GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 13 (2012) 458–465
Basic and Applied Ecology
www.elsevier.com/locate/baae

Influence of surrounding vegetation on insect herbivory: A matter of spatial scale and herbivore specialisation

Brice Giffard[a,b,*], Hervé Jactel[b], Emmanuel Corcket[a], Luc Barbaro[b]

[a] *Univ. Bordeaux, UMR 1202, BIOGECO, F-33405 Talence, France*
[b] *INRA, UMR 1202, BIOGECO, F-33610 Cestas, France*

Received 7 September 2011; accepted 9 August 2012

Abstract

The diversity of surrounding vegetation is thought to modify the interactions between a focal plant and its herbivores, disrupting (associational resistance) or enhancing (associational susceptibility) host plant location and colonisation. We compared the effects of host plant concentration on herbivory by generalist and specialist insects feeding on oak seedlings by increasing local concentration of seedlings. We also assessed the effects of the composition and structure of surrounding vegetation, both at stand and local levels. The damage caused by generalist leaf-feeding insects depended on the structure of plant communities at stand level, and increased with tree cover. By contrast, infestation by specialist leaf miners was affected by local understorey vegetation surrounding oak seedlings, and decreased with increasing shrub cover and stratification diversity. Leaf mine abundance was higher at higher oak seedling density, giving support to the host concentration hypothesis. However, the abundance of these specialist herbivores was also negatively correlated with damage caused by the generalist external leaf-feeders, suggesting competitive interactions.

Zusammenfassung

Es wird angenommen, dass die Diversität der umgebenden Vegetation die Interaktionen zwischen einer Pflanze und ihren Herbivoren beeinflusst, indem Wirtsfindung und -kolonisation gestört (associational resistance) oder gefördert (associational susceptibility) werden. Wir verglichen die Effekte der Wirtspflanzenkonzentration auf generalistische und spezialisierte Insekten, die an jungen Eichenpflanzen fraßen, indem wir die lokale Konzentration der Pflanzen erhöhten. Wir bestimmten außerdem die Effekte von Zusammensetzung und Struktur der umgebenden Vegetation für die Bestandsebene und im lokalen Maßstab. Der von generalistischen Blattfressern verursachte Fraßschaden hing von der Struktur der Pflanzengemeinschaft auf Bestandsebene ab und nahm mit dem Deckungsgrad der Bäume zu. Im Gegensatz dazu wurde der Befall durch die spezialisierten Blattminierer durch den Unterwuchs, der die Eichenpflanzen lokal umgab, beeinflusst. Der Befall nahm mit zunehmendem Deckungsgrad der Sträucher und zunehmender Diversität der Vegetationsschichten ab. Die Abundanz der Minen war höher bei höherer Dichte der Eichenpflanzen, was die Wirtskonzentrationshypothese unterstützt. Allerdings war die Abundanz dieser spezialisierten Herbivoren auch negativ mit den von generalistischen externen Blattfressern verursachten Fraßschäden korreliert, was auf Konkurrenz-Beziehungen hindeutet.

Keywords: Specialist; Generalist; Insect herbivory; Plant neighbours; Host plant concentration; Biodiversity

*Corresponding author at: Univ. Bordeaux, UMR 1202, BIOGECO, F-33405 Talence, France Tel.: +33 5 57122739; fax: +33 5 57122881.
E-mail address: brice.giffard@gmail.com (B. Giffard).

1439-1791/$ – see front matter
http://dx.doi.org/10.1016/j.baae.2012.08.004

Introduction

Interactions between plants and herbivores have long been viewed as binary relationships between resistance traits and herbivore communities, but the importance of the surrounding vegetation is increasingly recognised (Barbosa et al. 2009). The diversity of the surrounding vegetation has been reported to reduce herbivore damage to a focal plant, by providing associational resistance (Root 1973) in many ecosystems, such as crops (Tonhasca & Byrne 1994), forests (Jactel & Brockerhoff 2007; Vehviläinen, Koricheva, & Ruohomäki 2007) and grasslands (Unsicker et al. 2006). However, some studies have failed to confirm this relationship (Scherber et al. 2006; Vehviläinen, Koricheva, Ruohomäki, Johansson, & Valkonen 2006), or even reported the opposite response: associational susceptibility with higher herbivory in more diverse plant communities (Schuldt et al. 2010; Vehviläinen et al. 2007).

