlkofer *et al.* unpublished data, see chapter 6). Increased connectedness between plant stems decreased the searching time of parasitoid wasps, because connection points between plants caused the loss of time, the reversion of movement direction or initiated the leaving of the respective vegetation structure.

#### *The role of plant architecture regarding carnivore movement*

In contrast to vegetation structure the influence of plant architecture has received more attention in terms of predator and parasitoid movement patterns. Grevstad and Klepetka (1992) examined the foraging behaviour of four coccinellid species on four *Brassica* plant species that differed widely in their structures and surface textures. Predation rates were significantly influenced by plant variety, which the authors attributed to direct effects of plant morphology on predator mobility, falling frequency and prey accessibility. Notably, the slippery surface of plant leaves increased the falling frequency of the adult predators. Interestingly, this disadvantage for predator movement could be compensated on one tested plant species through more complex plant architecture. This plant species possessed more edges and less smooth surfaces that reduced the frequency of falling from this plant while foraging compared to the other two species tested. Similar results were reported by Kareiva and Sahakian (1990), which detected that ladybeetles fall of the slippery surface of bean plants. In this study, coccinellids were able to move better and had higher predation rates on a plant variety with a diminished number of leaves. Besides movement ability and

movement pattern, plant structural traits can affect the allocation of searching time and patch leaving behaviour.

Andow and Prokrym (1990) analysed the foraging behaviour of a parasitoid wasp on simple and complex plant paper models in the presence and absence of hosts. Without hosts the searching time on simple models was higher compared to complex models, which was consistent with parasitism rate. The obtained results in this investigation further make evident that structural complexity *per se* may influence the giving-up-time of searching parasitoids. Weisser (1995) examined the effect of different plant architectural properties of host plants on the foraging behaviour of a parasitoid wasp that attacks aphids. Intact host plants were compared to manipulated host plants, which had all leaves adjacent to aphid colonies removed. Overall, the wasps stayed on manipulated plants longer within the aphid colony, but parasitised more aphids on intact plants, because the time the wasps actively searched for hosts was higher on intact plants. The observations clarified that leaves adjacent to aphid colonies facilitated the attack of aphids for the parasitoid females. Frazer and McGregor (1994) analysed the searching behaviour of seven coccinellid species on plant models mimicking the varying branching patterns and arrangement of leaves attached to plant stems. The different plant models significantly affected searching time and the method of leaving from the plant models (by walking or flying) in the different ladybeetle species. The authors assumed that the observed impact of architectural traits of the plant models could also considerably affect host finding success in the field.

#### *The role of plant surface texture regarding carnivore movement*

As already mentioned, aside from vegetation structure and plant architecture, the surface texture of plants, for example leaf pubescence or leaf epicuticular waxes, were shown to affect the movement ability and foraging behaviour of carnivores usually negatively (e.g. Coll *et al.* 1997, Romeis *et al.* 1998, Yang *et al.* 2000, Chang *et al.* 2006, Gentry and Barbosa 2006, Olson and Andow 2006). Coll *et al.* (1997) attributed variation in leaf pubescence to a reduced searching efficiency of the minute pirate bug *Orius insidiosus* on leaves of bean, corn and tomato. The differences in walking speed and turning rate of the observed predators corresponded with the trichome density of the plants, which was lowest in bean and highest in tomato. Olson and Andow (2006) analysed the walking pattern of a *Trichogramma* parasitoids on varying surfaces



stemming from leaf and non-leaf materials. In general, the presence and density of trichomes had a negative effect on the walking speed of the parasitoids. Romeis *et al.* (1998) reported that movement of *Trichogramma* wasps on pigeonpea pods and calyxes was inhibited by long trichomes and wasps were trapped by sticky trichome exudates, in contrast to trichomes on leaves which were pressed down to the surface making walking easier. This led further to virtually no parasitism of host eggs on pods and calyxes in comparison to eggs on leaves, which suffered from 55% parasitism rate. Eigenbrode (2004) summarised the impact that epicuticular waxy blooms have on the attachment and effectiveness of insect carnivores on plants. Overall, it became evident that leaf epicuticular waxes reduce the attachment of predators and parasitoids to plants and thereby reduce the foraging efficiency of the carnivores. However, plant surface texture does not only influence carnivorous arthropods in their movement behaviour, but also herbivorous arthropod species (Eigenbrode 2004, Müller and Riederer 2005), but due to differences in body size the impact might be more profound on carnivores.

