Spatial mechanisms promoting plant coexistence: the role of dispersal and competition

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To my little one, who I wish to inspire with the curiosity for the wonders of life.

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Summary

One of the great challenges in ecology is to explain how large numbers of plant species are able to coexist in natural communities. Understanding the mechanisms that promote and maintain coexistence is crucial if we are to counteract biodiversity loss. The role of spatial structure – i.e. how species are distributed over space – for maintaining plant coexistence has so far mainly been explored by theory. Spatial structure involves two main processes: dispersal and competition. Seed dispersal is the main force generating spatial structure. Since most plant species are dispersal limited, they show intraspecific aggregation. Competitive interactions between plants occur over relatively small spatial scales. Thus, for a single plant individual, only those plants growing nearby are relevant. Spatially limited dispersal together with local interactions can therefore result in individual neighbourhoods much different from mean population densities.

Theory suggests that seed dispersal may contribute substantially to population dynamics and plant coexistence. However, in natural communities, additional processes affect the survival and fitness of established individuals, and the consequences of seed dispersal for local community dynamics are still under-explored. Individual-based models examine population dynamics by modelling survival and growth for each individual separately. As a consequence, assumptions have to be made about the distances over which neighbourhood interactions occur and how these attenuate with distance. Theory has shown that a competitively weaker species can invade a population of a superior species if the average distance at which conspecifics compete is longer than the average distance at which heterospecifics compete (heteromyopia). However, empirical knowledge on the spatial scales of competition lags behind, and heteromyopia has not been reported so far. Arbuscular mycorrhizal fungi (AMF) are symbiotic fungi that colonise the roots of most plant species and enhance their hosts' nutrient supply. Increasing evidence for host-specificity and the fact that AMF can connect the roots of many plant species suggest that they might be involved in the spatial scales of competiton.

The major goal of my thesis was to help close the current gap between theory and data in spatial ecology. I experimentally tested basic model assumptions and theoretical predictions on how dispersal and competition may contribute to maintain plant species coexistence. In a field experiment, I examined the consequences of seed dispersal distance for spatial pattern and local population dynamics of the perennial forb *Prunella grandiflora*. I found that only individuals in the vegetative but not in the reproductive stage responded to dispersal manipulation. Increasing dispersal distance lead to more vegetative individuals, and decreasing dispersal distance resulted in a more aggregated spatial distribution. In two target–

neighbour competition experiments I tested for heteromyopia in co-occurring forbs from calcareous grasslands. I explored the spatial scales of intra- and interspecific competitive interactions, how these attenuate with distance and the role of AMF therein. Although the distances over which intra- and interspecific competition could be detected varied substantially, I found no evidence for hetereomyopia. AMF neither influenced the distances over which competition occurred nor how the strength of competition declined over distance. However, AMF reduced the effects of relative size differences between neighbouring plants. The intensity of competitive interactions was primarily determined by relative size differences between target and neighbour plants, irrespective of their con- or heterospecific status. However, a conspecific neighbour may be more important than a heterospecific neighbour but only as the neighbour becomes very large compared to the target individual (size–identity interaction). Finally, I also tested for within-population host-specificity of genetically different isolates of *Glomus intraradices*. The different AMF isolates altered plant biomass and differed in their efficiency to colonise plant roots. Interestingly, plant species differed substantially in their susceptibility to different functional differences between these isolates, and this seemed to be positively linked to the percentage root colonisation.

The results of my thesis emphasise the importance of both dispersal and competition as spatial mechanisms promoting plant coexistence and point towards novel aspects of AMF in spatial plant ecology. I could confirm theory in that dispersal affects local population dynamics of natural plant communities – at least in the short run. However, it still remains to be demonstrated into what direction long-term population dynamics under manipulated seed dispersal would go and whether short time advantages would persist. From my target–neighbour experiments, I conclude that resource competition and AMF can be ruled out as potential mechanisms for heteromyopia. Other mechanisms (e.g. host-specific enemies or allelopathy) still remain to be explored, and diverse tropical forests are therefore perhaps the most likely candidate systems for heteromyopia. My results suggest that species-specific relative size differences between neighbouring plants are likely to be key factor determining the intensity of competitive interactions and must be incorporated into theory. The indicated size–identity interaction is well worth further investigation: it might make seedling establishment near a heterospecific of a given size more likely than near a conspecific and could further influence the performance of individuals at later stages. This may promote coexistence and help maintain community diversity. AMF might further aid seedling establishment and the coexistence of differently sized species by reducing the effects of size differences between neighbouring plants. Genetically-based heterogeneity in the

benefits provided by AMF may further interact with small-scale environmental heterogeneity in the field, which could have profound consequences for plant population and community dynamics.

Chapter 1: General introduction

One of the great challenges in ecology is to explain how large numbers of plant species are able to coexist in natural communities. Nearly half a century ago, Hutchinson (1961) formulated the "paradox of the plankton", stating that many plankton species coexist in relatively homogenous aquatic habitats, all competing for the same resources. However, according to the "principle of competitive exclusion" (Hardin, 1960), species competing for the same resource cannot coexist: the one species being best at exploiting this resource, i.e. the one which can persist at the lowest level of resource availability, will eventually outcompete all the other. More generally, the so-called **biodiversity paradox** (Clark *et al.*, 2007) arises because all photosynthetic plants compete for the same limited resources – light, water and nutrients. Hundreds of tree species can be found on a single hectare of rain forest (e.g. Stoll & Newbery, 2005) and one square meter of certain temperate grasslands can harbour up to 40 herbaceous plant species (Silvertown & Law, 1987). But how is it possible that we find so many plant species coexisting if resources are limited and competition for them is fierce?

Understanding the mechanisms that promote and maintain coexistence is not only interesting for basic ecology but also crucial if we are to counteract biodiversity loss. We need to understand how communities are structured and held together in order to prevent massive species extinctions and consequential changes in ecosystem composition and functioning.

Numerous mechanisms have been proposed to promote plant species coexistence (Barot, 2004). Classical mechanisms that lead to stable coexistence require that species differ in their **niches**, i.e. are ecologically different. Such niches can be based on differences in morphology (Cody, 1991), physiology (McKane *et al.*, 2002) or demography (Levine & HilleRisLambers, 2009). For example, Silvertown *et al.* (1999) could show that diverse communities in flood-plain meadows are structured by interspecific competition along soil moisture gradients. Life–history trade-offs may further result in "strategical" niches. The well-known competition–colonisation trade-off arises because a plant has a limited amount of resources available for reproduction. According to the competition–colonisation trade-off, a plant species is either a good coloniser (many small seeds) or a good competitor (few large seeds) (c.f. e.g. Turnbull *et al.*, 1999). In synthesis, niche differences stabilise competitor dynamics by giving species higher per capita population growth rates when rare than when common, and stable coexistence occurs when these stabilising effects overcome species differences in overall competitive ability (Levine & HilleRisLambers, 2009). The biggest difficulty with testing for niche differentiation lies in identifying the correct traits to measure (Silvertown *et al.*, 2001). Further, explaining species coexistence in the absence of conspicuous life-history trade-offs and in relatively homogenous environments remains a very difficult task (Clark *et al.*, 2003; Hubbell, 2005; Nee & Colegrave, 2006).

The view that niche differences are key to coexistence has recently been challenged by the **neutral theory of biodiversity** (Hubbell, 2001). Neutral theory assumes that competitors are ecologically equivalent: all species exhibit the same per capita demographic dynamics, and diversity is determined by the rates of random extinction and speciation events. According to this, coexistence is just an appearance due to ecologists looking at a slow exclusion process within a too short time window relative to process speed (Barot, 2004). Since all species are considered ecologically equivalent, in a truly neutral community one could eliminate all but one species without affecting the biogeochemical functioning of the community at all (Purves & Pacala, 2005). This concept is intriguing because it can explain some aggregate properties of ecological communities, e.g. the distribution of population sizes (Fisher *et al.*, 1943; Sugihara, 1980; Hubbell, 2001), without the need to determine any species differences. However, as Purves and Pacala (2005) have demonstrated, the fit between neutral models and observed patterns does not imply that real communities are neutral. A review on empirical tests of neutral theory has revealed an overwhelming weight of evidence against it (McGill *et al.*, 2006). A recent study by Levine and HilleRisLambers (2009), using a combination of field-parameterised population models and experimental manipulation, provided strong evidence for niche structuring in annual plant communities. Contrary to neutral theory, population growth rates increased when species became rare. However, the biological details behind the observed niche differences in this study remain unknown.

Spatial structure

Much effort of modern ecological theory has been put in investigating the role of spatial structure – i.e. how species are distributed over space – for species coexistence. Classical ecological theory has assumed random mixing of individuals and species in the landscape; this is the so-called **mean-field approach** (Pacala & Silander, 1985; Pacala, 1997; Pacala & Levin, 1997; Stoll & Weiner, 2000; Murrell *et al.*, 2001). While this may be appropriate for mobile animals, it does not necessarily hold for plants. Plants stand still, and this makes their ecology inherently spatial (Cousens *et al.*, 2008).

Seed dispersal is the main force, generating such spatial structure. Dispersal is often spatially limited which leads to **intraspecific aggregation** – synonymous to "species segregation" – (Pacala, 1997). Since most interactions between plants occur over small spatial scales (Mack & Harper, 1977; Antonovics & Levin, 1980; Pacala & Silander, 1987, 1990), individual neighbourhoods much different from mean population densities can result (Stoll & Weiner, 2000; Murrell & Law, 2003). Dispersal is believed to set the template from which community patterns develop (Levine & Murrell, 2003) and is well documented to influence population spread and persistence (Harper, 1977; Hanski & Gilpin, 1997; Clark *et al.*, 1998; Cain *et al.*, 2000; Cousens *et al.*, 2008). The distance over which an individual disperses its seeds may have profound consequences. Once a seed has landed and a seedling emerged, there is little escape from the local environment and neighbouring plants (Murrell, 2009). It has been shown theoretically that both short and long dispersal distances might be advantageous (Bolker & Pacala, 1999; Levin *et al.*, 2003; Levine & Murrell, 2003; Satterthwaite, 2007). A long dispersal distance enables the colonisation of new, potentially suitable habitats and thereby increases a species' spread and abundance and maintains gene flow. However, dispersing seeds over a long distance is costly, and **dispersal limitation** is considered to be the rule for most plant species. Dispersal nearby, on the other hand, may guarantee suitable growth conditions, and propagules may take over the space once inhabited by their mother plant (**site preference**).

Due to intraspecific aggregation, the frequency of intraspecific to interspecific interactions is expected to be greater than suggested by the mean-field approach. As a major consequence the exclusion of inferior competitors is slowed down because only those individuals on the edges of conspecific clusters compete with heterospecifics. This has been shown both theoretically (Weiner & Conte, 1981; Pacala & Levin, 1997; Murrell *et al.*, 2002) and experimentally (Schmidt, 1981; Stoll & Prati, 2001; Monzeglio & Stoll, 2005, 2008; Wassmuth *et al.*, 2009). However, strong interspecific competition at the edges of conspecific clusters will eventually result in the stronger competitor beating the weaker species (Chesson & Neuhauser, 2002). Therefore, the role of spatial structure in maintaining plant species diversity remains controversial (Pacala & Levin, 1997; Barot, 2004). A number of theoretical studies have investigated how spatial structure may affect equilibrium densities for both populations and communities (e.g. Anderson & Neuhauser, 2002; Bolker *et al.*, 2003; Law *et al.*, 2003; Snyder, 2008). However, empirical information lags behind, and most of the spatial mechanisms for coexistence have yet to be rigorously tested (Tilman & Kareiva, 1997; Amarasekare, 2003; Barot, 2004).

Heteromyopia

During the last three decades, focus of theory has been shifted from the mean-field approach, towards the level of the individual plant (for an overview see Berger *et al.*, 2008). Classical ecological theory uses average population properties, such as population density, birth, death and growth rates. In contrast, **individual-based ecology** (Grimm & Railsback, 2005) explicitly focuses on the processes by which survival and growth of individuals are affected, and population and community dynamics emerge from these as a consequence. Individual-based models take on the "**plant's-eye view**" (Turkington & Harper, 1979) and examine population dynamics by modelling survival and growth for each individual separately. As a consequence, assumptions have to be made about the distances over which neighbourhood interactions occur and how these attenuate with distance (e.g. Bolker & Pacala, 1999; Murrell & Law, 2003; Snyder & Chesson, 2004).

