GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 15 (2014) 685–692

Basic and Applied Ecology

www.elsevier.com/locate/baae

Does insect herbivory on oak depend on the diversity of tree stands?

Urwa Alalouni[a,*], Roland Brandl[a], Harald Auge[b], Martin Schädler[b]

[a]*Department of Animal Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, 35032 Marburg, Germany*
[b]*Department Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Straße 4, 06110 Halle, Germany*

Received 13 February 2014; accepted 28 August 2014
Available online 6 September 2014

Abstract

Studies on the effects of plant diversity on insect herbivory have produced conflicting results. Plant diversity has been reported to cause positive and negative responses of herbivores. Explanations for these conflicting responses include not only various population-level processes but also changes in plant quality that lead to changes in herbivore performance. In a tree diversity experiment, we investigated the effects of tree diversity on insect herbivory on oak in general and whether the effects of tree diversity on herbivore damage are reflected by the performance (leaf consumption, growth) of the generalist herbivore *Lymantria dispar*. Our study showed that the feeding damage caused by naturally occurring herbivores on oak trees decreased with increasing diversity of tree stands. The performance of *L. dispar* on oak leaves was not affected by tree diversity, neither in field nor laboratory experiments. Our results can be explained by the various processes behind the hypothesis of associational resistance.

Zusammenfassung

Studien zum Einfluss von Pflanzendiversität auf Herbivorie durch Insekten ergaben bisher keine einheitlichen Ergebnisse. Es wird sowohl über eine Ab- als auch eine Zunahme der Herbivorie mit ansteigender Anzahl an Pflanzenarten berichtet. Erklärungen für diese Muster umfassen zum einen diverse populationsbiologische Mechanismen, zum anderen aber auch Änderungen der Qualität des Pflanzengewebes mit zunehmender Pflanzendiversität, welches das Wachstum der Herbivoren beeinflusst. In einem Diversitätsexperiment mit Bäumen, haben wir den Einfluss der Baumdiversität auf den Fraßdruck von herbivoren Insekten auf Eiche sowie auf Fraß und Wachstum eines generalistischen Herbivoren (*Lymantria dispar*) untersucht. Insbesondere sollte geprüft werden, ob sich der Einfluss der Diversität des Baumbestandes auf Herbivorie mit Änderungen in Fraß und Wachstum an diesen Bäumen erklären lässt. In unserem Experiment konnten wir zeigen, dass mit zunehmender Diversität von Baumbeständen der Fraßschaden durch Herbivorie abnahm, es konnte aber kein Einfluss der Baumdiversität auf den Fraß und das Wachstum von *L. dispar* Larven festgestellt werden. Daraus schließen wir, dass die Abnahme des Fraßschadens im Freiland auf die verschiedenen Prozesse der Assoziationsresistenz zurückzuführen ist.

Keywords: Tree diversity; Plant–insect interaction; Associational resistance; Plant quality

*Corresponding author. Tel.: +49 6421 2826819; fax: +49 6421 28 23387.
E-mail addresses: alalouni@staff.marburg-uni.de, alalouni@staff.uni-marburg.de (U. Alalouni).

http://dx.doi.org/10.1016/j.baae.2014.08.013
1439-1791/

Introduction

Plant diversity affects plant–herbivore interactions in a wide range of ecosystems (Coley & Barone 1996; Mulder, Koricheva, Huss-Danell, Hogberg, & Joshi 1999; Jactel & Brockerhoff 2007; Scherber et al. 2010; Haddad, Crutsinger, Gross, Haarstad, & Tilman 2011). However, the magnitude and direction of the effects vary considerably among studies. Whilst a number of studies show that herbivore abundance and damage increase with increasing plant diversity (Mulder et al. 1999; Prieur-Richard, Lavorel, Linhart, & Dos Santos 2002; Schuldt et al. 2010), other studies demonstrate a decrease in abundance and damage with increasing plant diversity (Scherber et al. 2006; Jactel & Brockerhoff 2007; Unsicker, Oswald, Koehler, & Weisser 2008). Some studies indicate that neither abundance of nor damage by herbivores uniformly increases or decreases with plant diversity. Instead, diversity effects are variable and dependent on the identity of the host tree, stand characteristics, as well as the type of herbivores (Vehvilainen, Koricheva, Ruohomaki, Johansson, & Valkonen 2006; Vehvilainen, Koricheva, & Ruohomaki 2007).