*The role of vegetation structure regarding suitable microclimatic conditions for carnivores within habitats*

Besides the discussed direct impact of structural complexity on carnivore behaviour also indirect effects such as microclimatic conditions, which are influenced by plant structures, may play a role. Two studies provide indications that abiotic conditions do affect carnivore performance. In a field study, Meiners and Obermaier (2004) revealed that parasitism success was positively influenced by a sunny microclimate. Dyer and Landis (1997) investigated the abundance of the parasitoid, *Eriborus terebrans*, attacking the European cornborer, *Ostrinia nubilalis*, in cornfields and biotopes adjacent to the crop planting. The within-field distribution of parasitoids was assessed near a wooded field margin, near an herbaceous field margin and in the interior of cornfields. First and second generations of the parasitoids showed differences in their distribution between the sampled biotope types. The authors proposed that microclimatic conditions present in adjacent woody habitats, but unavailable in early-season cornfields significantly affected the distribution of the parasitoids aside from the availability of nutritional resources.

## **The interplay between plant species diversity and structural complexity – effects on chemical diversity and arthropod orientation**

### **Effects of plant species diversity on volatile chemical diversity**

#### *Origin of volatile chemical diversity*

The biochemistry of plants is characterised by an enormous diversity and variability of compounds. Different plant species vary largely in their content of plant secondary metabolites (for reviews see Hadacek 2002, Ober 2005). Approximately 200,000 different plant compounds have been identified to date (Ober 2005). A fraction of these plant secondary metabolites represent volatile compounds with a low molecular weight, lipophilic character and high vapour pressure that allows them to easily cross cell membranes and evaporate into the atmosphere (Pichersky *et al.* 2006). In headspace analyses about 1700 different volatile constituents from more than 90 plant families could be detected so far (for reviews see Dudareva *et al.* 2006, Knudsen *et al.* 2006). Three major groups of plant volatiles can be differentiated: terpenoids, phenylpropanoids/benzenoids and fatty acid derivatives (Dudareva *et al.* 2006). The most proliferated group of volatile compounds are the terpenoids (Theis and Lerdaу 2003, Dudareva *et al.* 2006, Cheng *et al.* 2007).

Some of the secondary plant compounds appear to be ubiquitous to all plant species, for example the ‘green leaf volatiles’ (GLVs) that are formed in high amounts after damage of plant tissue (Visser *et al.* 1978, Matsui 2006). On the other hand, the constituents of odour bouquets can differ largely from one plant species to another (e.g. Cornu *et al.* 2001, Sartoratto and Augusto 2003, Bukovinszky *et al.* 2005). Hence, within a habitat the composition and chemical diversity of the volatile bouquet might change with plant species composition. Further, specific secondary metabolites are found predominantly in only a few plant taxa (Schoonhoven *et al.* 2005, Pichersky *et al.* 2006). Glucosinolates for example, whose hydrolysis products have volatile character, occur almost exclusively in one plant order that includes among others the well-studied Brassicaceae plant family (for reviews see Halkier and Gershenzon 2006, Renwick 2002). Nevertheless, the glucosinolates are further a good example that one class of compounds can show a high diversity between different plant species, even when closely related (Fahey *et al.* 2001, Benderoth *et al.* 2006). Besides interspecific