Recent theory has shown that it is important to address the question whether intra- and interspecific neighbourhood interactions occur over different distances (Murrell *et al.*, 2002; Murrell & Law, 2003; Snyder & Chesson, 2004; Snyder, 2008). Most theory has so far assumed equal interaction distances within and between species with the consequence that spatial structure alone is often not sufficient to maintain coexistence. However, relaxing this assumption can have profound consequences for species coexistence (Murrell *et al.*, 2002; Murrell & Law, 2003). Using an individual-based model, Murrell and Law (2003) have shown that a competitively weaker species can invade a population of a superior species if the average distance at which conspecifics compete is longer than the average distance at which heterospecifics compete. The authors proposed the term "heteromyopia" for this mechanism, i.e. plant individuals are "short-sighted" in sensing neighbours of other species relative to their own. Under heteromyopia, intraspecific competition lowers the density of a more common species, creating small gaps that can be invaded by a rarer species, thereby facilitating coexistence (Amarasekare, 2003; Murrell & Law, 2003; Barot, 2004). Despite its potential implications for species coexistence, empirical evidence for heteromyopia is still outstanding.

Arbuscular mycorrhizal fungi

About two-thirds of terrestrial plants associate with arbuscular mycorrhizal fungi (AMF; class Zygomycetes, order Glomales) (Smith & Read, 1997). Arbuscular mycorrhizal fungi form finely branched hyphal structures within root cells, the so-called "arbuscules", over which phosphate and, to a limited extend, also nitrogen, potassium and zinc are exchanged for carbon (Read, 2002). However, the benefits plants gain from AMF go far beyond improved nutrient acquisition and include enhanced stress, pathogene and herbivore tolerance (Newsham *et al.*, 1995; Smith & Read, 1997; Kula *et al.*, 2005). Arbuscular mycorrhizal fungi seem to be involved at all levels of ecosystem complexity: they have been shown to play an important role for plant–plant interactions (Hartnett *et al.*, 1993; Facelli *et al.*, 1999; Ronsheim & Anderson, 2001; van der Heijden *et al.*, 2003b; Ayres *et al.*, 2006), plant population dynamics (Allsopp & Stock, 1992; Koide & Dickie, 2002), plant–herbivore interactions (Goverde *et al.*, 2000; Kula *et al.*, 2005), plant diversity (van der Heijden *et al.*, 1998b; Hartnett & Wilson, 1999), ecosystem properties and processes (van der Heijden *et al.*, 1998b; Rillig, 2004; Fitter, 2005), and establishment of invasive plant species (Marler *et al.*, 1999; Callaway *et al.*, 2008).

Arbuscular mycorrhizal fungi have long been considered to show no **host-specificity** because of their broad host range, the small number of about 150 described species, and the unpredictability in the distribution of species assemblages (Sanders, 2002). However, this view has changed dramatically since different AMF species have been shown to induce differential plant growth response (Streitwolf-Engel *et al.*, 1997; van der Heijden *et al.*, 1998a; van der Heijden *et al.*, 2003a), and AMF species composition has been shown to affect plant diversity and ecosystem productivity (van der Heijden *et al.*, 1998b). Similarly, AMF performance has been shown to depend on plant species identity (Helgason *et al.*, 2002). Moreover, there is recent evidence accumulating that also functional diversity within AMF species causes significant variation in plant and fungal growth performance (Koch *et al.*, 2006; Ehinger *et al.*, 2009).

Despite their obvious impact on plant species coexistence, the role of AMF in neighbourhood interactions is still under-explored. Experimental evidence suggests that the effects of AMF on plant competition and coexistence are not consistent but rather depend on the biological and environmental context (Umbanhowar & McCann, 2005). If co-occuring plant species differ in their mycorrhizal dependency, AMF can facilitate or hinder plant coexistence by reversing or emphasising competitive dominance (Grime *et al.*, 1987; Hartnett *et al.*, 1993; van der Heijden *et al.*, 1998b; Marler *et al.*, 1999). Arbuscular mycorrhizal fungi might play an important part in spatial plant ecology since they operate over relatively small spatial scales (Umbanhowar & McCann, 2005). If AMF could influence the interaction distances within and between species, they might even contribute to heteromyopia.

Aim of thesis

The major goal of my thesis was to help close the current gap between theory and data in spatial ecology. Spatial ecology is theoretically well established and more and more sophisticated models are derived therefrom. These models, like all models, are based on assumptions that simplify the complexity of natural systems as far as considered possible. Model predictions have led to new hypotheses on species coexistence. However, the next step in this process – hypotheses testing – has, in most cases, yet to be done. Moreover, many model assumptions lack a sound empirical basis. This is where this PhD thesis links in. I experimentally tested basic model assumptions and theoretical predictions of how the two spatial processes of dispersal and competition may contribute to maintain plant species coexistence.

Chapter 2 describes a field experiment in which I examined the role of seed dispersal distance for spatial pattern and population dynamics on a local, individual-based scale. In replicate plots on a calcareous grassland, I experimentally increased or decreased the distance over which seeds of the perennial forb *Prunella grandiflora* were distributed. I quantified the consequences of dispersal distance for the spatial pattern and the abundance of individuals compared to unmanipulated control plots, thereby testing for dispersal limitation versus site preference. This experiment aimed to shed some light on the question whether dispersal significantly affects spatial structure and population dynamics in natural communities as has been claimed by theory.

The greenhouse experiments described in **chapters 3 and 4** examined the most basic elements of individual-based models by studying pair-wise competition. I investigated how competition between con- and heterospecific neighbours declines with distance. These experiments provide the first experimental tests for heteromyopia. In both experiments I combined target individuals of herbaceous grassland species with either a con- or a heterospecific neighbor at 5, 10 or 15 cm distance and compared their performance with control plants grown in isolation. In the first experiment (**chapter 3**) I used four target species that were combined in two pairs (*Plantago lanceolata* and *Plantago media*; *Hieracium pilosella* and *Prunella grandiflora*). Target individuals of each plant species were either grown with a conspecific neighbor or with a heterospecific neighbor from the other species within the pair. The second experiment (**chapter 4**) carried this approach forward by additionally investigating whether AMF may influence the spatial scales of intra- and interspecific competition. The two competitively stronger plant species of the first experiment, *P. grandiflora* and *P. lanceolata*, were chosen as target species, combined with two heterospecific neighbour species (*P. lanceolata* and *H. pilosella* with *P. grandiflora*, and *P. grandiflora* and *P. media* with *P. lanceolata*) and either grown with or without AMF.

The greenhouse experiment described in **chapter 5** evaluated how within-population genetic variability of an AMF species affects growth performance of co-occurring plant species. The same plant species as in the previous competition experiments (chapters 3 and 4) were used. I further used five AMF isolates originating from one *Glomus intraradices* population from an agricultural field. These isolates have been shown to differ genetically (Koch *et al.*, 2004) and in their effects on plant growth (Koch *et al.*, 2006). Single plants were either inoculated with one of the five isolates or grown without AMF. Plant biomass and root colonisation under the different isolate treatments were compared within and among plant species. This experiment was originally designed as a pilot study to investigate within-population host-specificity of AMF. Isolates that differed in their effect on different host plant species could then be selected for future experiments investigating the role of AMF in neighbourhood interactions and heteromyopia.

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Chapter 2: Consequences of seed dispersal distance for spatial pattern and local population dynamics of *Prunella grandiflora*

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Manuscript in revision.

Plants stand still and wait to be counted.

John L. Harper

Summary

Plant ecology is inherently spatial: the fate of a plant is sealed where it emerges as a seedling. Dispersal at small scales is therefore considered to play a key role in local population dynamics. By dispersing away from the mother plant, recruits can colonise empty patches and avoid intraspecific competition. However, dispersal nearby may guarantee suitable growth conditions and be advantageous if intraspecific competition is relatively weak. We manipulated the seed dispersal distance of *Prunella grandiflora* for two-years in a field study on a calcareous grassland. We tested for effects of dispersal distance on the spatial pattern and local abundance of individuals within vegetative and reproductive stages. Seed dispersal distance of all naturally occurring reproductive individuals within each of five experimental plots (2 x 2 m) was either decreased to 2.5 cm around mother plants, increased to plot scale, or seeds were let to disperse naturally (control). The spatial pattern and the abundance of vegetative individuals were clearly affected, while reproductive individuals showed no significant response to seed dispersal manipulation. Under decreased dispersal distance, vegetative individuals became significantly more aggregated, however, increased dispersal distance did not result in a more random distribution. After two years, the level of aggregation was strongest under decreased and weakest under increased dispersal distance. Vegetative individuals increased in abundance in all dispersal treatments, but this increase was strongest under increased dispersal distance. At the end of our experiment, we found significantly more vegetative individuals under increased dispersal distance than under control and decreased dispersal distance. The common calcareous grassland species *Prunella grandiflora* profited from increased dispersal distance, with higher abundance and wider spatial distribution, while decreased dispersal slowed down natural population dynamics and limited the species' spread. *Synthesis:* This study provides experimental evidence that the distance over which seeds are dispersed contributes substantially to local population dynamics in natural plant communities.

Keywords: Calcareous grasslands, dispersal limitation, dispersal kernel, dispersal experiment, escape hypothesis, index of dispersion, spatial aggregation, seed limitation, site preference.

Introduction

Although plants are sessile, their ecology is inherently spatial (Cousens *et al.*, 2008). Seed dispersal is the movement of seeds through space (Begon *et al.*, 1996) and core determinant of where plants come to be located and struggle for life. Once a seed has landed and a seedling emerged, there is little escape from the local environment and neighbouring plants (Murrell, 2009). Therefore, spatial structure is considered crucial for population and community dynamics (Tilman & Kareiva, 1997). Dispersal is believed to set the template from which community patterns develop (Levine & Murrell, 2003) and is well documented to influence population spread and persistence (Harper, 1977; Hanski & Gilpin, 1997; Clark *et al.*, 1998; Cain *et al.*, 2000; Cousens *et al.*, 2008). Studying the ecology of dispersal involves a wide range of spatial scales (from the "plant's–eye view" (Turkington & Harper, 1979) over the population perspective to the meta-population level) and processes (*i.e.* individual growth, neighbourhood interactions, species coexistence, dynamics of meta-populations and global biodiversity patterns). The majority of dispersal studies have focussed on long-distance dispersal and the importance of small scale seed dispersal on the local abundance, distribution and coexistence of plant species is still under-explored (Schupp & Fuentes, 1995). Dispersal at small scales, however, is a key component of local population dynamics (Cousens *et al.*, 2008). Here, we focus on dispersal from a local, individual to population level perspective.

Besides dispersal, other spatial processes can interact to distribute species within a community (Nathan & Muller-Landau, 2000; Levine & Murrell, 2003). On the one hand, the abundance, spatial distribution and fecundity of reproductive plants as well as landscape structures that act as seed traps shape the seed dispersal pattern. On the other hand, many processes, including environmental factors and interactions between neighbouring plants, operate from seed arrival to maturity of adult plants, and it has been shown that the spatial distributions of seeds, seedlings and adult plants can differ strongly (Peart, 1989; Schupp & Fuentes, 1995; Houle, 1998). Therefore, the consequences of seed dispersal distance for community patterns are not clear *a priori*.

The distance over which seeds are dispersed can determine the frequency of intra- vs. interspecific contacts that recruits encounter. If dispersal distance is very short, offspring will experience strong competition with sibs and parents. This leads to self-thinning and results in a low establishment rate of recruits. In contrast, by dispersing away from the mother plant, the frequency of intraspecific contacts and kin competition are expected to decrease.

The advantage of bigger dispersal, however, depends on the species-specific relative strengths of intra- vs. interspecific competition. For example, competitively weak species may profit from intraspecific aggregation, while competitively strong species may profit from random dispersal (Schmidt, 1981; Stoll & Prati, 2001; Monzeglio & Stoll, 2005; Wassmuth *et al.*, 2009).