To account for the effects of plant diversity on plant–herbivore interactions, two general hypotheses have been introduced. In the first hypothesis, named "associational susceptibility", an increase in herbivore damage with increasing plant diversity is attributed to a "spill over" of herbivores (White & Whitham 2000; Brockerhoff, Liebhold, & Jactel 2006; Barbosa et al. 2009). In this case, herbivores, especially generalists, develop large populations on preferred host plants before shifting to other plants (Brown & Ewel 1987; Wada, Murakami, & Yoshida 2000; White & Whitham 2000; Jactel & Brockerhoff 2007). Moreover, herbivore performance increases with a diverse diet (Unsicker et al. 2008), which may also increase population growth and therefore abundance. The second hypothesis, "associational resistance", suggests that one or more processes could lead to a decrease in herbivore damage with increasing plant diversity. An increased diversity of plant species might support the abundance and efficiency of natural enemies (Andow 1991). As a result, a decrease of herbivore pressure is expected. Furthermore, herbivores, particularly specialists, are faced with a resource dilution in a diverse plant community (Tahvanainen & Root 1972; Root 1973; Barbosa et al. 2009). Additionally, increasing tree diversity in stands may decrease herbivore pressure due to the higher probability of focal trees being associated with taller neighbours, which decrease the apparency of the focal trees for herbivores (Castagneyrol et al. 2013).

Plant diversity, however, may also influence plant quality (i.e. nitrogen content of leaves), which in turn affects herbivore feeding. Such changes in plant quality may result from modifications of the soil conditions by co-occurring plant species. Numerous studies show that plants growing in monocultures support herbivores more than plants growing in mixed cultures owing to changes in plant quality (Bach 1980a,b, 1981; van Ruijven & Berendse 2003; Schenk 2006; Marquard et al. 2013). Furthermore, a reduction in plant diversity leads to changes in nutrient ratios and increasing variance in elemental composition of plants, which lead to changes in herbivore reactions (Abbas et al. 2013). This may also be the case in tree stands as it has been shown that total nitrogen uptake is higher in mixed tree communities (Lang et al. 2014).

Experimental studies on the consequences of species diversity on ecosystem properties and processes are, for obvious reasons, often performed with herbaceous plant species (Baeten et al. 2013). Yet trees, in comparison to many herbaceous plants, represent a more stable and predictable resource for herbivorous insects (Tscharntke & Brandl 2004; Vehvilainen et al. 2007). This predictability has even led to the suggestion that some herbivores may adapt to tree individuals (Raubenheimer & Simpson 1992; Ruhnke, Schädler, Matthies, Klotz, & Brandl 2006). Furthermore, the longer life span of trees than of herbaceous plants might cause pronounced effects of diversity for several reasons: (i) the long life span allows tree individuals to implement sophisticated defence strategies against herbivores, (ii) changes in the apparency and light environment of old trees might alter the levels of herbivory and (iii) old trees may change the abundances and efficiency of natural enemies (Moore & Francis 1991; Tylianakis, Didham, & Wratten 2004; Boege & Marquis 2005).

Here we studied the effects of tree diversity on insect herbivory and the performance of a generalist herbivore (*Lymantria dispar*). Our tree diversity experiment allowed us (a) to assess oak leaf damage caused by naturally occurring herbivores in the field and (b) to assess the performance (leaf consumption, growth) of *L. dispar* feeding on oak foliage in both field and laboratory experiments. We evaluated whether herbivore pressure increases or decreases with tree diversity. The herbivore performance data allowed us to evaluate whether the effects of tree diversity on herbivory can be explained by changes in leaf quality.

Materials and methods

Experimental design

The study was conducted using the infrastructure provided by the Kreinitz Tree Diversity Experiment in central Germany (51°23′N, 13°15′E, 110 m above sea level). This diversity experiment was established in fall 2005 on a former arable field abandoned in the 1990s. The experimental site is surrounded by a matrix of mature forest. The experiment was set up in two blocks; each block consisted of 49 plots of 25 m^2 (5 m × 5 m) that vary in diversity and composition of tree species. The tree species pool consists of 6 species native to central Europe: common beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.), Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.) and small-leaved lime (*Tilia cordata* Mill.). The plots were randomly assigned to 49 treatments representing 6 diversity levels: bare soil (no trees planted), monocultures (of each of the 6 tree species), all possible combinations of 2 species (15 combinations), all possible combinations of 3 species (20 combinations), all possible combinations of 5 species (6 combinations), and all 6 species. In 2005, 30 two-year-old tree saplings were planted in a regular pattern on each plot, with 1.0 m between rows and 0.8 m between trees in a row. The different species were randomly assigned to each planting position; during the first two years, dead individuals were replaced by saplings of the same species and age cohort. In our study, we used the 22 plots in each block that contained individuals of sessile oak. In the study year, oak trees had reached an average height of 1.9 m. Average height of the other species ranged from 0.96 m (beech) to 2.1 m (ash).

