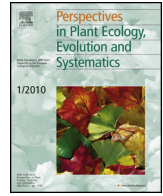




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Research article

Plasticity of functional traits of forb species in response to biodiversity



Annett Lipowsky^{a,b}, Christiane Roscher^{c,*}, Jens Schumacher^d, Stefan G. Michalski^c,
Marlén Gubsch^e, Nina Buchmann^e, Ernst-Detlef Schulze^b, Bernhard Schmid^a

^a Institute of Evolutionary Biology and Environmental Studies and Zurich-Basel Plant Science Center, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

^b Max Planck Institute for Biogeochemistry, POB 100164, 07701 Jena, Germany

^c UFZ, Helmholtz Centre for Environmental Research, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06120 Halle, Germany

^d Institute of Stochastics, Friedrich Schiller University Jena, Ernst-Abbe-Platz 2, 07743 Jena, Germany

^e Institute of Agricultural Sciences, ETH Zurich, Universitätsstrasse 2, 8092 Zurich, Switzerland

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ABSTRACT

In spite of increasing recognition that intraspecific variation may play an important role for niche differentiation, which is regarded as a promoter of species coexistence, the extent and structure of functional trait variation in response to plant neighbor diversity is poorly understood. We studied the plasticity of functional traits in vegetative and reproductive shoots of 27 non-legume forb species with different growth forms (reptant, rosulate, semirosulate) in experimental grasslands (Jena Experiment) of varying species richness and functional group composition (with and without legumes). Traits related to whole-shoot structure differed strongly among forb species with different growth forms, while leaf traits associated with light acquisition (specific leaf area, foliar $\delta^{13}\text{C}$ values) and traits associated with nitrogen nutrition (shoot biomass:N ratios, leaf nitrogen concentrations, foliar $\delta^{15}\text{N}$ values) were highly plastic within forb species. Plant height generally increased with increasing species richness. Plasticities to increased species richness in leaf traits (leaf length, SLA, foliar $\delta^{13}\text{C}$) varied among growth forms and depended on developmental stage. The presence of legumes generally increased plastic responses in light-acquisition traits in the same direction as increasing species richness. Greater tissue nitrogen concentrations and unchanged foliar $\delta^{15}\text{N}$ values of forb species in the presence of legumes suggested that the fertilizing effect of nitrogen-fixing legumes was due to the supply of unconsumed mineral nitrogen. Stronger correlations between trait means and trait plasticities in size-related traits suggested a functional convergence in response to light competition. A more variable spectrum in the plasticities of traits not associated with plant size indicated a greater functional separation among species. Our results suggest that both interspecific differences and intraspecific trait plasticity affect niche partitioning among forb species and are important for their coexistence in multi-species assemblages.

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Introduction

Niche differentiation, which is considered as a key to species coexistence and the maintenance of biodiversity, requires functional differences among species (Levine and Hille Ris Lambers, 2009). An increasing number of studies in natural and experimental ecosystems have emphasized the usefulness of functional trait-based approaches in the search of reliable predictors for ecosystem functioning (e.g., Díaz et al., 2007; Milcu et al., 2014; Mokany et al., 2008; Roscher et al., 2013). In this context, functional traits

are morphological, physiological or phenological characteristics measurable at the individual level (Violle et al., 2007). In many previous studies, it is assumed that intraspecific trait variation is of marginal importance relative to interspecific trait differences (McGill et al., 2006). However, several recent studies have documented that intraspecific trait variation represents a substantial proportion of the overall trait variability of plant communities (e.g., Albert et al., 2010; Hulshof and Swenson, 2010; Messier et al., 2010) and may be important for species coexistence and plant community assembly (e.g., Jung et al., 2010; Le Bagousse-Pinguet et al., 2014).

The set of trait values characterizing a species results from trade-offs among different functional requirements. They involve genetic or physiological constraints on certain trait combinations

* Corresponding author. Tel.: +49 345 5585223; fax: +49 345 5585329.
E-mail address: christiane.roscher@ufz.de (C. Roscher).

(“fundamental trade-offs”), which could result in species-specific abilities to interact with other species or to respond to environmental variation (“secondary trade-offs”, Suding et al., 2003). However, trait variation extends beyond such between-species differences due to within-species genetic variation or phenotypic plasticity. Environment-induced phenotypic plasticity is particularly important for plant species with a sessile life-form to respond to a wide variety of ecological conditions (Valladares et al., 2007).

The environment plant individuals experience in communities of increasing plant diversity varies in multiple ways due to a greater diversity in neighbor identities and increased plant density (Marquard et al., 2009), a more complete use of resources such as nutrients (Oelmann et al., 2007; Palmberg et al., 2005), light and space (Lorentzen et al., 2008; Spehn et al., 2000), and varied biotic interactions with higher trophic levels such as herbivores and pathogens (Knops et al., 1999). In addition to pure species-richness effects, interactions between legumes and non-legumes have been identified as a key mechanism of functional complementarity, whereby legumes may improve nitrogen-availability for non-legume species through symbiotic fixation of atmospheric N₂ (Temperton et al., 2007). Plasticity in functional traits related to light and nutrient acquisition provide one possibility how plant individuals may cope with diversity-induced environmental changes. Typical morphological adjustments in response to reduced light in the canopy shade of taller neighbors are the formation of larger and thinner leaves (shade tolerance) or an increase in stem length (shade avoidance) (Valladares and Niinemets, 2008). Stable carbon isotope ratios ($\delta^{13}\text{C}$) in plant tissue give valuable information about photosynthetic activity or stomatal conductance, which depend on light availability, air humidity and plant nutrition (Dawson et al., 2002; Farquhar et al., 1989). Stable nitrogen isotope ratios ($\delta^{15}\text{N}$) in non-legume plant species can provide information about the provision of depleted legume-derived N in communities with legumes or a shift in the uptake of different N forms (Craine et al., 2009; Högborg, 1997).