variation of volatile plant compounds, intraspecific variation between individual plants may additionally enhance the diversity of odour blends prevailing in the environment. In the case of the terpenoids, in several herbaceous and woody plant species, chemotypes are distinguishable, which differ in their amount and type of volatile compounds, although they are belonging to the same species by definition. For instance, chemotypes occur in populations of thyme (*Thymus vulgaris*, Lamiaceae) or yarrow (*Achillea millefolium*, Asteraceae) and in Scots pine trees (*Pinus sylvestris*, Pinaceae) (Theis and Lerda 2003, Orav *et al.* 2006, Thoss *et al.* 2007). Beyond differences among and within plant species, the variability of synthesis and emission of volatiles between different plant parts may add to the diversity of habitat odour bouquets. On intraplant level different parts such as leaves, buds, flowers or seeds may emit qualitatively and quantitatively different blends of volatiles (Knudsen *et al.* 1993, Irwin and Dorsett 2002, Pichersky and Gershenzon 2002). The overall variation in blend composition is further temporarily altered by induction of individual plants present in the habitat or parts of plants in response to either tissue damage caused by mechanical wounding, herbivore feeding, egg deposition or in response to plant-to-plant communication (e.g. Mumm *et al.* 2004, Van den Boom *et al.* 2004, Dicke *et al.* 2003, Ruther and Fürstenau 2005, Thoss and Byers 2006). Moreover, investigations with cultivated plants such as maize and rice revealed a high variability between different cultivars regarding the amounts and identity of emitted induced volatiles (Gouinguéné *et al.* 2001, Lou *et al.* 2006).

#### *Measuring volatile chemical diversity*

The measurement of chemical diversity of odour blends includes the determination of the qualitative and/or quantitative differences in compound composition. For qualitative analyses indices can be employed, which have been developed to describe the biodiversity of species within habitats, for example the Shannon-Wiener index. The chemodiversity index after Iason *et al.* (2005) determines the proportional concentration of a single compound in relation to the total number of detected compounds which are most concentrated in all samples. In this example the total number of components in the calculation were constant, thus, the determination of the chemical diversity was a measure of equitability of concentrations (see also Thoss and Byers 2006). Additionally, in this study Simpson's index was used as an alternative measure of chemodiversity in monoterpene content of individual Scots pine trees.

Further, Horn's index of similarity (also known as Morisita-Horn index, cf. Cramer and Willig [2005]) could be applied for the analysis of a volatile blend, which considers aside from compound identity also the abundances of these compounds. Bukovinszky *et al.* (2005) determined the similarities of volatile profiles measured from different *Brassica* plant species and the non-*Brassica* species malting barley (*Hordeum vulgare*, Poaceae). In their approach based on the Horn index they combined hierarchic clustering and a multidimensional scaling method to visualise the dissimilarities between the volatile bouquets of the investigated plant species. In general, multivariate data analysis might be a useful tool for a quantitative analysis of volatile patterns. Mumm *et al.* (2004) analysed and compared the headspace of egg-carrying and artificially wounded black pine (*Pinus nigra*, Pinaceae) and Scots pine (*Pinus sylvestris*, Pinaceae) twigs. Quantitative differences between volatiles blends of volatiles from differently treated twigs were compared with principal component analysis and additional discriminant analysis in order to separate specific clusters of components between different treatments and tree species. Another possibility to investigate volatile patterns quantitatively is to analyse each compound detected as a part of a blend and not as a compound released singly (Pareja *et al.* 2007). This procedure would be more closely to natural conditions, because plants always emit a mixture of varying compounds simultaneously, and thus, the individual components of these blends are not independent. Pareja *et al.* (2007) used an approach that combined several statistical methods to analyse the relative quantitative contributions of single compounds to an odour blend as a whole by multivariate analyses of the amounts of all compounds at the same time. Thereby the authors were able to determine fine-tuned increases and decreases of single compounds in the emitted volatile blend of herbivore-infested and uninfested brown knapweed (*Centaurea jacea*, Asteraceae) plants.

### **Effects of vegetation structure on odour blends and odour plumes**

#### *Influence of aerodynamic characteristics of vegetation structures on the dispersion of volatile compounds*

In the field, the dynamics of the occurring airflow are a product of the direct interaction between the structure of the ground surface and the physical characteristics