Herbivore damage in the field

In July 2009, herbivore damage on oak trees was assessed on all 44 plots with oaks. On each plot, one oak individual was randomly selected. To avoid edge effects, we selected only individuals from the inner area of the plots. We randomly selected two branches from both upper and lower layers of the chosen individual as tree layer has been shown to affect herbivore damage (Raubenheimer & Simpson 1992; Ruhnke, Schädler, Klotz, Matthies, & Brandl 2009). For each branch, we inspected 16–20 leaves for signs of insect herbivory. We counted leaves with damage caused by leaf chewers, hole feeders, gallers, miners, rollers and skeletonizers and the presence of sap-sucking insects. Leaves from the two branches from each layer were pooled, and the percentage of damaged leaves per tree and layer was calculated. In addition to the calculation of total damage, we also calculated the cumulative damage as the sum of the number of leaves of each damage type (values may exceed 100%). Only damage caused by chewers and hole feeders were common enough to allow separate analyses.

The effects of tree diversity on larval performance

The performance (leaf consumption and growth) of the gypsy moth (*L. dispar* L.; New Jersey strain) was measured in the field and laboratory. These caterpillars are generalist herbivores that feed on a wide range of tree species (Alalouni, Schädler, & Brandl 2013). They are highly sensitive to changes in leaf quality and are therefore a suitable integrative indicator for evaluating tissue quality (Barbosa & Greenblatt 1979; for *Quercus robur* see Giertych, Bakowski, Karolewski, Zytkowiak, & Grzebyta 2005). Prior to the experiments, groups of 10 larvae were reared on an artificial diet in plastic boxes ($15 \times 11 \times 6\,cm^3$). Feeding was stopped one day before field and laboratory experiments.

In the field experiment, we used 3 larvae per plot (132 larvae). Each larva was weighed and then placed on a randomly selected branch of an oak tree on inner areas of the plot. We covered the branch area of each larva with a fine-meshed bag. After two weeks, we measured the final weight of each larva.

In the laboratory experiment, we used 3 larvae per plot (132 larvae). Each larva was weighed and placed into an individual Petri dish (three Petri dishes per plot). We fed the larvae on oak leaves; i.e. oak leaves from the same tree on the same plot on which the larvae in the field were tested. For this experiment, we collected only leaves without any visible signs of herbivory or pathogens from the plots. The breeding room conditions were set to 23–25 °C, 70–75% humidity and a light:dark regime of 18:6 h for the entire experiment. After 5 days, we measured the final weight of each larva. We also estimated the dry mass of consumed leaves by calculating the difference between the dry weight of used leaves before and after feeding. We estimated the water content per plot by weighing four leaves of the tested oak trees in each plot, drying them and then estimating the percentage of water content. Values from the three Petri dishes of each plot were averaged and used as replicates for the analyses.

Statistical analysis of herbivore damage in the field

Tree diversity was represented in five different diversity levels (1, 2, 3, 5, and 6) as described above, i.e. level 1 represented an oak monoculture on the plot, while level 6 represented the combination of all tree species. Diversity was based on the different species combinations (tree composition) such that levels 2, 3 and 5 have different sub-levels based on species combinations. The effect of tree diversity on leaf damage in the field was tested using a generalized linear mixed model with block, tree diversity (categorical), species composition, tree individual and layer as factors. Block, tree individual and species composition were considered random factors. Species composition was nested within tree diversity, and the upper and lower layers were regarded as split-plots within individuals. The model was calculated as a binary response model with logit link function, and linear contrasts were used to test the a priori hypothesis that diversity caused a gradual change of response variables (Proc Glimmix, SAS 9.2).

Statistical analysis of the effects of tree diversity on larval performance

We tested the effects of diversity on the performance of the gypsy moth larvae (leaf consumption, growth) using nested ANCOVAs for both laboratory and field experiments. Again, block and tree composition were included as random effects, and tree composition nested within diversity. To account for initial differences of larvae, initial larval weight was used as a covariate (Type I sum of squares) of final weight and