By dispersing away from the mother plant, offspring may escape from host specific enemies (“escape hypothesis” e.g. Howe & Smallwood, 1982). It has been shown repeatedly, that establishment rate and survival of seedlings increases with distance from the mother plant, due to reduced seed predator, herbivore or pathogen pressure (Janzen, 1970; Connell, 1971; Augspurger, 1983; McCanny & Cavers, 1987), although this might not be a universal phenomenon (Condit *et al.*, 1992). A long dispersal distance enables the colonisation of new, potentially suitable habitats and thereby increases a species’ spread and abundance and maintains gene flow. However, dispersal nearby may guarantee suitable growth conditions (“site preference”, e.g. Donohue, 1997). Especially in short-lived, monocarpic species, propagules have a good chance of taking over the space once inhabited by their mother plant. If habitat quality is very heterogeneous and if the spatial scales of good and bad microsites are small enough to fall into a species’ dispersal capacity, then short dispersal may be favourable (Levin *et al.*, 2003). The chance to find a suitable site has been shown to decrease with distance to the mother plant (Augspurger & Kitajima, 1992).

Although seed dispersal patterns are thought to be important for population structure and dynamics, most experimental studies on seed dispersal have investigated the issue of seed limitation rather than consequences of seed dispersal distance or pattern. Plants are generally assumed to be seed limited, that is, a species’ distribution is primarily limited by seed availability at the local scale (Munzbergova & Herben, 2005). Typically, seed limitation has been tested with seed addition experiments, where seeds are added to existing populations or sown in unoccupied sites and the resulting seedling numbers compared with unmanipulated control plots (for a review see e.g. Turnbull *et al.*, 2000). If population size increases following seed addition, the species is considered to be seed limited, if not the species is rather considered to be microsite limited (Nathan & Muller-Landau, 2000). However, seed addition experiments have been criticised because they manipulate not only the quantity of seeds dispersed (more seeds are dispersed than produced on a site) but also the quality of seed dispersal (seeds are dispersed over larger distances than naturally) (Munzbergova & Herben, 2005; Clark *et al.*, 2007). The term dispersal limitation, where seeds do not reach all suitable sites, is often used on a regional scale, for meta-population dynamics (Munzbergova &

Herben, 2005). In this context, it has recently been shown that dispersal limitation affects the diversity and productivity of local grassland communities (Stein *et al.*, 2008). However, variation in seed dispersal distances within a single region is another important component of dispersal limitation (Satterthwaite, 2007).

Theoretical papers have explicitly addressed the role of seed dispersal distance for local population and community dynamics and have also explored potential advantages of short dispersal (Bolker & Pacala, 1999; Levin *et al.*, 2003; Levine & Murrell, 2003; Satterthwaite, 2007). These papers strongly advocate experiments that directly manipulate dispersal kernels. Rather than providing extra seeds, experimental studies should manipulate the spatial distribution of seeds by first collecting all seeds produced in a plot and then dispersing them randomly or locally (Bolker & Pacala, 1999; Levine & Murrell, 2003). The resulting abundance, distribution and coexistence of species within such replicate plots should then be compared to that in unmanipulated control plots.

The present experiment pursued this approach: in replicate plots on a calcareous grassland we experimentally increased or decreased the distance over which seeds from established *Prunella grandiflora* plants were distributed and quantified the consequences for the spatial pattern and the abundance of individuals compared to unmanipulated control plots. The aim of our experiment was to test for dispersal limitation versus site preference. We expected the spatial pattern to become more aggregated under decreased dispersal distance and to become more random under increased dispersal distance. We hypothesized that, if *P. grandiflora* was dispersal limited, it should become more abundant under increased dispersal distance but less abundant under decreased dispersal distance, while the opposite would indicate site preference. Since *P. grandiflora* is a perennial forb, we discriminated between flowering and non-flowering individuals in order to determine whether dispersal manipulation affected the reproductive and vegetative stages differently.

Material and methods

Study site and species description

This study was conducted on a calcareous grassland in Movelier, located in the north-western Swiss Jura mountains (47°24´N, 7°19´E). The study site is situated on a south-south-east-facing slope (inclination 20–22°) at an altitude of 780 m. Half of the site is surrounded by deciduous forest. The vegetation is characteristic for the Teucro-Mesobrometum. Until 1993, the site was grazed by cattle and moderately fertilized. Since then, management activities have been reduced to one single hay cut per year in late autumn. For the duration of our experiment, the main meadow was cut with a scythe mower and the hay raked off in the second half of October each year. Further details, including vascular plant species list, can be found in Zschokke *et al.* (2000).

Prunella grandiflora (L.) Scholler (big self-heal, *Lamiaceae*) is a perennial forb, with its main abundance on chalk-rich, semi-arid grasslands (Lauber & Wagner, 2007). It is typical for species-rich calcareous grasslands in north-western Switzerland and very abundant on our study site. With an average height of 10 – 20 cm (up to 30 cm) it is smaller than the majority of forbs and dominating grasses. *Prunella grandiflora* forms no stolons but occasional stem sprouting can be observed. On our study site, the species flowers from June to October, and seeds mature between August and November (D. R. Vogt, personal observations). The species naturally disperses its seeds via a ballistic, ombrochorous dispersal mechanism. As seeds mature, the infrutescences dry out. During rain, calyces take up water and begin to open, hitting raindrops then catapult the seeds out of the lomenta. The natural dispersal kernel of *P. grandiflora* is not known, but has been extensively studied under laboratory conditions (Sack, 2003). In this study, dispersal occurred up to 1 m. 16% of seeds landed within 7.5 cm and 63% within 30 cm. These results, however, refer to isolated plants and dispersal without any obstacles. In a natural community plants are surrounded by vegetation and moreover, *P. grandiflora* is among the smaller plant species on our study site. We therefore assume that dispersal will occur over a smaller range under natural conditions.

Experimental set up

The experiment was set up in August 2006 and lasted until October 2008, spanning three field seasons. We established five blocks (4 x 10 m), distributed over the whole study site and separated from each other by 15 to 30 m. Blocks were chosen semi-randomly, *i.e.* a randomly chosen location was selected when an appropriate number of *P. grandiflora* plants could be visually detected. In each block, we marked three plots (2 x 2 m), separated from each other by 1 m. Plots were further divided into 64 subplots (0.25 x 0.25 m). Each block contained one replicate of three dispersal treatments (see below), randomly assigned to the plots. The corners of each plot were permanently marked with iron tubes, plunged into the ground. Subplot markings – wooden sticks connected with cord – were removed for hay cut and reinstalled afterwards.

Dispersal treatments

The seed dispersal distance of all *P. grandiflora* individuals within one plot was either decreased or increased, or seeds were let to disperse naturally (control). To manipulate seed dispersal, we first collected all seeds produced in a plot and then dispersed them by hand. In the decreased dispersal distance treatment, seeds were collected from each individual separately and distributed within 2.5 cm around the mother plant. In the increased dispersal distance treatment, all collected seeds per plot were mixed, weighted and divided into 16 portions of equal weight. Each portion was then randomly distributed over four adjacent subplots taken together (0.5 x 0.5 m). In the control treatment, plots were left untouched until harvest. Decreasing dispersal distance resulted in an aggregated distribution of seeds, while increasing dispersal distance resulted in a random distribution of seeds.

Data collection

To prevent natural dispersal and loss of seeds under manipulated dispersal, inflorescences were wrapped with small net bags after petals had fallen off. Ripe fruits from these plots were harvested continuously between August and October each year, and the corresponding mother plants were labelled with plastic markers. Seeds were prepared out of fruits, counted and stored at room temperature until sowing. Flower buds and fruits of *P. grandiflora* individuals growing outside of the plots but within the blocks were removed regularly to exclude external seed input into plots.

For the decreased dispersal distance treatment, the number of seeds was counted for each flowering plant every year. For the increased dispersal distance treatment, in 2006 and 2007, all collected fruits were pooled, and only the total number of seeds per plot could be determined. In 2008, however, the number of seeds was also determined for each flowering plant. We have no knowledge of the number of seeds that were produced and dispersed within control plots.

Within each plot, 16 subplots (1/4 of plot area) were randomly selected for further data collection, the same subplots being used each year. On each selected subplot, we counted the number of *P. grandiflora* plants in reproductive (flowering) and vegetative stages and cut biomass at 5 cm above ground level. In 2008, we additionally cut and collected the vegetation of all selected subplots (referred to as “matrix biomass” from hereafter) at 5 cm above ground level. All collected biomass was dried at 60°C for 48h and weighted. The remaining vegetation on the plots was cut with a motor scythe at yearly hay cut. Data were collected between October 6 and 25 in 2006, October 8 and 11 in 2007, and between September 15 and 19 in 2008. Seeds were sown on 31 October in 2006 and 2007.

Index of dispersion

The spatial pattern of *P. grandiflora* plants on plots was estimated from the number of individuals on the selected subplots. For each plot, we calculated the index of dispersion (I), also called the variance-to-mean ratio

$$I = s^2 / \bar{x}$$

where $\bar{x}$ is the mean and s^2 is the variance of the number of individuals on subplots (for further details see Krebs, 1999). Separate indices of dispersion were calculated for the vegetative (I_{veg}) and the reproductive (I_{rep}) stages. If the spatial pattern is random, count data should follow a Poisson distribution where the variance equals the mean and therefore it is expected that $I = 1.0$. Under regular pattern, the variance will be less than the mean, with $I \rightarrow 0$, while under aggregated pattern, the variance will be larger than the mean, resulting in $I > 1.0$.

Statistical analyses

Spatial pattern

The index of dispersion can be tested for significant deviation from randomness with a two-tailed chi-square test with

$$\chi^2 = I(n-1)$$

where n is the number of subplots counted. If the observed χ^2 lies within the critical values for the expected χ^2 with $(n - 1)$ degrees of freedom, then the distribution does not deviate from a random distribution. Larger values of χ^2 indicate an aggregated distribution, and smaller values indicate a regular pattern. We calculated the 95% confidence interval (CI) for I under random distribution by back-transforming the corresponding χ^2 values ($CI = 0.42–1.83$). To determine the spatial pattern under the different dispersal treatments we checked whether the mean I per treatment lay within, above or below the CI (random, aggregated and regular pattern, respectively).

One subplot under increased dispersal distance contained an extremely high number of vegetative individuals in all three years (26, 36 and 35 respectively), accounting for up to 42% of the total number of vegetative individuals on the selected subplots within this plot. This led to an exceptionally high *I*-value that strongly influenced the mean *I*-value for increased dispersal distance (always indicating strong aggregation). We therefore decided to exclude this particular subplot from all spatial pattern analyses. Thus, for the corresponding plot, only 15 instead of 16 subplots were used to calculate *I*. The corresponding CI for increased dispersal distance was slightly larger ($I = 0.40–1.87$) but is not shown extra because it allocated the same spatial pattern to the plot as the corresponding CI for 16 subplots.

To test whether the index of dispersion changed significantly over time and whether this change differed between dispersal treatments, we used linear mixed-effects models with plot as random factor, taking repeated measures into account (three measures per plot). *I*-values of vegetative individuals were Box-Cox transformed ($\lambda = 0.2$) to meet the requirements of a normal distribution.

Abundance

We tested for effects of seed dispersal distance on the number of individuals at the end of our experiment using ANCOVAs, including the following three covariates: initial number of individuals (= number in 2006), number of reproductive individuals of previous years (summed up over 2006 and 2007; approximation for the number of dispersed seeds) and biomass of matrix vegetation in 2008 (log-transformed). These covariates differed between blocks. In the ANCOVAs, *i.e.* after correction for differences in these covariates, block effects were no longer significant. This indicates that the significant variation among blocks was “captured” by the covariates. Therefore, we no longer included block effects in our analyses. We further used ANCOVAs to test for effects of dispersal distance on the number of individuals after one year of dispersal manipulation (two covariates: initial number of individuals and number of reproductive individuals of previous year). However, we found no significant treatment effects, and these results are not reported.

Data on the number of individuals showed strong over-dispersion (residual deviance larger than residual degrees of freedom) and were therefore analysed using generalised linear models, assuming a quasi-Poisson error distribution. In contrast to a Poisson distribution, the dispersion parameter for a quasi-Poisson distribution is not fixed at 1.0, but calculated by dividing residual deviance by residual degrees of freedom to model over-dispersion (Crawley, 2007).