of the air (Moen 1974). Where a directed air stream meets vegetation structures it is disrupted and turbulences, i.e. large and small-scale eddies, develop. In general, the variation in wind velocity between two air masses leads to the formation of turbulences, which happens for example when a sweep of air hits the boundary of a plant canopy. The faster moving air from above makes the slower moving air beneath rise. Thereby, the faster air stream combines with the slower one and thus, also carries along volatile compounds emitted by the plants, resulting in thorough mixing of the air above the plant canopy (reviewed in Conover 2007). Turbulences are either the result of thermal or mechanical conditions prevailing in the environment. Thermal turbulences are caused by convective currents as a result of variations in air temperature. Convective currents above plant canopies can develop when solar radiation hits only the outer areas of a plant canopy, but does not reach the inner areas or the ground (Sun and Mahrt 1995, Sun 1999, Zhang *et al.* 2007). This can also have profound implications for microclimatic conditions above and within plant canopies in terms of light intensity, relative humidity and soil moisture, which might further influence the release of volatiles (Plaza *et al.* 2005, Llusia *et al.* 2006). The reasons for mechanical turbulences are frictional forces, i.e. the aerodynamic resistance caused by the surface structure of the vegetation. The term ‘aerodynamic roughness’ describes the extent of aerodynamic resistance vegetation structures generate (Moen 1974, Conover 2007). The aerodynamic roughness of plant canopies is directly related to their geometry and characteristics such as height, density and shape of the vegetation have a major impact on the variations in wind velocity and with it on turbulence intensity (Moen 1974, Ma and Daggupaty 2000, Dong *et al.* 2001, Whicker *et al.* 2002, Li *et al.* 2005). Thereby, homogeneous canopies form rather smooth surfaces with low turbulence intensity, whereas heterogeneous canopies represent rough surfaces with a high turbulence intensity occurring above or within them.

Specific types of plant canopies differ considerably in their aerodynamic roughness. The highest amount of air turbulence regarding grass or forb-dominated vegetation is achieved with a mixture of grasses and forbs varying in height and shape, because this creates a surface with a high aerodynamic roughness (Conover 2007). In intermediate vegetation types, such as savannas where open, grassy areas are intermingled with rather isolated standing bushes or trees, the sparsely occurring surface features enhance turbulence intensity and may lead to a rapid dispersion of volatile compounds. The wind profiles of canopies composed only of forbs differ

significantly from the ones of pure grass canopies, because the majority of leaves and the plant stems are concentrated at different heights. The speed of air streams in dense standing grasses in meadows slows down exponentially with depth into the canopy and the almost windless zone a few centimetres above the ground is interrupted frequently by gusts (Aylor *et al.* 1993). As the long and flexible leaves and stems of the grasses usually cause an upward distraction of the airflow, odorant particles released by grass canopies may experience fast dispersion into the atmosphere (Conover 2007). In contrast, in forb-dominated canopies with a high leaf density at the top level of the canopy, the airflow is slowed down already on the surface of the canopy. Measurements within soybean canopies revealed that the wind velocity is slower within rows than between the rows (Baldocchi *et al.* 1983). Therefore, it is likely that within dense forb canopies the dispersion of volatiles happens much slower than in grasslands, because odorant particles keep concentrated below the forb canopy and mixing of different odorant particles is reduced. This might also be the case in uniformly grown forests with a closed canopy. Wind velocity is usually retarded by the leaves and branches within the crown area, thus within the subcanopy of a forest wind velocities are much slower than above the canopy, but the intensity of turbulences is higher there (Baldocchi and Meyers 1988, Amiro 1990). Investigations in Sitka spruce (*Picea sitchensis*, Pinaceae) stands varying in spacing between the trees conducted by Green *et al.* (1995) revealed that the narrower the trees were placed to each other the more wind speed was reduced below the canopy in the trunk space. However, when understory vegetation is absent, wind speed may increase again in the subcanopy area (Baldocchi and Meyers 1988). Moreover, comparable to habitats characterised by grasses or forbs, in forests the dynamics of the airflow strongly depend on the type of forest, i.e. the trees species identity and composition and the growth structure, whether the canopy is even (for instance in forest plantations) or gaps occur between trees (for instance in undisturbed old growth forests) (Amiro 1990, Lee 2000). Wherever gaps occur within the forest canopy the turbulence intensity increases at these edges, because different vegetation structures meet and aerodynamic roughness is enhanced (Zhang *et al.* 2007).