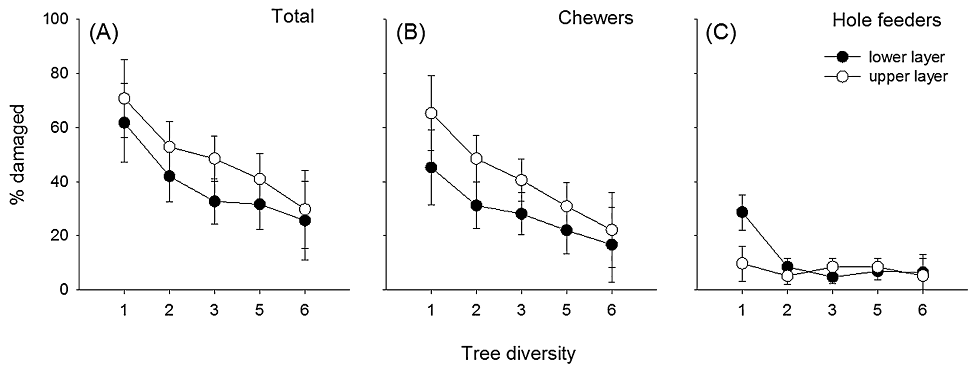

Fig. 1. Damage caused by herbivores feeding on oak foliage in the field. (A) Total damage, (B) damage caused by leaf chewers, and (C) damage caused hole feeders. Values are means ± standard errors.

consumed leaf mass (Raubenheimer & Simpson 1992; Ruhnke et al. 2009). For the analysis of biomass gain of larvae, consumed leaf material was used as covariate, giving an estimate of the efficiency of conversion of ingested food into body mass (Waldbauer 1968). Linear contrasts were used to test the a priori hypothesis that diversity caused a gradual change of response variables (Proc Mixed, SAS 9.2). Prior to the analyses, we tested the assumptions of ANOVA (normal distribution, heteroscedasticity) by visual inspection of residuals.

Results

The proportion of oak leaves on both tree layers damaged by herbivores in the field decreased with tree diversity (overall $F_{4,17} = 2.59$, $P = 0.08$; linear contrast $P < 0.05$; Fig. 1A). The same pattern was found for the percentage of leaves with damage caused by leaf-chewing insects (Fig. 1B; tree diversity: $F_{1,17} = 2.95$, $P = 0.05$; linear contrast: $P < 0.05$), but not for damage caused by hole-feeding insects (Fig. 1C; tree diversity: $F_{1,17} = 1.40$, $P > 0.1$).

Leaf damage was not dependent on tree species composition (all $P > 0.1$). Total leaf damage was generally higher in the upper tree layer (lower layer: 39% ± 8.6%; upper layer 49% ± 8.6%; $F_{1,39} = 16.5$, $P = 0.002$). Damage caused by leaf chewers was also generally higher in the upper tree layer (lower layer: 29% ± 7.9%; upper layer: 42% ± 7.9%; $F_{1,39} = 27.4$, $P < 0.001$). For hole feeders, the effect of tree diversity was dependent on tree layer (significant interaction: $F_{1,39} = 6.51$, $P = 0.004$). Only in the lower layer was damage by hole feeders higher in oak monocultures (Fig. 1C).

Tree diversity and composition showed no effects on the larval consumption and growth, neither in the field nor in the laboratory (ANCOVA: $P > 0.1$ for all tests; Fig. 2).

Discussion

The genus *Quercus* harbours more species of phytophagous insects than any other tree genus in Germany (Brändle & Brandl 2001). This may in part explain the high herbivory damage on leaves observed, with up to about 70% in oak monocultures. Furthermore, we found that an increase in tree diversity was associated with reduction in the total damage caused by herbivores. Our study also showed that tree diversity had no effects on the performance of gypsy moth larvae.

Our results do not support the associational susceptibility hypothesis and suggest that the patterns in herbivore damage in the investigated system are not explained by changes in leaf quality. Thus, the various processes behind the associational resistance hypothesis provide possible explanations for our results. First, control of herbivores by natural enemies (Root 1973; Wilby & Thomas 2002; Sobek, Scherber, Steffan-Dewenter, & Tscharntke 2009) might be involved in the decreased leaf damage observed with increasing diversity of tree stands. Tree diversity might supply natural enemies with appropriate resources and habitats, thereby increasing their efficiency in controlling populations of insect herbivores (Wilby & Thomas 2002; Jactel, Brockerhoff, & Duelli 2005; Cardinale et al. 2006; Barbosa et al. 2009). Second, tree diversity might divert herbivores, particularly specialists, from their preferred hosts. This disruption involves optical and chemical processes (Floater & Zalucki 2000; McNair, Gries, & Gries 2000; Dulaurent et al. 2012) in which visual and olfactory cues of non-host or less-preferred trees hinder phytophagous insects from finding their host trees (Finch, Billiald, & Collier 2003; Reeves, Lorch, & Kershner 2009; Jactel, Birgersson, Andersson, & Schlyter 2011). Furthermore, a decrease of tree apparency with increasing tree diversity might contribute to the reduction of damage detected in our experiment (Castagneyrol et al. 2013).