Intraspecific density and matrix biomass

We analysed the relationships between the number of vegetative individuals, the number of reproductive individuals and matrix biomass, using data from 2008 only. We tested several regression models (linear, log-linear, quadratic and cubic) against the corresponding null model for each dispersal treatment separately ($\alpha = 0.05$; under quasi-Poisson error distribution the change in residual deviance compared to the null model follows an F-distribution). If more than one model explained data significantly better than the null model, we tested them against each other. If those models were equal ($p > 0.1$), the simplest model (in terms of number of parameters) was chosen. We report p-values of selected models tested against the null model. Predicted values of significant regressions are shown in figures. Data showed strong over-dispersion and we therefore used generalized linear models assuming a quasi-Poisson error distribution (c.f. above) for all density–dependence analyses.

All statistical analyses were performed with the statistical program R, version 2.8.1 (R Development Core Team, 2008).

Results

Spatial pattern analysis

Initially, individuals in the vegetative stage were significantly aggregated (mean of all plots: $I_{veg} = 2.11$, $p < 0.05$), while individuals in the reproductive stage were randomly distributed (mean of all plots: $I_{rep} = 1.59$) (Fig. 1). Moreover, on each plot, vegetative individuals showed a higher level of aggregation than reproductive individuals ($I_{veg} > I_{rep}$; paired t-test: $t_{14} = 2.43$, $p < 0.05$). At the end of our experiment, we found strong differences in the spatial pattern of vegetative individuals: spatial aggregation was significantly stronger under decreased dispersal distance compared to unmanipulated and increased dispersal distance (Tukey's honest significance test: decreased dispersal distance vs. control: $p < 0.05$; decreased vs. increased dispersal distance: $p < 0.001$; control vs. increased dispersal distance: n.s.). The final spatial pattern of reproductive individuals did not differ between dispersal treatments.

When data of all dispersal treatments were pooled, I of both stages increased over time (Table 1). However, this effect differed between the dispersal treatments and was mainly due to increasing aggregation of individuals under decreased dispersal distances. We found no correlation between I in 2006 and 2008 for either stage, thus the resulting spatial patterns were independent of the initial spatial pattern.

Abundance and population dynamics

Initially, the plots assigned to the different dispersal treatments did not differ in their average number of vegetative or reproductive individuals (ANOVAs: vegetative individuals: $F_{2/12} = 0.8$, $p = 0.466$; reproductive individuals: $F_{2/12} = 0.4$, $p = 0.675$). After two years, however, the manipulation of seed dispersal distance significantly affected the number of vegetative individuals (Table 2, Fig. 2). On average, there were more vegetative individuals under increased dispersal distance (96 ± 9; predicted mean and one standard error, adjusted for covariates) than under unmanipulated (66 ± 7) and decreased dispersal distance (67 ± 7). Further, all covariates (the number of reproductive individuals of previous years, the initial number of vegetative individuals and the biomass of the matrix vegetation) significantly influenced the number of vegetative individuals (Table 2). In contrast, the number of reproductive individuals in 2008 was affected only by the number of reproductive individuals of previous years, and we found no effects of dispersal treatments.

Intraspecific density and matrix biomass

The abundance of vegetative individuals increased with the abundance of reproductive individuals, and these relations differed between the three dispersal treatments (Fig. 3; comparisons with null model: decreased dispersal distance: $F_{1/78} = 26.3$, $p < 0.001$; control: $F_{1/78} = 10.4$, $p = 0.002$; increased dispersal distance: n.s., average number of 7.8 individuals predicted). When there were no or only a few reproductive individuals per subplot, the predicted numbers of vegetative individuals were larger under increased dispersal distance compared to unmanipulated and decreased dispersal distance. However, with increasing number of reproductive individuals per subplot, the number of predicted vegetative individuals increased more under decreased dispersal distance, followed by unmanipulated and increased dispersal distance.

The number of vegetative individuals further showed a clear negative density–dependence with matrix biomass under increased and unmanipulated dispersal distance, but not under decreased dispersal distance (Fig. 4; comparisons with null model: decreased dispersal distance: n.s., average number of 3.9 individuals predicted; control: $F_{1/78} = 39.0$, $p < 0.001$; increased dispersal distance: $F_{1/77} = 34.5$, $p < 0.001$). Independent of the dispersal treatment, we found no significant relationship between the number of reproductive individuals and matrix biomass (data not shown).

Discussion

The spatial distribution and the abundance of plant individuals within populations fluctuate naturally. Dispersal is generally believed to play an important role for the development of community patterns (Tilman & Kareiva, 1997; Nathan & Muller-Landau, 2000; Levin *et al.*, 2003; Levine & Murrell, 2003; Cousens *et al.*, 2008). The field study presented here provides experimental evidence that the distance over which seeds are dispersed indeed contributes to these patterns. Our results suggest that *P. grandiflora* may benefit from increased dispersal distance, which indicates dispersal limitation. Below we first elaborate on the consequences of seed dispersal distance and relate these to other mechanisms, such as density-dependence. We then discuss a central question that emerges from our experiment and similar studies: if a larger dispersal distance seems to be advantageous, why has it not evolved?

Consequences of dispersal distance and its interaction with density effects

Our study has shown that seed dispersal distance has direct consequences for the abundance and spatial distribution of recruits in natural plant populations. Data from the control plots show that local *P. grandiflora* populations fluctuate from year to year: during our experiment, the number of vegetative individuals doubled, while the number of reproductive individuals was more or less constant. However, the spatial pattern of both stages did not change significantly during our experiment in the control plots. Manipulating seed dispersal distance significantly influenced individuals in the vegetative stage: this lead, on the one hand, to a stronger spatial aggregation (decreased dispersal distance) and on the other hand, to a larger abundance (increased dispersal distance). This suggests that seed dispersal distance contributes to population dynamics. However, our study also pointed out that other mechanisms, related to intra- and interspecific density, shape a species' abundance and fecundity and may interact with dispersal distance. Furthermore, we found no significant response of reproductive individuals to dispersal manipulation.

By manipulating the dispersal distance we have uncoupled the natural small-scale auto-correlation between reproducing individuals and recruits. The number of vegetative individuals was positively related to the number of reproductive individuals under unmanipulated and under decreased dispersal distance. However, we found no such relation under increased dispersal distance: recruits established (spatially) independently of their mother plant or any other adult conspecifics. This indicates that *P. grandiflora* shows no site preference but benefits – in terms of recruit establishment – from an increased dispersal distance by colonising more suitable patches.

While we found clear effects of dispersal distance on the spatial pattern and abundance of the vegetative stage, the reproductive stage did not respond to dispersal manipulation. This seems most likely due to a time-lag in response. The initial spatial distribution and abundance sets a template from which the new patterns result from manipulated dispersal scale, thus it takes time to override the original signature in a long-lived species. Many of the initial individuals will have survived until the end of our experiment, thereby "echoing" the initial spatial pattern. If we were to find effects of dispersal distance, this should primarily evolve from individuals emerging from experimentally dispersed seeds. Significant effects in the vegetative stage became visible only after the second year of dispersal manipulation. Moreover, since *P. grandiflora* takes at least one year before flowering, reproductive individuals are expected to react slower than vegetative individuals. Therefore, we assume that our study was too short to capture the response of the reproductive stage.

If a larger dispersal distance is advantageous, why has it not evolved?

Prunella grandiflora profited from increased dispersal distance with a larger abundance and a wider spatial distribution of the vegetative stage. Decreasing dispersal distance, however, slowed down the increase in abundance and limited the species' distribution. Furthermore, the local abundance of vegetative individuals was not correlated to that of reproductive individuals. Thus, *P. grandiflora* showed no indications of site preference and would likely perform better if individuals could disperse their seeds over larger distances. These findings indicate dispersal limitation.

Many studies have shown dispersal limitation in a wide range of community types (e.g. Turnbull *et al.*, 1999; Ehrlen & Eriksson, 2000; Bossuyt *et al.*, 2004; Cascante-Marin *et al.*, 2009). The relative importance of dispersal limitation may, however, depend on the spatial and temporal heterogeneity (Moore, 2009) and on the spatial scale of observation (Freestone & Inouye, 2006; Girdler & Barrie, 2008). Plants are considered dispersal limited if their performance would be enhanced with larger dispersal distances, e.g. by successful colonisation of suitable patches or by an escape from enemies (Augspurger, 1983). We think that in our case, increased successful colonisations predominated and that the potential for escaping (above-ground) enemies was limited on such a local scale (but see Petermann *et al.*, 2008).

For most plant species a larger dispersal distance would thus be better. But why did it not evolve? It could either be the case that trade-offs or other constraints – such as the competition-colonisation trade-off, limited fecundity or environmental heterogeneity – prevent the evolution of longer dispersal distances; or it could be that the observed phenomena from which dispersal limitation is commonly concluded are not relevant for plants in the long run and that many plant species are in fact not dispersal limited. We first discuss several reasons that might prevent the evolution of larger dispersal distances and then elaborate on the importance of discriminating short-term from long-term beneficial effects.

According to the competition–colonisation trade-off a plant species is either a good coloniser or a good competitor (e.g. Turnbull *et al.*, 1999). Colonisers are often pioneer species that produce many small seeds, which disperse easily but loose competition against larger seeded species. Competitors produce few large seeds with poor primary dispersal and often rely on costly secondary dispersal. However, there are many "intermediate strategists" coexisting within a certain community, and a plant may be both a colonist and a persistent (Howe & Smallwood, 1982). Recently, it has been shown that tropical tree species, sharing the same mode of seed dispersal, exhibit a large interspecific variation in primary seed dispersal distances (Muller-Landau *et al.*, 2008). Seed mass was found to be a key factor explaining this variation so that a plant's abundance and spatial distribution seems to be restricted due to the costs related to dispersal that increase with seed mass. Another selective trade-off may exist between fecundity and dispersal ability. Using an individual-based model, Satterthwaite (2007) showed that the response of final population size to local or global seed dispersal is a function of fecundity and whether or not present individuals make safe sites, at least temporarily, unavailable (e.g. by leaving litter after dying or by persisting over more than one season). The models also suggest that larger dispersal distances could be selected against at low fecundities (typical for low productive habitats such as calcareous grasslands), since the probability of colonising distant sites may be small even if all seeds disperse.

We should, however, also consider that larger dispersal distances might not be evolutionary stable. It could be that an increased abundance and a wider spatial distribution are only advantageous at the short term and that recruits on suboptimal patches will suffer from decreased survival, growth and fecundity on the long run. Most studies, ours included, have been conducted over relatively short time periods. Microsite quality might be less important at the juvenile stage, allowing seedlings to establish basically on every site that seeds reach, while the requirements of adult plants might be more specific, so that patch quality will act as a sieve, selecting for individuals on optimal sites (Murrell, 2009). In addition, unknown or unobserved positive effects of short dispersal, e.g. connection to an established mycorrhizal network or attraction of pollinators, might counterbalance the disadvantages compared to increased dispersal distances. Moreover, we speculate that reduced seedling establishment around mother plants might result from a kind of "birth control", guaranteeing that those few individuals that survive reach the adult stage and reproduce.

Conclusions

The aim of the present study was primarily to test whether the spatial scale over which seeds are dispersed has significant consequences for population dynamics when all other contributing factors (c.f. Levine & Murrell, 2003) are unaltered. Our results provide experimental support that seed dispersal scale contributes significantly to local population dynamics under natural, field conditions, as has been claimed by theory (Tilman & Kareiva, 1997; Nathan & Muller-Landau, 2000; Levin *et al.*, 2003; Levine & Murrell, 2003; Cousens *et al.*, 2008). An important next step would be to manipulate the dispersal scales of co-occurring strong and week competitors simultaneously and to test for theoretically derived dispersal strategies (c.f. Bolker & Pacala, 1999). Experiments should also examine into what direction long-term population dynamics under manipulated seed dispersal go and whether short time advantages persist.

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Table 1: Results of ANOVA testing for effects of two years of manipulated seed dispersal distance (decreased, increased or unmanipulated) on the spatial pattern (Index of dispersion) of vegetative and reproductive *Prunella grandiflora* individuals.

		Vegetative stage		Reproductive stage	
Source	df	F	p	F	p
Intercept	1/27	6114.1	< 0.001	283.0	< 0.001
Time	1/27	7.9	0.009	5.5	0.027
Dispersal	2/12	4.0	0.046	4.3	0.038
Dispersal x Time	2/27	0.8	0.480	2.3	0.123

Note: Linear mixed-effects model, plot was included as random factor to account for repeated measures.