*Influence of vegetation structure on odour plume structure and concentrations of volatile compounds*

Volatile compounds that are used as cues for location of host plants and prey or hosts have to exceed certain threshold concentrations in the air so that arthropods can detect these cues with their olfactory system. The concentrations of specific volatile chemical signals within the atmosphere are closely related to the shape and structure of the odour plume, which constitutes a highly intermittent stimulus (Murlis *et al.* 2000). Regarding shape and structure, both spatial and temporal aspects of an odour plume play a major role in the ability of arthropods to detect relevant volatile cues and follow them to their source of origin (reviewed in Murlis *et al.* 1992, Vickers 2006). The formation of odour plumes happens, when volatile chemical compounds are emitted by a source and are carried away by the wind. The appearance of these plumes can be described as discrete undulating cloud whose fine-scale structure is determined by individual intertwined air filaments containing either odour particles or clean air (Murlis *et al.* 1992, Bernays and Chapman 1994, Schoonhoven *et al.* 2005). On a large scale the shape of the plume as a meandering cloud may affect the odour-induced anemotactic responses exhibited by walking or flying arthropods orienting in upwind direction (Willis *et al.* 1994, Willis and Avondet 2005). On a small scale the fluctuating odour concentrations within the filaments may influence the neural processing of the odour signal and the following orientation response of arthropods to the source (Mafrá-Neto and Cardé 1994, 1998, Vickers and Baker 1994, Geier *et al.* 1999, Vickers *et al.* 2001). A specifically important characteristic of odour plumes is the intensity of the odour signal, i.e. the quantity of volatile compounds in a given space at a given time point and the distribution of these compounds, i.e. the rate at which concentrations change over time (Vickers 2006). These qualitative and quantitative properties of odour plumes depend on the chemical and physical characteristics of the containing odorant particles, the size of the source and its location and most of all wind speed (Murlis *et al.* 1992). Wind velocity and turbulence intensity are the main factors influencing the shape of an odour plume and the occurring concentrations of compounds within the plume.

Wind speed and airflow dynamics in turn may depend on plant structural complexity of the vegetation within habitats. Hence, vegetation structure may determine whether volatile compounds disperse in the air and become thoroughly mixed within and above the plant canopy or concentrate below the canopy, and

whether the containing volatiles drift along a more linear guided band or spread out into a rather homogeneous cloud (cf. Conover 2007 and literature therein). In general, the further away from the source the lower is usually the concentration of the volatiles within the plume, because the volatiles get diluted when moving away from the source (Murlis *et al.* 1992). However, it is known from investigations with pheromone plumes in the field that the surrounding vegetation absorbs volatile chemical compounds and later rereleases these absorbed volatiles again into the air and thus, new odour sources of a specific signal may be generated and can additionally influence the concentration of volatile cues in the atmosphere and the searching behaviour of arthropods (Perry *et al.* 1988, Karg *et al.* 1994, Suckling *et al.* 1996). Detailed studies with the help of smoke puffs or soap bubbles revealed that the movement direction of plumes and their linearity can vary considerably between different locations of the odour source and the surrounding vegetation structures. Over open habitat such as crop fields or grasslands individual segments of plumes may continue to follow a nearly straight line over a distance of about 20 m from the source (David *et al.* 1982, 1983). Under these conditions flying insects can relatively easy achieve to find the way to the source, when performing typical optomotor anemotactic upwind and crosswind flight behaviour (Willis and Cardé 1990, Vickers and Baker 1996). Within closed habitats such as forests, however, different aerodynamic conditions prevail and individual odour segments show highly non-linear trajectories even within few metres, which might affect severely the ability of arthropods to locate an odour source (Elkinton *et al.* 1987, Perry *et al.* 1988, Brady *et al.* 1989). The highly intermittent signal of fluctuating filaments of volatiles within plumes seems to be necessary for the maintenance of upwind flight, which was not initiated in homogenous clouds of volatiles in some searching insects (Kennedy *et al.* 1980, Baker *et al.* 1985, but see: Justus and Cardé 2002, Justus *et al.* 2002).

However, the knowledge that is available about odour plumes and the behavioural implications for arthropod searching behaviour was in the majority gathered in studies about moth pheromones and how male moths find females under various conditions. In contrast, hardly anything is known about how carnivore arthropods follow odour plumes generated by plants to locate their prey or hosts (Conover 2007). Furthermore, in experimental investigations about pheromone plumes the source of the odour is usually represented by a point source, which might not be



transferable to situations where whole plants or groups of plants represent the odour source.