Castagneyrol, Jactel, Vacher, Brockerhoff, and Koricheva (2014) have demonstrated that the effects of tree diversity also depend on the phylogenetic diversity of tree species mixtures as well as herbivore specialization. In their study, the associational resistance against generalist herbivores is high in phylogenetically diverse tree mixtures, whilst herbivory by specialists is generally low in such mixtures. Our experiment was not designed to test for effects of phylogenetic

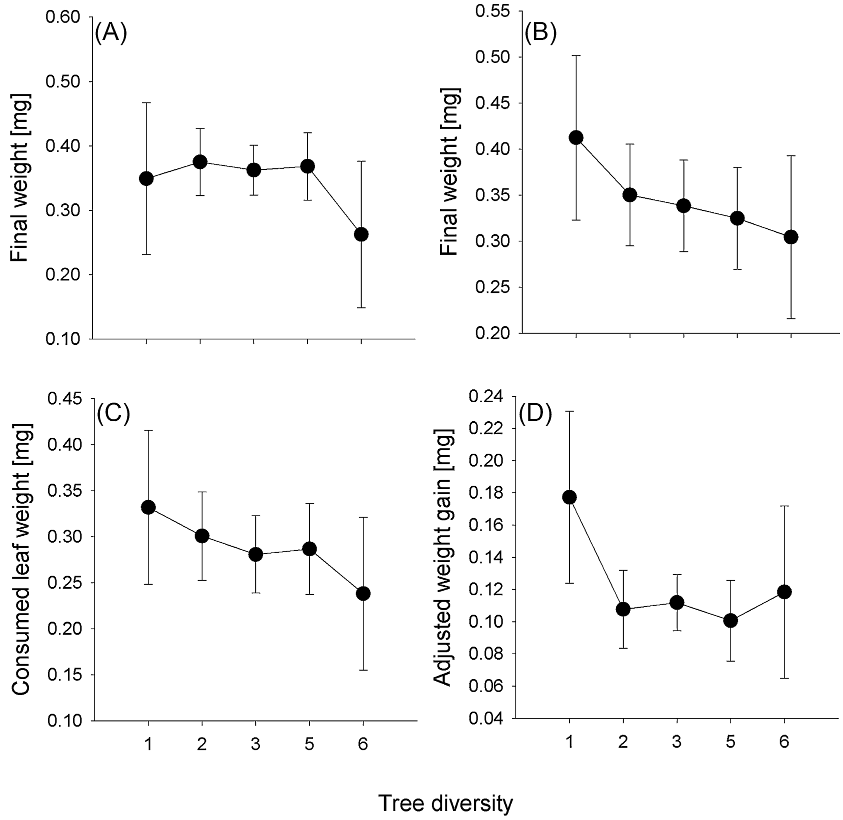

Fig. 2. Effects (means ± standard errors) of tree diversity on (A) final weight of *Lymantria dispar* larvae feeding on oak leaves, adjusted for the initial weight of larvae, (B) final weight of larvae feeding on oak leaves in the laboratory, adjusted for the initial weight of larvae, (C) consumed leaf dry weight in the laboratory, adjusted for the initial weight of larvae and (D) larval weight gain in the laboratory, adjusted for consumed leaf material. For details, see Materials and methods section.

diversity, but the absence of any significant effects of species composition on herbivory indicated that phylogenetic diversity was of little importance for our results.

Some studies have led to speculations that herbivores should change their performance with changes in plant quality owing to tree diversity (Bach 1980a,b) as well as composition of tree species (Moore & Francis 1991). For example, the consumption and growth of a generalist herbivore is significantly greater on oak leaves from experimental oak–spruce mixtures than from oak–adler mixtures or/and pure oak stands (Moore & Francis 1991). In our experiment, tree diversity and composition had no effect on the performance of the gypsy moth larvae. If herbivore performance depends on the quality of the diet, then our results implied that there is no change in plant quality across the experimental levels of tree diversity. But cautionary notes are in order to qualify our findings. First of all, changes in leaf quality (e.g. due to complementary effects of tree mixtures) are expected to increase over time, and the tree stands used for our experiments may have been too young to show such effects (Moore & Francis 1991; Boege & Marquis 2005). Moreover, the performance of herbivores on trees depends not only on leaf quality (Moore & Francis 1991) but also on other factors that involve leaf distribution across the canopy, time of bud break, the physical structure and biochemical processes. Plant quality also depends on the genotype and may therefore vary among and within tree individuals (Dudt & Shure 1994; Laitinen, Julkunen-Tiitto, & Rousi 2000; Osier, Hwang, & Lindroth 2000; Osier & Lindroth 2001; Henriksson et al. 2003). Clearly, the plethora of factors influencing feeding behaviour and development of herbivorous insects (Osier et al., 2000; Fortin & Mauffette 2002; Osier & Lindroth 2004) might dilute diversity effects.

