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Intraspecific trait variation and allocation strategies of calcareous grassland species: Results from a restoration experiment

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Abstract

Intra- and interspecific trait variation express the response of plants dealing with different environmental conditions. We measured root and leaf traits on 14 species of calcareous grasslands in a restoration experiment. We aimed at identifying intraspecific differences in biomass allocation and functional plant traits under contrasting soil conditions by comparing plants growing in ancient grassland and two restored grasslands on ex-arable land, one of them with topsoil removal. Relative importance of trait variation within and among species, and among site was assessed by variance partitioning. Interspecific variation was more important than intraspecific variation, but the contribution of the latter to total variation was considerable, especially for specific leaf area. Changes in soil properties due to topsoil removal resulted in lower values of plant height, specific leaf area and specific root length compared to the control (ancient grassland). Soil fertility found in the treatment without top soil removal did not affect plant plasticity compared to the control. The study species showed two allocation strategies in relation to resource stress, while the responses of individual traits to the soil treatments were consistent across species. We conclude that caution must be taken when using mean trait values for plastic species or when working with environmental gradients.

Zusammenfassung

Intra- und interspezifische Variation von Pflanzeneigenschaften (‚plant traits') ist Ausdruck der Reaktion von Pflanzenarten auf unterschiedliche Standortverhältnisse. Kontrastierende Standortbedingungen eines Renaturierungsexperimentes bildeten einen geeigneten Rahmen für eine Untersuchung der Wurzel- und Blatteigenschaften von 14 Kalkmagerrasenarten. Die Studie fokussierte auf Unterschiede in der Biomasse-Allokation und ausgewählten Pflanzenmerkmalen zwischen Individuen, die auf einem erhaltenen (historischen) Kalkmagerrasen wuchsen, und solchen auf zwei renaturierten Flächen (mit oder ohne Oberbodenabtrag) mit Acker als Vornutzung. Untersucht wurde die relative Variation der Pflanzeneigenschaften zwischen Individuen, Arten und Untersuchungsflächen. Die interspezifische Variation war stärker als die intraspezische, besonders bei der spezifischen

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Blattfläche. Oberbodenabtrag führte zu geringerer Pflanzenhöhe, und niedrigeren Werten für spezifische Blattfläche und spezifische Wurzellänge verglichen mit dem historischen Magerrasen. Die höheren Nährstoffgehalte der Ackerflächen ohne Bodenabtrag beeinflussten die Plastizität der Pflanzenarten nicht. Die Magerrasenarten zeigten zwei unterschiedliche Allokationsstrategien als Reaktion auf ungünstige Bodenverhältnisse, während die Veränderungen der einzelnen Pflanzeneigenschaften bei allen Arten ähnlich ausfielen. Die Ergebnisse legen nahe, dass die Verwendung von gemittelten Werten von Pflanzeneigenschaften bei plastischen Arten entlang von Umweltgradienten problematisch ist.

Keywords: Biomass; Leaf traits; Multi-species experiment; Plasticity; Root traits; Topsoil removal

Introduction

Trait variability is an important element of plant strategies because it allows plants to grow and to reproduce under environmental conditions with different degrees of stress, disturbance and strength of biotic interactions (Weiner 2004; Craine 2009; Fort, Cruz, & Jouany, 2014). If the expression of a plant trait is an indicator of the ecological niche filled by a species (Mason, de Bello, Doležal, & Lepš, 2011), examining the ecological niche breadth and the resulting consequences for population and community dynamics (Bolnick et al. 2011) requires a quantification of the plasticity of species' traits across varying environmental conditions (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Albert, Grassein, Schurr, Vieilledent, & Violle, 2011).

Recent studies on the functional structure of plant communities suggest that competitive hierarchies exist, in which there is an optimal range of trait values that allow species to successfully compete for limiting resources (Kunstler et al. 2012; Fort et al. 2014; Herben & Goldberg 2014), but this trait optimum may shift along environmental gradients. If a species is sufficiently plastic to adjust the expression of traits relevant for resource acquisition and turnover towards the required optimum, it will be more likely to persist in a broad range of environments.

In ecological restoration, species are often transferred to sites that show marked differences in soil conditions compared to the source habitat. For example, in restoring calcareous grasslands in Central Europe, a well-established method is transferring hay to ex-arable land, sometimes preceded by topsoil removal (Kiehl & Pfadenhauer 2007). The objective of the latter is to reduce nutrient loads and seed banks from previous land use to establish species-rich calcareous grasslands (Kiehl, Thormann, & Pfadenhauer, 2006). This restoration practice results in three types of sites with strongly contrasting soil moisture and nutrient contents, i.e. nutrient-poor ancient grasslands, and restored grasslands either with or without nutrient-rich soil. Plant species occurring in these sites should show some trait plasticity relevant to the respective resource supply.

In this study, we make use of the contrasting site conditions of a nutrient-poor ancient grassland and two restoration sites on ex-arable land, one of which restored by topsoil removal. The aim was to study the effects of different levels of water and nutrient supply on intraspecific trait variability and allocation strategies. For this purpose, we investigated a set of above- and below-ground traits related to resource acquisition, growth rate and competitive vigour in 14 species. We hypothesised that (i) intraspecific trait variability is higher among than within sites; (ii) intraspecific trait variability is species- and trait-dependent, i.e. species respond differently to the environmental constraints; (iii) traits related to resource acquisition and growth rate have lower values in the harsher environment; and (iv) investment in below-ground structures is higher under harsher conditions.

Multi-species experiments are a powerful approach to identify general ecological patterns (van Kleunen, Dawson, Bossdorf, & Fischer, 2014). Our study is one of the first multi-species experiments to analyze the extent of functional trait variability of plant traits under varying levels of abiotic stress, especially in a restoration context. Importantly, we also provide information on the variability of root traits, which play a significant role for acquisition, storage and cycling of resources (Freschet, Cornelissen, van Logtestijn, & Aerts, 2010), especially at sites with rare disturbance, and low availability of water and nutrients.

Materials and methods

Study location

The study was conducted in the 'Garchinger Heide' nature reserve (48°18′N, 11°39′E, 469 m a.s.l., 27 ha), one of the few remnants of species-rich calcareous grasslands on calcaric leptosol (IUSS 2006) in the Munich Gravel Plain, Germany. The shallow soils are nutrient-poor and relatively dry, despite mean annual precipitation around 880 mm and mean annual temperature 8.1 °C (Kiehl & Pfadenhauer 2007). Areas surrounding the remnant grassland were converted into arable land in the early 20th century (Pfadenhauer 2001). These areas were restored in 1993, aiming to re-establish the characteristic community of reference grasslands. Three adjacent sites were chosen for our study (Fig. 1): two restoration sites on ex-arable land, i.e. one with (TR) and another without topsoil removal (NR), and a control site (AG, ancient grassland; Table 1). On TR, 30–40 cm topsoil was removed in 1993 down to the calcareous gravel. The remaining soil