GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 10 (2009) 726–736
Basic and Applied Ecology
www.elsevier.de/baae

Variability in leaf traits, insect herbivory and herbivore performance within and among individuals of four broad-leaved tree species

Haike Ruhnke[a], Martin Schädler[b,*], Stefan Klotz[a], Diethart Matthies[c], Roland Brandl[b]

[a]*Department of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle, Germany*
[b]*Unit of Plant Ecology, Department of Biology, Philipps-University Marburg, Marburg, Germany*
[c]*Unit of Animal Ecology, Department of Biology, Philipps-University Marburg, Marburg, Germany*

Received 30 December 2008; accepted 19 June 2009

Abstract

Individual plants may vary in their suitability as hosts for insect herbivores. The adaptive deme formation hypothesis predicts that this variability will lead to the fine-scale adaptation of herbivorous insects to host individuals. We studied individual and temporal variation in the quality of leaves of the tree species ash, lime, common oak, and sycamore in the field as food for herbivores. We determined herbivore attack and leaf consumption and performance of the generalist caterpillars of *Spodoptera littoralis* in the laboratory. We further assessed the concentrations of carbon, nitrogen and water in the leaves.

All measures of leaf tissue quality varied among and within individuals for all tree species. The level of herbivory differed among the tree individuals in lime, oak and sycamore, but not in ash. Within host individuals, differences in herbivory between the upper and lower crown layer varied in direction and magnitude depending on tree species. In feeding experiments, herbivore performance also varied among and within tree individuals. However, variation in palatability was not consistently related to the leaf traits measured or to herbivory levels in the field. The ranking of individuals with respect to the quality of leaf tissue for herbivorous insects varied between years in lime and oak. Thus, trees of both species might present moving targets for herbivores which prevents fine-scale adaptations. In contrast, among individuals of ash and sycamore the pattern of insect performance remained constant over 2 years. These species may be more suitable hosts for the formation of adapted demes in herbivores.

Zusammenfassung

Die Eignung als Wirtspflanze für herbivore Insekten kann zwischen einzelnen Individuen einer Pflanzenart variieren. Die "*adaptive deme formation hypothesis*" sagt eine kleinräumige Anpassung herbivorer Insekten an diese Variabilität der Wirtsindividuen vorher. Wir untersuchten die individuelle und zeitliche Variabilität der Blattqualität von Gemeiner Esche, Winter-Linde, Stiel-Eiche und Berg-Ahorn im Feld als Nahrung für Herbivore. Wir bestimmten die Fraßintensität im Feld und die Reaktion der generalistischen Raupen von *Spodoptera littoralis* im Labor. Weiterhin bestimmten wir den Gehalt an Kohlenstoff, Stickstoff und Wasser in den Blättern.

*Corresponding author. Tel.: +49 6421 2823382; fax: +49 6421 2823387.
E-mail address: schaedler@staff.uni-marburg.de (M. Schädler).

1439-1791/$ - see front matter © 2009 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.
doi:10.1016/j.baae.2009.06.006

Alle gemessenen Blattqualitätsmerkmale variierten zwischen und inerhalb der untersuchten Individuen für alle Baumarten. Das Ausmaß des Herbivorenfraßes variierte zwischen den Individuen von Linde, Eiche und Ahorn, jedoch nicht von Esche. Innerhalb der Baumindividuen gab es Unterschiede in der Herbivorie an Blättern aus der unteren und der oberen Schicht der Baumkrone, welche jedoch bezüglich ihrer Stärke und Richtung zwischen den Baumarten variierten. Die Reaktion der Herbivoren in den Fraßexperimenten variierte ebenfalls zwischen und innerhalb der Baumindividuen. Diese Variabilität war jedoch nicht durchgängig mit im Feld erhobenen Blatt- oder Herbivoriemerkmalen erklärbar. Die Rangfolge der Individuen einer Baumart bezüglich ihrer Blatt- oder Herbivoriemerkmale war nicht gleich in den zwei Untersuchungsjahren für Linde und Eiche. Baumindividuen dieser Arten repräsentieren daher eher „*moving targets*"für Herbivore, welche eine kleinräumige Anpassung verhindern. Dagegen war das Muster der Reaktion der Herbivoren auf Blätter der jeweiligen Individuen von Esche und Ahorn in beiden Jahren konstant. Diese beiden Arten können daher als geeignete Wirte für die Herausbildung von adaptierten *demes* herbivorer Arten angesehen werden.