Table 2: Results of ANCOVA testing for effects of abundance of reproductive individuals in previous years, initial abundance of vegetative individuals, biomass of the matrix vegetation in 2008 and seed dispersal distance (decreased, increased or unmanipulated) on the abundance of vegetative and reproductive *Prunella grandiflora* individuals after two years of seed dispersal manipulation.

	Vegetative individuals				Reproductive individuals			
Source	df	Deviance	F	p	df	Deviance	F	p
Reproductive individuals 2006 & 2007[ab]	1	435.8	107.5	< 0.001	1	31.6	13.0	0.005
Vegetative individuals 2006[a]	1	50.2	12.4	0.007				
Matrix vegetation[a]	1	33.1	8.2	0.019	1	3.3	1.4	0.269
Dispersal	2	38.5	4.7	0.039	2	5.2	1.1	0.378
Residuals	9	36.1			10	25.2		

Note: Generalised linear model, assuming a quasi-Poisson error distribution. Dispersion parameter was taken to be 4.05 for vegetative individuals and 2.43 for reproductive individuals.

[a] Covariates.

[b] The number of reproductive individuals, summed-up over the two previous years, was included for both stages as an approximation of the number of dispersed seeds.

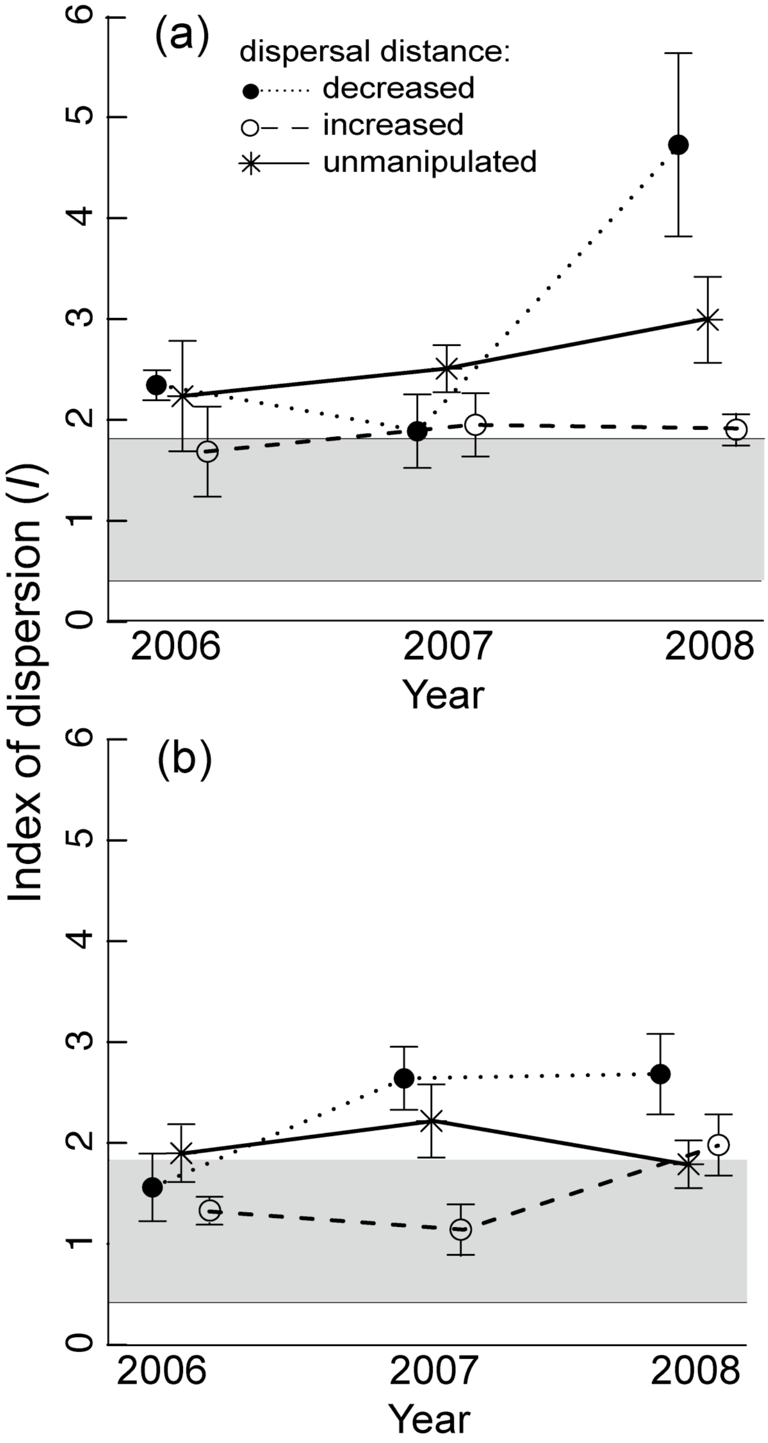

Fig. 1: Index of dispersion for (a) vegetative and (b) reproductive *Prunella grandiflora* individuals under decreased, increased or unmanipulated seed dispersal distance from 2006 to 2008. Mean values ± one standard error are shown (n=5 plots, 16 subplots per plot selected). Grey areas represent the 95% confidence interval (CI) for a random pattern. Mean values above the 95% CI indicate aggregated spatial pattern, mean values below the 95% CI would indicate regular spatial pattern.

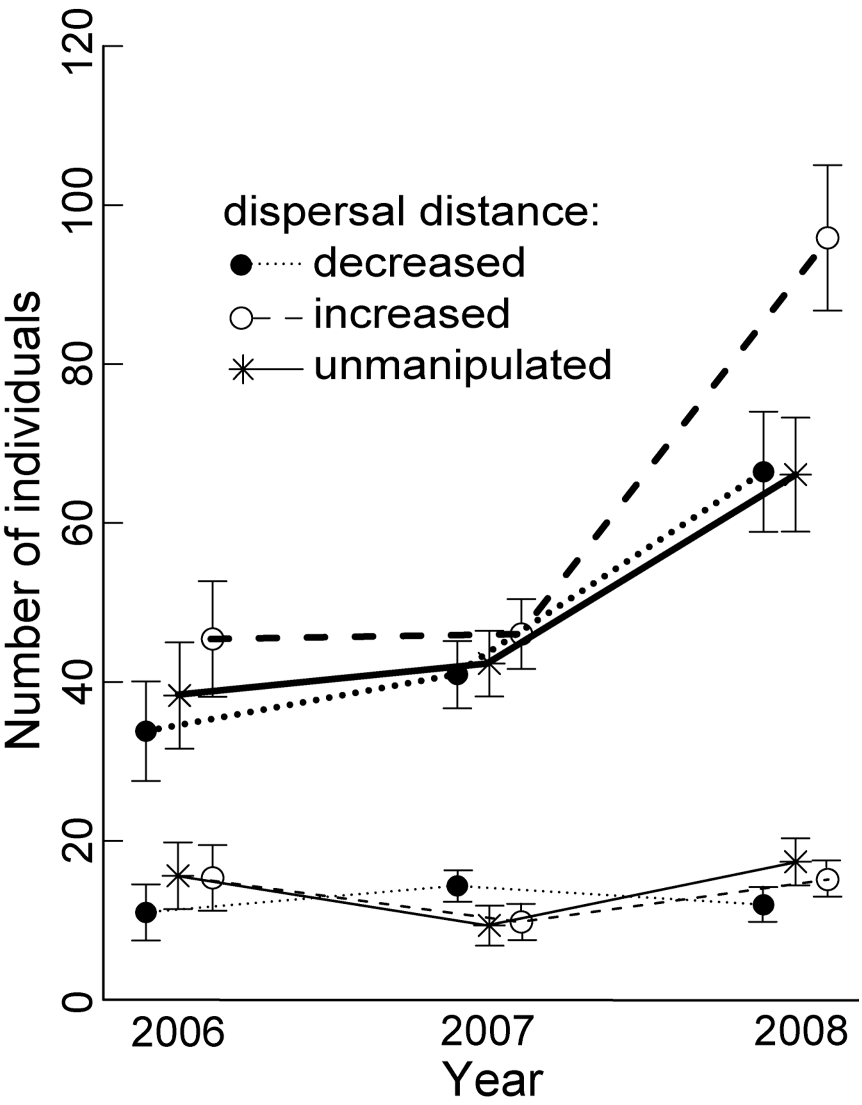

Fig. 2: Predicted number of vegetative (upper thick lines) and reproductive (lower thin lines) *Prunella grandiflora* individuals over three years (2006–2008) under decreased, increased or unmanipulated seed dispersal distance. Mean values ± one standard error are shown (n=5 plots, 16 subplots per plot selected). Predictions are from separate analyses per stage and year (generalised linear models, assuming quasipoisson error distribution, adjusted for covariates).

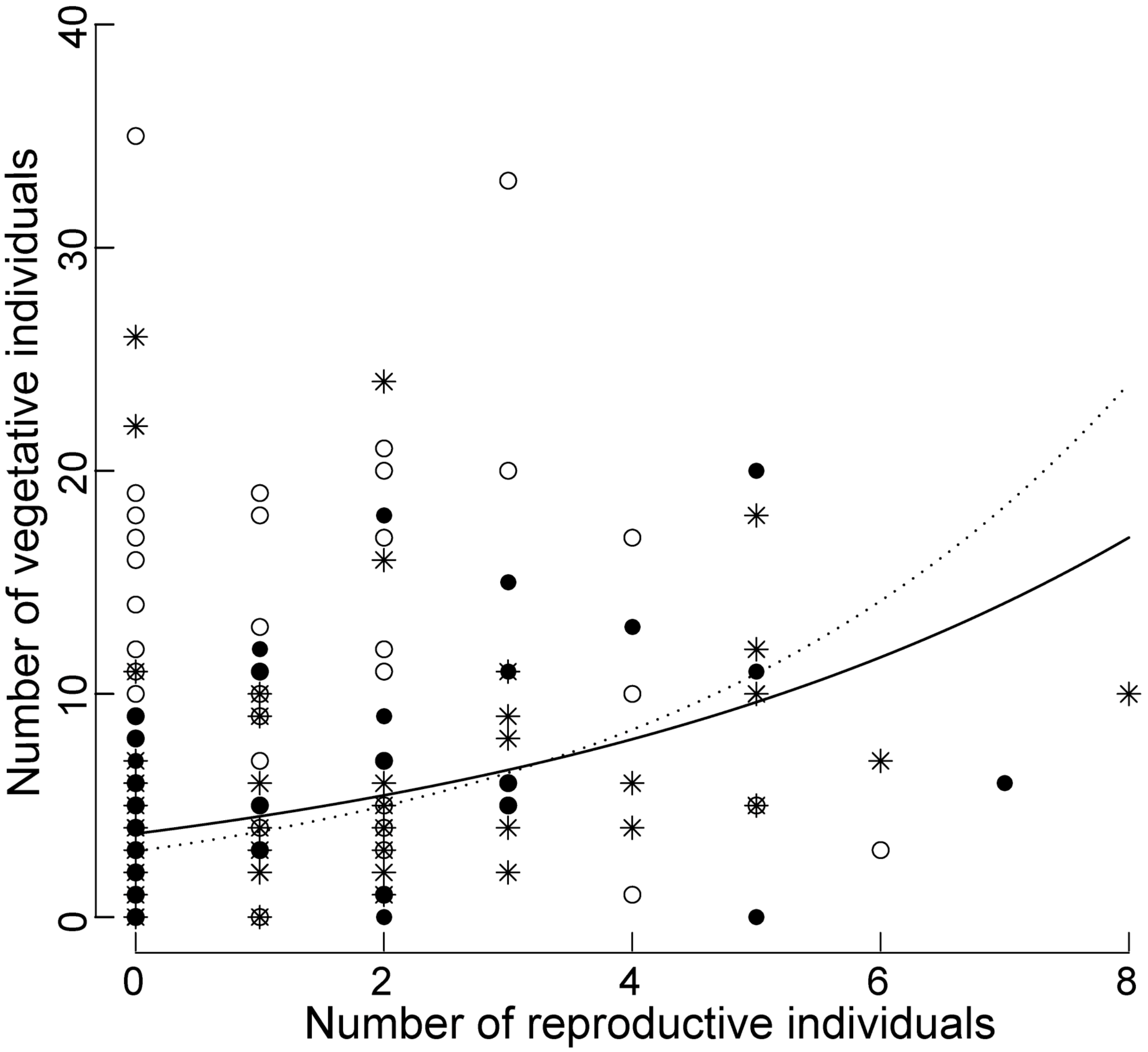

Fig. 3: Relation between vegetative and reproductive *Prunella grandiflora* individuals in 2008 under decreased (filled circles, dotted line), increased (open circles) or unmanipulated (asterisks, continuous line) seed dispersal distance. Curves show predicted values from separate analyses per treatment, where significant.