### **Chemical diversity and its impact on herbivore and carnivore orientation**

The general or specific plant derived signals, which herbivores and carnivores use to locate their host plants and their prey or hosts, are commonly represented by mixtures of different volatile components (Städler 2002, Dicke *et al.* 2003, Schoonhoven *et al.* 2005). Therefore, the capability of arthropods to process complex odour stimuli in the peripheral and the central nervous system plays a key role regarding their behavioural responses (reviewed in Isman 1992, Mustaparta 2002, Ache and Young 2005). The recognition of an odour signal within the habitat and the following behavioural response involves both the quality and the quantity of the volatile signal (for reviews see Visser 1986, Vickers 2006). The information of relevant volatile cues may often be determined by the identity of individual (key) compounds and the specific composition of an odour blend out of different chemical compounds (e.g. Pettersson *et al.* 2001, de Boer *et al.* 2004, Bengtsson *et al.* 2006, Cunningham *et al.* 2006). On the other hand, the total amount of individual compounds and/or the relative ratios of the concentrations of individual compounds to each other in a blend may convey important information for searching arthropods (Visser and Avé 1978, Wright and Smith 2004b, Wright *et al.* 2005, Tasin *et al.* 2006). For some arthropod species both key compounds and the relative ratios of the occurring compounds in a blend might determine the behavioural response (Al Abassi *et al.* 2000, Breed *et al.* 2004). Further, the overall intensity of a volatile cue as a whole might be important for arthropod response (Wright and Smith 2004a).

However, the response of arthropods to volatile cues might be modified by the overall occurring odour bouquet prevailing in the environment. The presence of non-host plant volatiles in natural habitats can profoundly affect the detection and processing of relevant volatile signals and thus, the subsequently displayed behaviour of arthropods as initially described in this review. As outlined before, arthropods may encounter in their natural environment a huge number of volatiles due to high plant species diversity, which may lead to an enhanced chemical diversity through release of various volatile compounds into the air. In natural ecosystems, it is therefore argued