Results of previous studies have suggested that there is no general pattern of variations in leaf palatability among the various layers of the canopy (Rowe & Potter 1996; Reynolds & Crossley 1997; Fortin & Mauffette 2002; Ruhnke et al. 2009). Such a variation in tissue quality across canopy layers varies not only between tree species and tree individuals, but also between years (Ruhnke et al. 2009), which makes trees “moving” targets for herbivores. In our experiment, we found higher herbivory damage in the upper layers of individual oaks than in the lower layer (except for hole feeders). However, we are not able to offer a specific explanation of this finding, which may range from a higher proportion of young leaves in the upper layer (young leaves have a high nitrogen content and low tannin concentrations) to microclimatic effects (Murakami & Wada 1997; Murakami, Yoshida, Hara, & Toda 2005).

In conclusion, our study showed that damage caused by herbivores decreases with increasing tree diversity, which is in line with several recent studies (Jactel & Brockerhoff 2007; Kaitaniemi, Riihimaki, Koricheva, & Vehvilainen 2007). This reduction in tree damage seems to be due to processes that increase associational resistance to herbivores. However, our results provide no insights into the possible mechanisms behind the associational resistance hypothesis. Therefore, further investigations are necessary to analyse the host-search behaviour of herbivores as well as the abundance of natural enemies in relation to plant diversity.

Acknowledgments

We thank Dr. Dörte Goertz (Institut für Forstentomologie, Forstpathologie und Forstschutz, Vienna, Austria) for providing us with gypsy moth egg masses and for important tips on rearing the larvae. We also thank Karen Brune for editing the manuscript. The Kreinitz experiment is a cooperative research initiative, and we thank the many people who have assisted with the establishment and maintenance of the experiment and who are too numerous to be listed. In particular, we acknowledge the Departments of Community Ecology, Soil Ecology, Soil Physics and Environmental Microbiology and the team of the Bad Lauchstädt field station of the Helmholtz Centre for Environmental Research - UFZ.

References

Abbas, M., Ebeling, A., Oelmann, Y., Ptacnik, R., Roscher, C., Weigelt, A., et al. (2013). Biodiversity effects on plant stoichiometry. *PLoS One*, 8.

Alalouni, U., Schädler, M., & Brandl, R. (2013). Natural enemies and environmental factors affecting the population dynamics of the gypsy moth. *Journal of Applied Entomology*, *137*, 721–738.

Andow, D. A. (1991). Vegetational diversity and arthropod population response. *Annual Review of Entomology*, *36*, 561–586.

Bach, C. E. (1980a). Effects of plant diversity and time of colonization on an herbivore–plant interaction. *Oecologia*, *44*, 319–326.

Bach, C. E. (1980b). Effects of plant-density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Aclymma Vittata* (FAB). *Ecology*, *61*, 1515–1530.

Bach, C. E. (1981). Host plant-growth form and diversity – effects on abundance and feeding preference of a specialists herbivore, *Aclymma Vittata* (Coleoptera, Chrysomelidae). *Oecologia*, *50*, 370–375.

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finer, L., et al. (2013). A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology Evolution and Systematics*, *15*, 281–291.

Barbosa, P., & Greenblatt, J. (1979). Suitability, digestibility and assimilation of various host plants of the gypsy moth *Lymantria dispar* L. (Lepidoptera, Lymantriidae). *Oecologia*, *43*, 111–119.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology Evolution and Systematics*, *40*, 1–20.

Boege, K., & Marquis, R. J. (2005). Facing herbivory as you grow up: The ontogeny of resistance in plants. *Trends in Ecology & Evolution*, *20*, 441–448.

Brändle, M., & Brandl, R. (2001). Species richness of insects and mites on trees: Expanding Southwood. *Journal of Animal Ecology*, *70*, 491–504.

Brockerhoff, E. G., Liebhold, A. M., & Jactel, H. (2006). The ecology of forest insect invasions and advances in their management. *Canadian Journal of Forest Research*, *36*, 263–268.

Brown, B. J., & Ewel, J. J. (1987). Herbivory in complex and simple tropical successional ecosystems. *Ecology*, *68*, 108–116.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., et al. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, *443*, 989–992.

Castagneyrol, B., Giffard, B., Pere, C., & Jactel, H. (2013). Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology*, *101*, 418–429.

Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E. G., & Koricheva, J. (2014). Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *Journal of Applied Ecology*, *51*, 134–141.

Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, *27*, 305–335.

Dudt, J. F., & Shure, D. J. (1994). The influence of light and nutrients on foliar phenolics and insects herbivory. *Ecology*, *75*, 86–98.