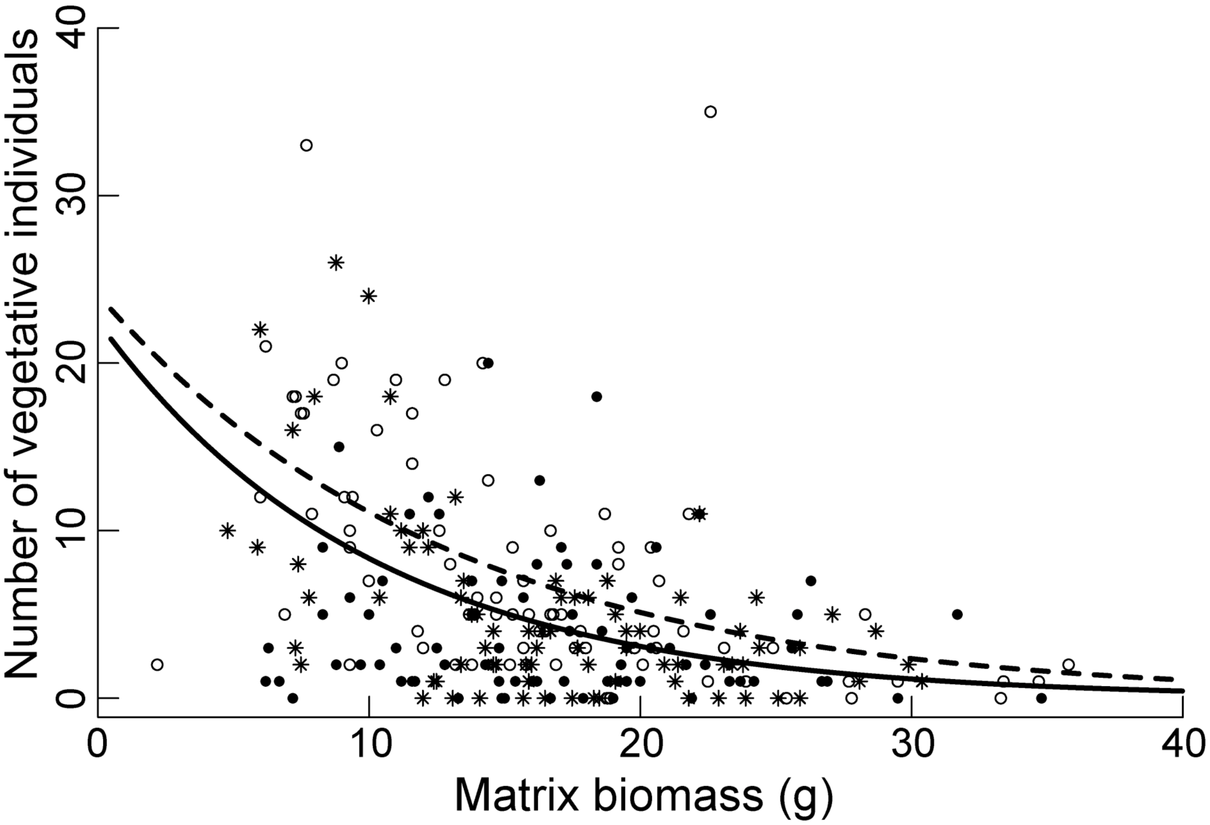

Fig. 4: Number of vegetative *Prunella grandiflora* individuals in 2008 in relation to matrix biomass under decreased (filled circles), increased (open circles, dashed line) or unmanipulated (asterisks, continuous line) seed dispersal distance. Curves show predicted values from separate analyses per treatment, where significant.

Chapter 3: Testing spatial theories of plant coexistence: No consistent differences in intra- and interspecific interaction distances

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Appendices: Online Appendix A (including Figure A1), Online Appendix B (including Table B1).

Abstract

Plants stand still and interact with their immediate neighbors, and theory has shown that the distances over which these interactions occur may have important consequences for population and community dynamics. In particular, if intraspecific competition occurs over longer distances than interspecific competition (heteromyopia), coexistence can be promoted. We examined how intraspecific and interspecific competition scales with neighbor distance in a target–neighbor greenhouse competition experiment. Individuals from co-occurring forbs from calcareous grasslands were grown in isolation and with single conspecific or heterospecific neighbors at 5, 10 or 15 cm distance (*Plantago lanceolata* versus *Plantago media* and *Hieracium pilosella* versus *Prunella grandiflora*). Neighbor effects were strong and declined with distance. Interaction distances varied greatly within and between species but we found no evidence for heteromyopia. Instead neighbor identity effects were mostly explained by relative size differences between target and neighbor. We found a complex interaction between final neighbor size and identity, such that neighbor identity may only become important as the neighbor becomes very large compared to the target individual. Our results suggest that species-specific size differences between neighboring individuals determine both the strength of competitive interactions and the distance over which these occur.

Keywords: Competition experiment, heteromyopia, individual-based models, log response ratio, neighborhood.

Introduction

The role of spatial structure in maintaining plant species diversity is a fundamental and controversial issue in ecology (Pacala and Levin 1997; Barot 2004). Plants stand still and interactions between individuals usually occur within their immediate neighborhood (Mack and Harper 1977; Antonovics and Levin 1980; Pacala and Silander 1987; Pacala and Silander 1990; Stoll and Weiner 2000). Spatially limited dispersal, together with local interactions, can lead to individual neighborhoods much different from mean population densities (Murrell and Law 2003). Local dispersal leads to aggregations of conspecifics (Pacala 1997), and because competition is also expected to occur over small spatial scales, the frequency of intraspecific to interspecific interactions is expected to be greater than suggested by the landscape or patch-scale densities. As a major consequence the exclusion of inferior competitors is slowed down because only those individuals on the edges of conspecific clusters compete with heterospecifics, and this has been shown both theoretically (Weiner and Conte 1981; Pacala and Levin 1997; Murrell et al. 2002) and experimentally (Schmidt 1981; Stoll and Prati 2001; Monzeglio and Stoll 2005; Monzeglio and Stoll 2008).

A number of theoretical studies have investigated how spatial structure may affect equilibrium densities for both populations and communities (e.g. Anderson and Neuhauser 2002; Bolker et al. 2003; Law et al. 2003; Snyder 2008), yet empirical information lags behind, and most of the spatial mechanisms for coexistence have yet to be rigorously tested (Tilman and Kareiva 1997; Amarasekare 2003; Barot 2004). During the last three decades, focus has been shifted from the mean-field or population-level approach, which assumes random mixing of species and individuals in the landscape, towards the level of the individual plant (for an overview see Berger et al. 2008). Individual-based models examine population dynamics by modeling survival and growth for each individual separately (Grimm and Railsback 2005), so assumptions have to be made about the distances over which individuals interact (e.g. Bolker and Pacala 1999; Murrell and Law 2003; Snyder and Chesson 2004). So-called competition or interaction kernels are functions that describe the growth, survival and reproduction of an individual by means of its own size and the size of and distance to its neighbors (Law et al. 2001). However, despite their theoretical importance, very little is known about the actual shape of such competition kernels, and a wide variety of mathematical functions and assumptions have been used to incorporate them into models (see Purves and Law 2002).

Much of the knowledge on the spatial scales of competition is derived from neighborhood analyses of forest systems, but so far no general picture has emerged as to the extent neighbor identity (i.e. conspecifics versus heterospecifics) influences the competitive effect and size of the neighborhood. While some studies have concluded that neighborhood sizes do not differ for con- and heterospecific neighbors (Hubbell et al. 2001; Uriarte et al. 2004), other studies have shown that conspecific neighbors are of greater importance and differ in interaction radii from heterospecific neighbors (Peters 2003; Stoll and Newbery 2005; Queenborough et al. 2007).

Despite a large body of competition studies in herbaceous systems (see e.g. Goldberg and Barton 1992; Gurevitch et al. 1992), the spatial scales of interactions in these communities have been rarely investigated. In grassland communities it has been shown that above- and below-ground interactions do not necessarily occur over the same spatial scales (Milbau et al. 2007), and this inevitably means neighborhood size depends on the processes taken into account, because they will ultimately influence the functional shape of interaction kernels. Experimental studies on *Arabidopsis thaliana* have assessed the effect of size and distance of conspecific neighbors in target–neighbor pairs of plants of different age and separated by different distances (Purves and Law 2002), and fitted a dynamic competition kernel that was a simple function proportional to the logarithm of neighbor size and decreasing with distance. This approach has been carried forward in even-aged multi-individual stands of *A. thaliana*, where competition was found to increase with plant size and to attenuate rapidly at distances of only a few centimeters (Schneider et al. 2006). These two studies experimentally tested basic assumptions of complex theoretical models in a simple and straightforward way. However, they focused on monospecific stands and there are only a few experiments that have measured heterospecific competition kernels. In a rare multi-species example, the zones of influence for two competing weed species were found to differ, both within and between species (Pacala and Silander 1990); but in this case the authors concluded that, because of weak aggregation and enormous plasticity, a non-spatial model summarized the community dynamics sufficiently well.

Theory has shown that it is important to address the question of whether neighborhood sizes differ for con- vs. heterospecific neighbors. Most theory has so far assumed symmetric neighborhoods within and between species, i.e. equal interaction distances. However, relaxing this assumption—i.e. allowing the spatial scales of within- and between-species interactions to differ, while assuming equal interaction strength, integrated over all distances—can have profound consequences for community dynamics (Murrell et al.

2002; Murrell and Law 2003). Murrell and Law (2003) proposed the term heteromyopia for plant individuals that are “short-sighted” in sensing neighbors of other species relative to their own, and showed how this may be sufficient to allow an otherwise weaker competitor to invade a population of a superior species.

Spatially explicit individual-based models use so-called competition kernels to describe how the strength of competitive interactions declines with distances (c.f. fig. 1). Theory typically uses competition kernels that sum to one with the overall intensity scaled by a separate parameter, the competition coefficient. The competition coefficient allows one to separate out shape effects of the competition kernel from the per-capita effect of a competitor. Modeling competition kernels this way means that if individuals are arranged randomly across the landscape, the outcome of competition only depends on the magnitude of the scaling coefficients (in other words, the mean-field model is recovered (Murrell and Law 2003)). One can therefore think of a competition kernel as a probability density function, covering an area of 100% competition (the ecological neighborhood *sensu* Antonovics and Levin (1980)). Multiplying the competition kernel by the competition coefficient raises or lowers the entire surface of the kernel and results in the actual function describing the strength of competition. In order to get larger within than between species interaction distances, the intraspecific competition kernel should be of a platikurtic shape and the interspecific one of a leptokurtic shape, which forces the two kernel functions to cross (fig. 1). The key feature of heteromyopia is that interspecific interactions must be more intense than intraspecific interactions at short distances, whereas at longer distances, this relationship should be reversed. This pattern promotes coexistence by allowing conspecific clusters to build up, which leaves gaps in the landscape for other species to exploit; and the species remain segregated because of the rapid removal nearby heterospecific neighbors (Murrell and Law 2003; Snyder and Chesson 2004). Other outcomes are possible, and there is now a growing body of theory that shows how different scales for conspecific and heterospecific interactions may influence the outcome of competition (Murrell et al. 2002; Murrell and Law 2003; Snyder and Chesson 2004; Snyder 2008); yet its relevance to real communities remains an open question, and to our knowledge, heteromyopia has not been tested.