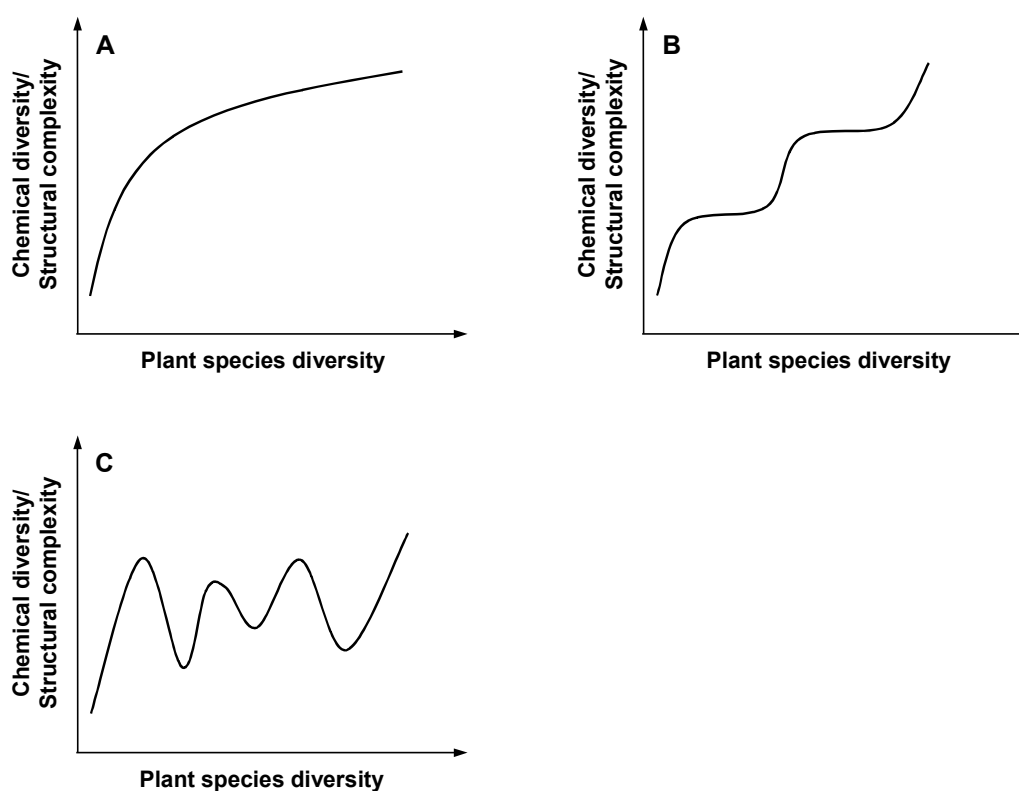
that typically occurring higher plant diversity might also generate higher signal diversity, because volatile signals derived from host plants are intermingled with volatiles released by non-host plants (Visser 1986, Hadacek 2002, Zhang and Schlyter 2004). Whether or not herbivorous as well as carnivorous arthropods are capable to filter the relevant information out of the chemical diversity of environmental odour bouquets may depend on their dietary specificity. Generalist and specialist herbivorous arthropods may differ in their neural abilities regarding the recognition and processing of volatile cues (Isman 1992, Bernays 2001, Mustaparta 2002). In this context it is assumed that specialist herbivores possess better filtering abilities than generalists (Egan and Funk 2006). Likewise, specialist carnivores are expected to make use of specific infochemical cues, for example pheromones or induced plant volatiles, whereas generalists should use primarily unspecific cues that are commonly related to their various types of prey or hosts (Vet and Dicke 1992, Steidle and van Loon 2003). However, it is argued that an optimisation of the olfactory system in arthropods towards high specificity has been achieved only for the perception of conspecific pheromones, but not with regard to host recognition, at least with regard to herbivore species (Isman *et al.* 1992). In general, on the peripheral level herbivorous arthropods feature specific olfactory receptors with a high specificity to unique compounds, but also quite unspecific receptors with a broadly overlapping sensitivity to many stimulatory compounds (Isman *et al.* 1992, Schoonhoven *et al.* 2005, Hallem *et al.* 2006). In terms of plant derived volatiles, both generalist and specialist herbivores show sensitivity and selectivity to volatile compounds that are generally occurring in many plant species, but also to volatiles, which are rather specific for certain plant groups (Mustaparta *et al.* 2002, Barata *et al.* 2002). Therefore, when arthropods have to cope with complex odour mixtures variable responses may be the outcome. It is known that odorant mixtures can cause excitatory or inhibitory effects during neural processing of these signals in the brain (Akers and Getz 1993, Ache and Young 2005, Deisig *et al.* 2006). Inhibitory processes in the central nervous system might act as a potential means to optimise discrimination of odour compounds in a diverse blend by enforcing only relevant stimuli (Laurent *et al.* 1999, Deisig *et al.* 2006). On the other hand, there is also evidence that arthropods may have difficulties to discriminate between different compounds in an odour blend, especially when compounds are quite similar in chemical structure, and adequate behavioural response to a relevant cue within odour mixtures might be impeded (Chandra and Smith 1998, Smith 1998,

Meiners *et al.* 2003). Although in recent years huge efforts have been made to elucidate the complex mechanisms of odour signal processing in arthropods, our knowledge is presently still incomplete regarding the neuronal pathways from the periphery to the central nervous system (Städler 2002, Ache and Young 2005). Moreover, the obtained results so far rely mainly on investigations with herbivorous arthropods or bees, but carnivorous species were scarcely considered.

*Proposed relationships between plant species diversity, chemical diversity and structural complexity of habitats*

Up to now, no hypothesis has been formulated that clearly points out the possible relationship between plant species diversity, structural complexity and volatile chemical diversity. Therefore in this review, we put forward three hypotheses, which describe how plant species diversity and vegetation structure might be related to the occurring odour bouquet in arthropod habitats. The proposed hypotheses have been developed on the basis of previously stated hypotheses on general species biodiversity within habitats (see Lawton 1994, Johnson *et al.* 1996, Naeem 1998). First, one could assume that the chemical diversity of an odour blend will rapidly increase with the gradual increase of plant species diversity and structural complexity within the habitat, provided that each new plant species adds different chemical compounds to the overall habitat odour blend. This assumption would further imply that plant species diversity directly correlates with structural complexity and that enhanced structural complexity concurrently increases volatile chemical diversity by augmenting turbulence intensity and ensuring vigorous mixing of volatiles in the atmosphere. For example, in studies investigating the successional processes of habitats it has been shown that structural heterogeneity increases during the course of succession (Cook *et al.* 2005, Martinko *et al.* 2006). However, as plants produce not an infinite number of volatile compounds the increase in volatile chemical diversity may slow down eventually and the chemical diversity might even approximate a plateau (Fig. 1A). A proposed second hypothesis takes into account that volatile chemical diversity and structural complexity do not change gradually with plant species diversity, but rather with the diversity of plant taxa. Regarding chemical diversity particular volatile chemical compounds are restricted to specific plant groups and closely related plant species might release quite similar odour blends (Schoonhoven *et al.* 2005, Pichersky *et al.* 2006). Plant groups, which contain specific compounds, might therefore represent distinct chemical