In temperate grasslands, forb species constitute a large proportion of species diversity and represent a variety of growth forms. Species of a given growth form often share similar functional traits and respond similarly to environmental variation (Chapin, 1993; Klimešová et al., 2008; Liira et al., 2002). Perennial species in temperate grasslands usually represent a mixture of individuals in various developmental stages. Plant functioning also depends on morpho-physiological changes through various stages of plant development, which may involve gradual changes in growth form (Gatsuk et al., 1980) and modified plastic responses to environmental changes (Niinemets, 2004). However, differences in functional trait means or plasticities among co-existing species might also be limited by evolutionary constraints within phylogenetic groups (Crisp and Cook, 2012; Felsenstein, 1985). Even though some plant traits may evolve rapidly, others do not (Thompson, 2009) and rapid multivariate evolutionary change in plant functional traits may be impossible.

In the current study, we investigated traits of aboveground plant organs related to light-acquisition and nitrogen-nutrition, and measured plant performance in terms of biomass and reproductive structures of non-legume forb species in experimental grassland of varying species richness and in the presence or absence of legume species. The study was conducted in a long-term biodiversity experiment (Jena Experiment; Roscher et al., 2004). We sampled traits of 27 non-legume forb species including two developmental stages (vegetative, reproductive). The studied forb species differed in growth forms and represented a broad range of phylogenetic relatedness levels. Specifically, we asked the following questions (Fig. 1): (1) Do forb species with different growth forms differ in mean values of functional traits? (2) Are there common effects of

plant diversity (species richness, legume presence/absence) on the plasticity of functional traits in forb species with different growth forms and representing different developmental stages? (3) Are trait values and trait plasticities in response to increased plant diversity related across different forb species suggesting common functional trade-offs? (4) Are trait means and plasticities more closely correlated between phylogenetically related than phylogenetically unrelated species?

Material and methods

Design of the Jena Experiment

The study was carried out in a large grassland biodiversity experiment, the Jena Experiment, established in spring 2002 (Roscher et al., 2004). The experimental site is a former arable field located in the floodplain of the river Saale near Jena (Germany; 50°55'N, 11°35'E, 130 m a.s.l.). The area around Jena is characterized by mean annual air temperatures of 9.3 °C and a mean annual precipitation of 587 mm (Kluge and Müller-Westermeier, 2000). The soil of the field site is developed from up to 2 m thick fluvial sediments and varies in texture from sandy loam near the riverside to silty clay with increasing distance from the river. Because of this gradient in soil characteristics, the experimental area was divided into four blocks parallel to the river.

Eighty-two experimental plant communities of varying species richness and composition were assembled from a pool of 60 species typically found in Central European semi-natural, species-rich grasslands (Molinio-Arrhenatheretea; Ellenberg, 1988). Based on a cluster analysis of a literature-based matrix of morphological, physiological and phenological traits, the 60 plant species were classified into four functional groups: 16 grasses, 12 small forbs, 20 tall forbs, and 12 legumes (Roscher et al., 2004). The five species-richness levels of 1, 2, 4, 8 or 16 species were near-orthogonally crossed with four levels of functional group richness (1 to 4). Each species-richness level had 16 replicates (except for the 16-species mixtures with 14 replicates because pure legume and small-forb communities were not possible). In addition, four plots were established with all 60 species. Mixture compositions were determined by random draws from the species pool, and communities of the same richness level were allowed to partly overlap with regard to the species they contained. Each community was sown on a plot of 20 × 20 m. Monocultures of all experimental species were established on smaller plots of 3.5 × 3.5 m. Plots were weeded twice per year (early April and July) to maintain the sown species compositions. Each year, plots were mown in early June and September to mimic the usual management of extensive hay meadows. The plots did not receive any fertilizer.

Data collection

In this study, traits of the 27 well-established non-legume forb species (12 small forbs and 15 tall forbs) of the experimental pool of 60 species (Supplementary material, Table A.1) were analyzed. Measurements took place during two harvests at estimated peak biomass before mowing (late May and August 2006) in monoculture and mixture plots four years after establishment of the biodiversity experiment. For the 60-species mixtures, two plots were sampled. Individual shoots served as basic unit for all measurements because in many herbaceous species a reliable distinction of genetic plant individuals (genets in the sense of Harper, 1977) is not possible. Five shoots per species and plot were studied when only vegetative plants occurred. Three vegetative and three reproductive shoots were sampled in cases when shoots of

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