The present experiment aimed to help close the gap between theory and data and to evaluate potential differences in within- and between-species interaction distances. Competition in nature results from a complex interplay of components, such as neighbor number, size, identity and distance. To advance our understanding of local competition, one has to reduce this complexity to its components and to vary these experimentally (Purves and

Law 2002; Ramseier and Weiner 2006). Greenhouse experiments allow to control for environmental heterogeneity and to isolate the actual effects of the components in focus from natural complexity. We examined the most basic elements of individual-based models by studying pair-wise interactions addressing resource competition. In a target–neighbor competition experiment, we combined target individuals of four herbaceous grassland species with either a con- or a heterospecific neighbor at several distances and compared performance with control plants grown in isolation. We expected neighbor individuals to have a negative effect on target individuals and the strength of this effect to decline with distance. We hypothesized that, if species are not equal (as opposed to neutral, e.g. Bell 2000; Hubbell 2001), the competitive response to con- and heterospecific neighbors and the distances over which con- and heterospecific neighbors compete should differ from each other. If heteromyopia contributes to coexistence, conspecific neighbors should compete over longer distances than heterospecific neighbors, and interspecific competition should be more intense at close distances but decline more rapidly with distance compared to intraspecific competition. Finally, we examined the importance of neighbor identity in relation to neighbor size.

Material and methods

Plant species

Heteromyopia has been hypothesized as a coexistence mechanism for similar competitors. We therefore decided to work with morphologically and ecologically similar species from diverse calcareous grasslands: *Hieracium pilosella* L. (mouse-ear hawkweed, *Asteraceae*), *Plantago lanceolata* L. (ribwort plantain, *Plantaginaceae*), *Plantago media* L. (hoary plantain, *Plantaginaceae*) and *Prunella grandiflora* (L.) Schaller et Jacq. (big self-heal, *Lamiaceae*). These species are perennial forbs, native to Europe with dry and semi-dry grasslands on alkaline soils among their main habitats. They are common, often growing together on calcareous grasslands.

Experimental design

The four experimental species were combined in two pairs (*P. lanceolata* and *P. media*; *H. pilosella* and *P. grandiflora*), representing different aspects of similarity. *Plantago lanceolata* and *P. media* are congenerics and keep a rosette growth form while *H. pilosella* and *P. grandiflora*, though taxonomically distant, share the capability of vegetative reproduction (tillers and reptant shoots, respectively). Target individuals of each plant species were either grown with a conspecific neighbor or with a heterospecific neighbor from the other species within the pair. As a control treatment, individuals of each species were grown without a neighbor. Target and control individuals were always placed at the same position within containers, and neighbors were placed at 5, 10 or 15 cm distance. This resulted in seven treatments per target species: one control treatment, three conspecific and three heterospecific neighbor treatments. Each combination was replicated four times, but for *P. media* the replicate number was reduced to three in two cases (heterospecific neighbor at 10 cm and conspecific neighbor at 15 cm distance) due to death of the target individuals after two months.

Growth conditions

The aim of our experiment was to compare intra- and interspecific competition on a local scale. Plants were therefore grown in relatively small containers (22 x 11.5 x 9 cm) to ensure competition and root contact. A total of 112 plastic containers were filled with 1.47 l substrate mixture consisting of 650 ml quartz sand (Sihelco 30, Sihelco AG, Rheinfelden, Switzerland), 170 ml sieved (2 mm) soil from a calcareous grassland and 650 ml sieved loess. Seeds were obtained from commercial Swiss ecotypes (fenaco, Winterthur, Switzerland) and directly sown into the containers (five seeds per individual's position). We used small plastic tubes to prevent relocation until primary leaves had emerged. After 24 days, all but the largest seedling at each individual's position were removed. A few individuals died during the first three weeks (nine *P. grandiflora* and three *P. media* individuals) and were replaced by transplanting separately raised seedlings. The experiment was set up in a greenhouse at the University of Basel on June 6 2006 and ran for 260 days until plant growth stopped. Replicates of all treatment combinations were equally distributed between two parallel greenhouse chambers. Within these chambers, containers were randomly placed on benches and re-randomized every three to four weeks. Plants were watered with distilled water as needed, several times a week, and from November 9 until the end of the experiment, additional lighting was supplied (16h/8h day/night regime).

Data collection

On days 27, 53, 85, 113, 182, 212, 247 and 260 after sowing, the number of leaves of all individuals and length and width of the three largest leaves were measured. Linear regressions between these measurements and above-ground biomass at harvest were used to estimate above-ground biomass during growth for control individuals. The resultant growth curves served as a description of intrinsic growth performance of the four target species (see online appendix A). After 260 days, all plants were harvested. Above-ground and below-ground biomass was separated and dry mass (48 hours at 60°C) determined per individual. We refer to above-ground biomass as measure of plant performance.

Statistical analyses

We analyzed our data focusing on three main aspects. Firstly, we estimated intra- and interspecific interaction distances based on our three experimental distances for each species separately. Secondly, we analyzed whether the average competitive response to neighbors differed between target species or neighbor identity and how the competitive response declined over distance. Thirdly, we tested whether neighbor identity effects where related to final neighbor size.

All statistical analyses were performed with the statistical program R, version 2.6.1 (R Development Core Team 2007). Data were transformed as necessary to meet the requirements of a normal distribution: Above-ground biomass of *P. lanceolata*, *P. media* and *P. grandiflora* was square root transformed for determination of interaction distances; lnRR data (description below) were square root transformed after addition of 0.25 since some values were negative.

Interaction distances

We defined interaction distance for species x on species y as the maximum distance at which the performance of an average target individual of species y growing with a neighbor of species x was significantly worse compared to an average isolated (control) individual of species y. This maximum distance is essentially measuring the zone of influence of one species on another, although in our experiment we do measure how the influence attenuates within the zone. Since above-ground biomass differed between species, we estimated intra- and interspecific interaction distances, using separate ANOVAs for each target species. These ANOVAs included neighbor treatment as factor with seven levels: one control treatment and six neighbor identity–distance treatments. We then defined the contrast matrices so that each neighbor treatment was tested against the control treatment within the separate ANOVAs. The aim of these analyses was to test whether intraspecific competition could be detected over larger distances than interspecific competition (heteromyopia).

Competitive response and neighbor distances

In order to analyze the general performance of target individuals, i.e. all species taken together, we calculated the log response ratio of each target individual based on above-ground biomass:

$$\mathrm{lnRR}_{ijd} = \ln\left(\overline{BM_i^c} \big/ BM_{ijd}^t\right)$$

where $\overline{BM_i^c}$ is the mean above-ground biomass of four control individuals of target species *i*, and BM_{ijd}^t is the above-ground biomass of a target individual of species *i* grown with a neighbor of species *j* (con- or heterospecific) at distance *d*. The log response ratio is a measure for the competitive response, i.e. how much a target individual suffered due to its neighbor (c.f. Goldberg et al. 1999; Weigelt and Jolliffe 2003). Since lnRR is standardized between all species it can be used to test for differences in average competitive response of target species to neighbor identity. We analyzed the competitive response of target individuals to their neighbors with an ANOVA testing for effects of target species, neighbor distance and neighbor identity and all second-order interactions. Greenhouse chambers differed in mean temperature and were therefore included as random block factor into the model. Since *P. lanceolata* showed no competitive response to its heterospecific neighbor (*P. media*), the analysis was performed with two data sets: Either including all four target species or with *P. lanceolata* excluded.

In these analyses, a significant interaction between distance and target species would indicate that lnRR declines differently with distance for the target species, and accordingly for a significant interaction between distance and neighbor identity. In other words, testing for distance effects means testing for differences in the slope of the respective regressions of lnRR against distance (figs. 2A, B and D). Equal slopes would indicate that identical competition kernels could be used for our species pairs. Even if the slopes were equal, different interaction distances within and between species could result, as long as the average response (or total competitive response, as in fig. 2) to con- and heterospecific neighbors differ (analogous to the competition coefficients that scale the competition kernels; fig. 2C). This would require significant main effects of target species or a significant interaction between target species and neighbor identity. A steeper slope for heterospecific than conspecific neighbors together with equal total competitive responses would result in heteromyopia (fig. 2D). Different slopes and different total competitive responses to con- and heterospecific neighbors may or may not result in different interaction distances (figs. 2A and

B). Both the slopes and the total competitive response to con- and heterospecific neighbors may differ between target species and may further depend on relative size differences between neighboring plants.

Size effects

Con- and heterospecific neighbors of three target species differed significantly in total biomass (two sample t-tests: *P. lanceolata*: $t_{22} = 6.5$, $p < 0.001$; *P. media*: $t_{20} = 3.9$, $p < 0.001$; *H. pilosella*: $t_{22} = 2.3$, $p < 0.05$). To test whether target species-specific response to neighbor identity, revealed by the ANOVA, were mainly due to such size differences, we performed the same analyses with an ANCOVA model that included final neighbor size as covariate. We used information criteria to select the best measure for neighbor size from a set of six ANCOVA models. We found the log-transformed relative total neighbor size (total neighbor biomass divided by total target biomass) to be the best measure of neighbor size. Detailed descriptions of statistical models and the model selection process are given in online appendix B.

Results

Effects of neighbor presence

Most target individuals grown with a neighbor were substantially smaller than control individuals grown alone, and the effects of neighbors decreased with distance (fig. 3). An exception was *P. lanceolata* when grown with its heterospecific neighbor *P. media*: above-ground biomass was not significantly reduced at any distance (fig 3A). In the case of *H. pilosella*, control individuals produced tillers, which resulted in substantially more above-ground biomass compared to target individuals, all staying within the rosette stage (fig 3C).

Interaction distances

We found no common pattern, i.e. intraspecific interaction distances being generally larger than interspecific interaction distances or vice versa, but rather, interaction distances seemed to be target–neighbor species-specific (fig. 3). Significant competition was still occurring at 15 cm distance in the case of *P. lanceolata* (conspecifics; fig. 3A) and *H. pilosella* (con- and heterospecifics; fig. 3C). For *P. media* interspecific competition occurred over a longer distance than intraspecific competition (10 cm, resp. 5 cm; fig. 3B), while the opposite was found for *P. grandiflora* (fig. 3D).

Average competitive response

In both ANOVAs and ANCOVAs log response ratio (lnRR) differed significantly among target species, while main effects of neighbor identity were not significant (table 1). This shows that target species differed in their average competitive response to a neighbor: *P. media* was the species most affected by its neighbors (average lnRR and standard error: 1.31 ± 0.21), followed by *H. pilosella* (1.02 ± 0.07), *P. grandiflora* (0.71 ± 0.13) and *P. lanceolata* (0.55 ± 0.10). However, there was no difference in the average competitive response to conspecific and heterospecific neighbors, i.e. all target species and neighbor distances taken together. The ANOVAs further indicated a strong interaction between target and neighbor species (table 1). However, this interaction became non-significant when neighbor size was taken into account (ANCOVAs). Thus, target–neighbor species-specific differences in competitive response were due to (species-specific) size differences between target and neighbor individuals.

Competitive response and neighbor distance

The competitive response clearly declined with neighbor distance (fig. 4). This effect was weaker when neighbor size was taken into account, which indicates some correlation of neighbor size with distance (c.f. F-values ANOVA vs. ANCOVA, table 1). Still, a neighbor, growing to a given size, became significantly less important the further away it was. The ANOVA revealed a significant interaction between target species and distance when data from all four species were used, which vanished when *P. lanceolata* was excluded (table 1). The cause therefore was that the competitive response of *P. lanceolata* did not decline with distance when grown with a conspecific neighbor and even increased with distance when grown with a heterospecific neighbor (fig. 4). We found no significant interaction between neighbor identity and distance. Thus, all species taken together, lnRR decreased equally over distance for con- and heterospecific neighbors, although we note that the variability of lnRR was substantially larger with heterospecific neighbors than conspecific neighbors, especially at close distances (fig. 4).

Size effects

Relative neighbor size was highly significant as a covariate (table 1 and fig. 5) and accounted for 70% of total variance, whether *P. lanceolata* was included or not. This was also reflected in the much better fit of all ANCOVA models compared to the ANOVA model when selecting for the best covariate (online appendix B). We found significant interactions between relative neighbor size and both target species and neighbor identity (fig. 5). Thus, not only did species differ in their average competitive response to a neighbor (main effect of target species), but also in how the strength of the competitive response scaled with relative neighbor size (fig. 5A). Moreover, the relative strength of the competitive response to con- and heterospecific neighbors changed with relative neighbor size (fig. 5B). While target individuals had a stronger response to heterospecific neighbors than to conspecific neighbors when the neighbors were smaller than the target, this relationship was reversed for neighbors being larger than the target individuals (note that the lines in fig. 5B cross at relative neighbor size around 1 (0 on the log-scale)). In other words, with increasing relative neighbor size, conspecific neighbors became more important than heterospecific neighbors.