Keywords: Adaptive deme formation; Broad-leaved trees; Canopy; Insect herbivory; Intraspecific variability; Palatability; Resource heterogeneity

Introduction

Leaf traits such as thickness, water content, C/N-ratio and the content of secondary compounds differ among individuals but also within individuals of a given tree species (among individuals: e.g. Laitinen, Julkunen-Tiitto, & Rousi 2000 ; Osier, Hwang, & Lindroth 2000b, within: e.g. Dudt & Shure 1994; Henriksson et al. 2003). These differences affect the feeding behaviour and development of insect herbivores (e.g. Ayres, Suomela, & MacLean 1987; Fortin & Mauffette 2002; Osier & Lindroth 2001). Ultimately, such differences in leaf quality among plant individuals may lead to the evolution of genetically distinct groups (demes) within herbivorous insect species that are adapted to individual plants (adaptive deme formation hypothesis, Edmunds & Alstad 1978). Because of their longevity, trees are the most likely host candidates for the formation of adaptive demes. However, most experimental tests have not supported the adaptive deme hypothesis (see Ruhnke, Schädler, Matthies, Klotz, & Brandl 2006) and the hypothesis is still controversial (e.g. Cobb & Whitham 1998; Van Zandt & Mopper 1998).

Important preconditions for the evolution of adaptive demes are that differences in leaf quality exist among host individuals (host heterogeneity) and that at least the relative differences in the suitability of individual host plants (the ranking of individuals) remains the same for several generations of insects. Resource heterogeneity has been studied in several tree species (e.g. Fortin & Mauffette 2002; Marquis 1988; Reynolds & Crossley 1997; Roslin et al. 2006; Rowe & Potter, 1996; Suomela & Nilson 1994). Most of these studies relied on chemical analyses, but some also studied palatability as an integrative and functionally relevant measure of resource heterogeneity. Few studies, however, have related levels of herbivore attack in the field to the palatability estimated in laboratory trials (Rowe & Potter 1996).

We investigated the intraspecific variability in insect herbivory and in the quality of leaf tissue for herbivorous insects in four broad-leaved tree species (*Fraxinus excelsior*, *Tilia cordata*, *Quercus robur*, and *Acer pseudoplatanus*) both among and within tree individuals in two consecutive years. For this, we assessed and compared measures of leaf quality, herbivore attack in the field and palatability in the laboratory. These data allowed us to answer the following questions: (1) do leaf traits differ among individual trees and between layers within a tree? (2) Are herbivory levels in the field as well as consumption and growth of a polyphagous insect herbivore in the laboratory related to leaf traits? Specifically, we would expect positive correlations to nitrogen and water content and negative correlations to carbon content. (3) Are differences in leaf traits and palatability consistent across years?

Methods

The study area and tree species

The study was performed in Central Germany in the "Leipzig flood-plain forest" (city of Leipzig, Saxony, Germany) which covers an area of ca. 1900 ha. In spring 2001, a construction crane was set up in this forest, which made it possible to work in the canopy of an area of 1.6 ha. In the crane plot, the vegetation is classified as a typical flood-plain forest (Querco-Ulmetum) on nutrient-rich loamy flood-plain soils (Morawetz & Horchler 2004). It is rich in species and dominated by ash, sycamore, oak, lime, maple and hornbeam. In this study, four of the dominant tree species were used: Ash