functional groups. In addition, plant groups are distinguishable according to their spatial growth form, for example plant height and branching order. Hence, certain plant species may further constitute functional groups with respect to plant architecture (see Hooper *et al.* 2005). In this case, chemical diversity in habitats may increase stepwise every time a new plant taxon with a divergent type of secondary plant metabolites or plant architecture is added to the plant species pool of the habitat (Fig. 1B).



**Figure 1.** Proposed relationships on the influence of plant species diversity and structural complexity on volatile chemical diversity within habitats of arthropods. (A) Continuous increase in diversity of volatile compounds and structural complexity with increasing plant species diversity. (B) Stepwise increase of volatile chemical diversity and structural complexity with increasing diversity of plant functional groups. (C) No direct correlation between volatile chemical diversity, structural complexity and plant species diversity.

Finally, plant species diversity might be a weak predictor for the composition of odour bouquets in the environment, because of a large inter- and intraspecific variability of plant secondary metabolism. Furthermore, the relationship between plant species diversity and structural complexity of the vegetation might vary largely with regard to

plant species composition and the analysed spatial scale, therefore generalisations might be difficult to deduce (González-Megías *et al.* 2007). The impact of vegetational complexity on the occurring airflow is highly variable over time and possesses a certain random character and thus, might not allow for making any predictions. In fact, the influence of the aerodynamic properties of vegetation structure on the specific qualitative and quantitative characteristics of odour blends is largely unknown to date. Thus, it also might be possible that no correlative relationship between plant species diversity, structural complexity and the volatile chemical diversity exists under natural conditions (Fig. 1C).

### **Concluding remarks**

Up to now, investigations that analysed the impact of plant species diversity and plant structural complexity on arthropods responses revealed positive, negative or even no effects both in natural and managed habitats. Therefore, predicting the impact of enhanced vegetational complexity on herbivorous and carnivorous arthropod species seems to be difficult. On the one hand, the large variability of analysed spatial scales might account for the contradictory results (Bommarco and Banks 2003). On the other hand, this may be also due to the fact that we still know very little about the acting mechanisms in diverse habitats in the field (Potting *et al.* 2005). Different mechanisms, underlying the behavioural responses of arthropods, have been elucidated to explain the observed variability of the obtained results, which considered the visual and olfactory orientation as well as the movement ability of arthropods. However, many studies that analysed the underlying mechanisms were performed in the laboratory, but the prevailing conditions in natural habitats may differ largely from the laboratory situation. This may be particularly the case with regard to the impact of diverse odour mixtures on arthropod orientation. The complexity of tested odour mixtures in laboratory experiments has been usually rather low compared to the composition of odour blends in natural environments. Moreover, the focus of these studies has been placed on herbivorous arthropods and their sensory processing abilities regarding odour blends. Under field conditions, investigations concentrated on the response of moth species to pheromone plumes. It is arguable whether these results are transferable to plant derived volatile cues which might not represent a distinct point

source of released volatiles. Therefore, research efforts should be expanded to a wider range of species, especially carnivorous ones, with regard to odour blends in more natural situations. This could help to complete the knowledge about the linkage between the sensory processes in the insect brain and arthropod behaviour in the field (van Naters and Carlson 2006). Furthermore, investigating the role of plant species diversity for volatile chemical diversity and the effect of structural complexity on the composition of odour bouquets occurring in the field further on might provide new insights in arthropod orientation behaviour. This may allow for better estimating the impact of vegetational complexity on arthropod responses.

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