Dulaurent, A.-M., Porte, A. J., van Halder, I., Vetillard, F., Menassieu, P., & Jactel, H. (2012). Hide and seek in forests: Colonization by the pine processionary moth is impeded by the presence of nonhost trees. *Agricultural and Forest Entomology*, *14*, 19–27.

Finch, S., Billiald, H., & Collier, R. H. (2003). Companion planting – do aromatic plants disrupt host-plant finding by the cabbage root fly and the onion fly more effectively than non-aromatic plants? *Entomologia Experimentalis Et Applicata*, *109*, 183–195.

Floater, G. J., & Zalucki, M. P. (2000). Habitat structure and egg distributions in the processionary caterpillar Ochrogaster lunifer: Lessons for conservation and pest management. *Journal of Applied Ecology*, *37*, 87–99.

Fortin, M., & Mauffette, Y. (2002). The suitability of leaves from different canopy layers for a generalist herbivore (Lepidoptera: Lasiocampidae) foraging on sugar maple. *Canadian Journal of Forest Research*, *32*, 379–389.

Giertych, M. J., Bakowski, M., Karolewski, P., Zytkowiak, R., & Grzebyta, J. (2005). Influence of mineral fertilization on food quality of oak leaves and utilization efficiency of food components by the gypsy moth. *Entomologia Experimentalis Et Applicata*, *117*, 59–69.

Haddad, N. M., Crutsinger, G. M., Gross, K., Haarstad, J., & Tilman, D. (2011). Plant diversity and the stability of foodwebs. *Ecology Letters*, *14*, 42–46.

Henriksson, J., Haukioja, E., Ossipov, V., Ossipova, S., Sillanpaa, S., Kapari, L., et al. (2003). Effects of host shading on consumption and growth of the geometrid Epirrita autumnata: Interactive roles of water, primary and secondary compounds. *Oikos*, *103*, 3–16.

Jactel, H., Birgersson, G., Andersson, S., & Schlyter, F. (2011). Non-host volatiles mediate associational resistance to the pine processionary moth. *Oecologia*, *166*, 703–711.

Jactel, H., Brockerhoff, E., & Duelli, P. (2005). A test of the biodiversity-stability theory: Meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. *Forest Diversity and Function: Temperate and Boreal Systems*, *176*, 235–262.

Jactel, H., & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters*, *10*, 835–848.

Kaitaniemi, P., Riihimaki, J., Koricheva, J., & Vehvilainen, H. (2007). Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fennica*, *41*, 259–268.

Laitinen, M. L., Julkunen-Tiitto, R., & Rousi, M. (2000). Variation in phenolic compounds within a birch (*Betula pendula*) population. *Journal of Chemical Ecology*, *26*, 1609–1622.

Lang, A. C., von Oheimb, G., Scherer-Lorenzen, M., Yang, B., Trogisch, S., Bruelheide, H., et al. (2014). Mixed afforestation of young subtropical trees promotes nitrogen acquisition and retention. *Journal of Applied Ecology*, *51*, 224–233.

Marquard, E., Schmid, B., Roscher, C., De Luca, E., Nadrowski, K., Weisser, W. W., et al. (2013). Changes in the abundance of grassland species in monocultures versus mixtures and their relation to biodiversity effects. *PLoS One*, *8*(9) http://dx.doi.org/10.1371/journal.pone.0075599

McNair, C., Gries, G., & Gries, R. (2000). Cherry bark tortrix, *Enarmonia formosana*: Olfactory recognition of and behavioral deterrence by nonhost angio- and gymnosperm volatiles. *Journal of Chemical Ecology*, *26*, 809–821.

Moore, R., & Francis, B. J. (1991). Factors influencing herbivory by insects on oak trees in pure stands and paired mixtures. *Journal of Applied Ecology*, *28*, 305–317.

Mulder, C. P. H., Koricheva, J., Huss-Danell, K., Hogberg, P., & Joshi, J. (1999). Insects affect relationships between plant species richness and ecosystem processes. *Ecology Letters*, *2*, 237–246.

Murakami, M., & Wada, N. (1997). Difference in leaf quality between canopy trees and seedlings affects migration and survival of spring-feeding moth larvae. *Canadian Journal of Forest Research*, *27*, 1351–1356.

Murakami, M., Yoshida, K., Hara, H., & Toda, M. J. (2005). Spatio-temporal variation in Lepidopteran larval assemblages associated with oak, *Quercus crispula*: The importance of leaf quality. *Ecological Entomology*, *30*, 521–531.

Osier, T. L., Hwang, S. Y., & Lindroth, R. L. (2000). Effects of phytochemical variation in quaking aspen *Populus tremuloides* clones on gypsy moth *Lymantria dispar* performance in the field and laboratory. *Ecological Entomology*, *25*, 197–207.