Resource concentration may account for a significant proportion of the decrease in damage due to specialist herbivores within diverse plant communities (Root 1973). The relative abundance and nature of the neighbouring plants determine the probability of a plant being colonised by herbivores (Barbosa et al. 2009). In more diverse plant communities, host plants are proportionally less frequent and non-host neighbouring plants can provide chemical or physical barriers to host plant location (Hambäck & Beckerman 2003; Jactel, Birgersson, Andersson, & Schlyter 2011; Randlkofer, Obermaier, Hilker, & Meiners 2010). For example, unpalatable or spiny shrubs may provide a physical barrier protecting tree seedling against mammalian grazers (Baraza, Zamora, & Hódar 2006).

These plant–herbivore interactions may also vary with the spatial scale at which they occur (Banks 1998; Gunton & Kunin 2007). The effect of plant neighbours on herbivory depends on the distance between a focal plant and its neighbours (Barbosa et al. 2009). Many studies have reported a significant influence of plant diversity on herbivores in small plots, whereas experiments over large spatial scales have tended to show no such benefits of plant diversity (Bommarco & Banks 2003).

Finally, the magnitude and direction of the relationship between plant diversity and insect herbivory seems to vary with the mobility of herbivores and their diet breadth (Banks 1998). Associational susceptibility would be expected to be most prevalent with polyphagous herbivores, because they are able to feed on multiple host plant species (Unsicker, Oswald, Koehler, & Weisser 2008), whereas specialist herbivores are limited by the numbers of suitable hosts (Bertheau, Brockerhoff, Roux-Morabito, Lieutier, & Jactel 2010). Plant neighbours may disrupt host finding by specialist insects, whereas generalist insects may simply shift from one host plant to another.

The objective of this study was therefore to investigate the effect of host concentration on insect herbivory on pedunculate oak *Quercus robur* seedlings, by manipulating the local concentration of focal host plants. We also investigated the influence of the composition (species diversity) and structure (cover and stratification) of the surrounding vegetation of oak seedlings at local and stand levels. We hypothesised that specialist and generalist herbivores associated with oak seedlings would not be influenced in the same direction and magnitude by surrounding vegetation. We compared the effect of neighbouring plants on specialist leaf miners and on generalist external feeders.

Methods

Study system

This study was conducted in the Landes de Gascogne forest, in south-western France, a region covered by one million hectares of native maritime pine plantations (*Pinus pinaster*). Pedunculate oak (*Q. robur*) regenerates naturally within pine stands and becomes co-dominant in older plantations. Other broadleaf species present are: chestnut (*Castanea sativa*), European holly (*Ilex aquifolium*), red and Holm oaks (*Q. rubra* and *Q. ilex*), and silver birch (*Betula pendula*). The predominant understorey species are common bracken (*Pteridium aquilinum*), moor grass (*Molinia caerulea*), dwarf and common gorse (*Ulex europaeus*, *U. minor*), heather species (*Erica scoparia*, *E. cinerea*, *Calluna vulgaris*), glossy buckthorn (*Frangula alnus*), blackberry (*Rubus* spp.) and European honeysuckle (*Lonicera periclymenum*).

Experimental design

We investigated the effects of host plant concentration and surrounding vegetation on insect herbivory in eight mixed stands of *Q. robur* and *P. pinaster* (40–45 years of age). We established two experimental plots within each stand (Fig. 1). In the low-host concentration treatment ("low HC plot"), three oak seedlings were planted about 60 cm apart in a 2.25 m^2 (1.5 m × 1.5 m) plot. In the high-host concentration treatment ("high HC plot"), we planted six additional seedlings around the three target seedlings, reducing the distance between seedlings to about 30 cm in a 2.25 m^2 plot (Fig. 1). In total, 96 one-year-old *Q. robur* seedlings were randomly transplanted in February 2009: 48 target seedlings (3 replicate seedlings × 2 plots × 8 stands) and 48 additional seedlings (6 replicates × 1 high HC plot × 8 stands). The oak seedlings had been grown in nursery for one year and were about 45 ± 2 cm high (mean ± SE) and had 47 ± 3 leaves.

Insect herbivory on focal species

Most of the insect damage occurring on *Q. robur* leaves is caused by generalist external leaf-feeders (chewer and skeletoniser guilds), principally lepidopteran larvae and grasshoppers, which are able to feed on several plant species.