Osier, T. L., & Lindroth, R. L. (2001). Effects of genotype, nutrient availability, and defoliation on aspen phytochemistry and insect performance. *Journal of Chemical Ecology*, *27*, 1289–1313.

Osier, T. L., & Lindroth, R. L. (2004). Long-term effects of defoliation on quaking aspen in relation to genotype and nutrient availability: Plant growth, phytochemistry and insect performance. *Oecologia*, *139*, 55–65.

Prieur-Richard, A. H., Lavorel, S., Linhart, Y. B., & Dos Santos, A. (2002). Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. *Oecologia*, *130*, 96–104.

Raubenheimer, D., & Simpson, S. L. (1992). Analysis of covariance: An alternative to nutritional indices. *Entomologia Experimentalis et Applicata*, *62*, 221–231.

Reeves, J. L., Lorch, P. D., & Kershner, M. W. (2009). Vision is important for plant location by the phytophagous aquatic specialist *Euhrychiopsis lecontei* Dietz (Coleoptera: Curculionidae). *Journal of Insect Behavior*, *22*, 54–64.

Reynolds, B. C., & Crossley, D. A. (1997). Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environmental Entomology*, *26*, 1232–1239.

Root, R. B. (1973). Organization of a plant arthropod association in simple and diverse habitats – Fauna of collards (*Brassica oleracea*). *Ecological Monographs*, *43*, 95–120.

Rowe, W. J., & Potter, D. A. (1996). Vertical stratification of feeding by Japanese beetles within linden tree canopies: Selective foraging or height per se? *Oecologia*, *108*, 459–466.

Ruhnke, H., Schädler, M., Matthies, D., Klotz, S., & Brandl, R. (2006). Are sawflies adapted to individual host trees? A test of the adaptive deme formation hypothesis. *Evolutionary Ecology Research*, *8*, 1039–1048.

Ruhnke, H., Schädler, M., Klotz, S., Matthies, D., & Brandl, R. (2009). Variability in leaf traits, insect herbivory and herbivore performance within and among individuals of four broad-leaved tree species. *Basic and Applied Ecology*, *10*, 726–736.

Schenk, H. J. (2006). Root competition: Beyond resource depletion. *Journal of Ecology*, *94*, 725–739.

Scherber, C., Mwangi, P. N., Temperton, V. M., Roscher, C., Schumacher, J., Schmid, B., et al. (2006). Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia*, *147*, 489–500.

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., et al. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, *468*, 553–556.

Schuldt, A., Baruffol, M., Boehnke, M., Bruelheide, H., Haerdtle, W., Lang, A. C., et al. (2010). Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology*, *98*, 917–926.

Sobek, S., Scherber, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia*, *160*, 279–288.

Tahvanainen, J. O., & Root, R. B. (1972). Influence of vegetational diversity on population ecology of a specialiyed herbivore, *Phyllotreta cruciferae* (Coleoptera-Chrysomelidae). *Oecologia*, *10*, 321–346.

Tscharntke, T., & Brandl, R. (2004). Plant–insect interactions in fragmented landscapes. *Annual Review of Entomology*, *49*, 405–430.

Tylianakis, J. M., Didham, R. K., & Wratten, S. D. (2004). Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology*, *85*, 658–666.

Unsicker, S. B., Oswald, A., Koehler, G., & Weisser, W. W. (2008). Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia*, *156*, 313–324.

van Ruijven, J., & Berendse, F. (2003). Positive effects of plant species diversity on productivity in the absence of legumes. *Ecology Letters*, *6*, 170–175.

Vehvilainen, H., Koricheva, J., Ruohomaki, K., Johansson, T., & Valkonen, S. (2006). Effects of tree stand species composition on insect herbivory of silver birch in boreal forests. *Basic and Applied Ecology*, *7*, 1–11.

Vehvilainen, H., Koricheva, J., & Ruohomaki, K. (2007). Tree species diversity influences herbivore abundance and damage: Meta-analysis of long-term forest experiments. *Oecologia*, *152*, 287–298.

Wada, N., Murakami, M., & Yoshida, K. (2000). Effects of herbivore-bearing adult trees of the oak *Quercus crispula* on the survival of their seedlings. *Ecological Research*, *15*, 219–227.

Waldbauer, G. P. (1968). The consumption and utilization of food by insects. *Advances in Insect Physiology*, *5*, 229–288.

White, J. A., & Whitham, T. G. (2000). Associational susceptibility of cottonwood to a box elder herbivore. *Ecology*, *81*, 1795–1803.

Wilby, A., & Thomas, M. B. (2002). Natural enemy diversity and pest control: Patterns of pest emergence with agricultural intensification. *Ecology Letters*, *5*, 353–360.