Discussion

The central goal of this investigation was to close the gap between theory and data in spatial plant ecology by investigating species-specific interactions between neighboring pairs of individuals. Such individual-level processes influence population and community dynamics (Grimm and Railsback 2005), and depend upon the spatial distance and the size differences between individuals and also upon their species identity. All of these variables have been incorporated into at least some theory for neighborhood competition in plants (e.g. Bolker and Pacala 1999; Law et al. 2001; Murrell and Law 2003; Snyder and Chesson 2004; Murrell 2009), and yet there is very little empirical information on how important each of these neighbor components are in determining the intensity of competition between two neighboring individuals. As we will discuss below, our investigation yielded three main results: (1) that there was no general pattern of within- and between-species interaction distances and consequently no evidence for heteromyopia; (2) that species-specific relative size differences between neighboring plants are likely to be key factor determining the intensity and distance of competitive interactions; and (3) that a conspecific neighbor may be more important than a heterospecific neighbor but only as the neighbor becomes very large compared to the target individual.

Interaction distances

Theory has shown that differences between pair-wise intra- and interspecific interaction distances can have profound consequences at the population and community level. The two defining features of the coexistence mechanism known as heteromyopia are for (1) interspecific competition to occur over shorter distances than intraspecific competition (Murrell et al. 2002; Murrell and Law 2003); and (2) that interspecific interactions are more intense than intraspecific interactions at short distances, whereas at longer distances, this relationship is reversed (c.f. fig. 1). However, our experiment revealed no empirical evidence for heteromyopia. The distances over which intra- and interspecific competition could be detected varied substantially but we found no general pattern, e.g. intraspecific interaction distances being larger than interspecific interaction distances. We found larger intra- than interspecific interaction distances only for the stronger competitors within each species pair, that is the species least affected by their neighbors; and we found no evidence for a reversal of the relative importance of intra- and interspecific competition at larger distances.

Within each of our two species pairs, one species turned out to be a stronger competitor than the other (namely *P. lanceolata* and *P. grandiflora*), and as a neighbor, resulted in larger interaction distances than the other species. These results are in accordance with a previous competition study on weed species, where neighbors of the stronger competitor affected growth of a focal plant over larger distances than neighbors of the weaker competitor (Pacala and Silander 1990). The competitive hierarchy between neighboring plants rather than identity per se might thus determine interaction distances. According to this, a neighbor that exerts a large competitive effect (c.f. Goldberg and Fleetwood 1987) will result in relatively large interaction distances, irrespective of a target's species identity, and this is probably due to a species' competitive ability often being correlated with average final plant size (Freckleton and Watkinson 2001). At the same time, a competitively tolerant target individual that shows a small competitive response will experience relatively small interaction distances, irrespective of a neighbor's species identity. Our study further revealed that the absolute distances over which competition persisted also depended on, and differed between, target species. Several studies have shown that competitive effect and response are not correlated (Goldberg and Landa 1991; Cahill et al. 2005; Fraser and Miletti 2008), and target–neighbor species-specific interaction distances might therefore result from different combinations of competitive abilities to suppress and tolerate neighbors.

Another spatial process, potentially maintaining coexistence, is intraspecific aggregation, whereby individuals mainly compete with conspecifics. It has been shown that intraspecific aggregation slows down the competitive exclusion of inferior species in annual (Stoll and Prati 2001; Monzeglio and Stoll 2005; Monzeglio and Stoll 2008) and perennial herbaceous species (Schmidt 1981). Besides reducing the frequency of interspecific interactions, intraspecific aggregation can enhance the local abundance of weak competitors and reduce that of strong competitors. This is because intraspecific competition is weaker than interspecific competition for inferior species and vice versa for superior species. Our findings are in accordance with this: the competitively inferior species did better with a conspecific neighbor, while the opposite was found for the competitively superior species. However, theory suggests that on its own, within-species aggregation and between-species segregation is insufficient to generate stable coexistence, i.e. expected recovery of all species from a low density, since the stronger species will still over-run clusters of the weaker species when they meet in space (Neuhauser and Pacala 1999).

If heteromyopia was a general coexistence mechanism we should have discovered a strong signal, independent of the biology of the investigated species. It has been hypothesized that heteromyopia might be aided by mechanisms that indirectly shape the competition kernels (Murrell and Law 2003). These might include host-specific vectors, such as specialist pathogens, herbivores or seed predators (Janzen 1970; Connell 1971), host-specific mycorrhizal fungi (Stoll and Newbery 2005) or allelopathy. In our experiment, host-specific enemies were excluded, our species associate with arbuscular mycorrhizal fungi (much less host-specific than e.g. ectomycorrhizal fungi), and the frequency and importance of allelopathy in plant–plant interactions is so far still widely unknown. Therefore, we assume that direct neighbor interactions, mainly belowground competition, dominated in our experimental system. From our results, we conclude that if heteromyopia should prove to be a general coexistence mechanism, it probably does not result from resource competition. Whether this conclusion can be generalized to other sessile communities beyond plants remains an open question. However, Noda (2009) suggested that heteromyopia is unlikely to operate in rocky intertidal sessile assemblages because neither host-specific enemies nor allelopathy have been reported from these assemblages.

Neighbor identity versus neigbor size

Our results clearly showed the performance of target individuals to be inhibited by the presence of a neighbor, and that the competitive response to it declined with distance. Species differed in how strongly they responded to their con- and heterospecific neighbors, but these neighbor identity effects were mainly due to species-specific size differences. Including neighbor size substantially increased empirical support of the statistical models (c.f. online appendix B). It is interesting to note that the size of the neighbor relative to the target individual, rather than the absolute size of the neighbor explained most variation in the results; and this emphasizes the importance of taking on the “plant’s eye view” (Turkington and Harper 1979) when examining and modeling plant–plant interactions.

The question whether competitive strength is determined by neighbor size or by neighbor identity has been investigated previously for three dune species in competition experiments using seedlings and adult plants (Weigelt et al. 2002). Competition intensity was analyzed for its relation with final neighbor size and neighbor identity, and the authors concluded that competition intensity generally depends on species-specific traits, such as biomass allocation strategies, while size differences are important only at early life stages, such as seedling establishment. This stands in contrast to our experiment where size differences between neighboring adult plants accounted for 70% of the variability in competitive response. One explanation for this disparity is that in our study plants were sown in pairs and grown together for the duration of the whole experiment. It could well be that differences in germination speed and species-specific growth rates have lead to differences in size at early life-stages. These differences might even have increased, during the course of our experiment (c.f. online appendix A).

It has been suggested that coexisting plant species are those that are equivalent in competitive ability for shared resources (Aarssen 1983). Consequently, competitive effects should be equivalent on a per-unit-size basis, but not necessarily on a per-individual basis since species vary greatly in average size. Goldberg and Werner (1983) have argued that competitive equivalence per-unit-size could be expected for three reasons: (1) all plant species compete for the same few resources; (2) individuals of any particular species-pair have a low encounter probability; and (3) competitive interactions are predominated by size asymmetries between individuals, so that if a neighbor is larger than a target individual, then the identity of the neighbor is of much lesser importance. This argument is supported by the results of an earlier comparison of competitive effects of seven plant species on *Solidago canadensis* (Goldberg 1987), and our results are similar in that strong neighbor effects were primarily due to species-specific differences in size.

Can we therefore conclude that on a per-unit-size basis species are ecologically equivalent? Our results provide evidence both for and against this. We found no difference in the average response to con- and heterospecific neighbors, when all species and neighbor sizes were taken together. Similarly, averaged over all species, there was no difference in how competitive response to con- and heterospecific neighbors declined with distance. This would imply that equal competition kernels could be used to model intra- and interspecific interactions. On the other hand, species differed in how their response scaled with neighbor size: The competitive response of *P. media* increased most rapidly with neighbor size and that of *P. lanceolata* least rapidly. This non-equivalence of species might be partly due to species-specific biomass allocation strategies. Moreover, when all species were taken together, the competitive response to conspecifics increased more rapidly with neighbor size than the competitive response to heterospecifics. Relative size differences between neighboring plants should therefore be accounted for by additional scaling parameters, allowing for flexible intra- and interspecific competition coefficients.

Size–identity interaction

A nearby neighbor that is much larger will have a large negative effect on an individual, regardless of its' species identity. However, our results suggest that there might be a general interaction between neighbor size and identity. Considering all species together, we found that the competitive response of a target individual was independent of neighbor identity, as long as the neighbor was of equal size or only slightly larger, but with increasing size differences, individuals became more sensitive towards conspecific neighbors (c.f. fig. 5B). If such a size–identity interaction should be frequently found in empirical data, this could have important implications for community dynamics. For example, it may well affect seedling establishment, making establishment near a heterospecific of a given size more likely than establishment near a conspecific. As has been shown repeatedly for tropical trees (e.g. Harms et al. 2000), seedling establishment near heterospecifics is often more likely compared to establishment near conspecifics. Moreover, our data suggest that a size–identity interaction could further influence the performance of individuals at later stages. Both processes may promote coexistence and help maintain community diversity. Specific target–neighbor experiments, combining seedlings and adult plants, would be needed to test this hypothesis.

Conclusions

As with every experiment, there are trade-offs between controlling for environmental variability and experimental artificiality. Plants in our experiment were grown in relatively small containers, in homogenous substrate, and in the greenhouse without natural enemies and climatic stress. Furthermore, our neighborhoods consisted of a single neighbor—a very unlikely situation in calcareous grasslands. Nevertheless, individual-based models are built upon such pair-wise neighbor-interactions, and the aim of our study was to experimentally test these basic elements of spatial theory. Bearing in mind these caveats, our study provided empirical evidence that both the intensity of competitive interactions and the distance over which these occur are primarily determined by the relative size differences between neighboring plants, irrespective of their con- or heterospecific identity. Species-specific size differences between individuals, most likely related to species-specific life–history traits, account for effects of neighbor identity. Discovering the various life-history traits that are associated with large or small neighborhood ranges is an important next step in uncovering the crucial processes that determine plant community structure and dynamics. Future research should also focus on the dynamics of the patterns observed in our experiment. For example, investigating the onset of competition and how this relates to species identity and size differences between neighbors would foster our understanding of the underlying processes of competition. Moreover, the observation that conspecific interactions may become more important than heterospecific interactions if size differences are large reveals the complex nature of size-based competition, and points to new processes that need to be explored by theoretical models.

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Table 1: Results of ANOVA versus ANCOVA testing for effects of neighbor size (CoV), target species (TG), neighbor distance (D: 5, 10 or 15 cm), neighbor identity (NB: conspecific or heterospecific) and pair-wise interactions on the log response ratio of target individuals of perennial forbs from calcareous grasslands.

	ANOVA +Pl		ANCOVA +Pl		ANOVA -Pl		ANCOVA -Pl	
Source	d.f	F	d.f.	F	d.f.	F	d.f.	F
Chamber[a]	1	1.9	1	4.6 *	1	0.4	1	1.1
CoV[b]			1	308.8 ***			1	214.6 ***
TG	3	9.5 ***	3	6.1 ***	2	5.4 **	2	6.6 **
D	1	23.2 ***	1	5.3 *	1	28.5 ***	1	5.6 *
NB	1	1.4	1	0.1	1	1.4	1	0.2
CoV x TG			3	3.6 *			2	4.6 *
CoV x D			1	0.2			1	2.8
CoV x NB			1	5.3 *			1	4.4 *
TG x D	3	4.2 **	3	2.3	2	0.8	2	0.5
TG x NB	3	12.1 ***	3	2.1	2	6.7 **	2	0.7
D x NB	1	2.3	1	0.7	1	0.8	1	0.1
Residuals	80		74		59		54	

Note: Log response ratio was calculated as $\ln\mathrm{RR}_{ijd} = \ln\left(\overline{BM_i^c} / BM_{ijd}^t\right)$ where $\overline{BM_i^c}$ is the mean above-ground biomass of four control individuals of target species *i*, and BM_{ijd}^t is the above-ground biomass of a target individual of species *i* grown with a neighbor of species *j* (con- or heterospecific) at distance *d*. Data included either all four target species (+Pl) or *Plantago lanceolata* was excluded (-Pl). Degrees of freedom (d.f.) and F-values (F) are shown

[a] Greenhouse chamber was included as random factor.

[b] Covariate: Log-transformed relative neighbor size (total neighbor biomass divided by total target biomass).

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

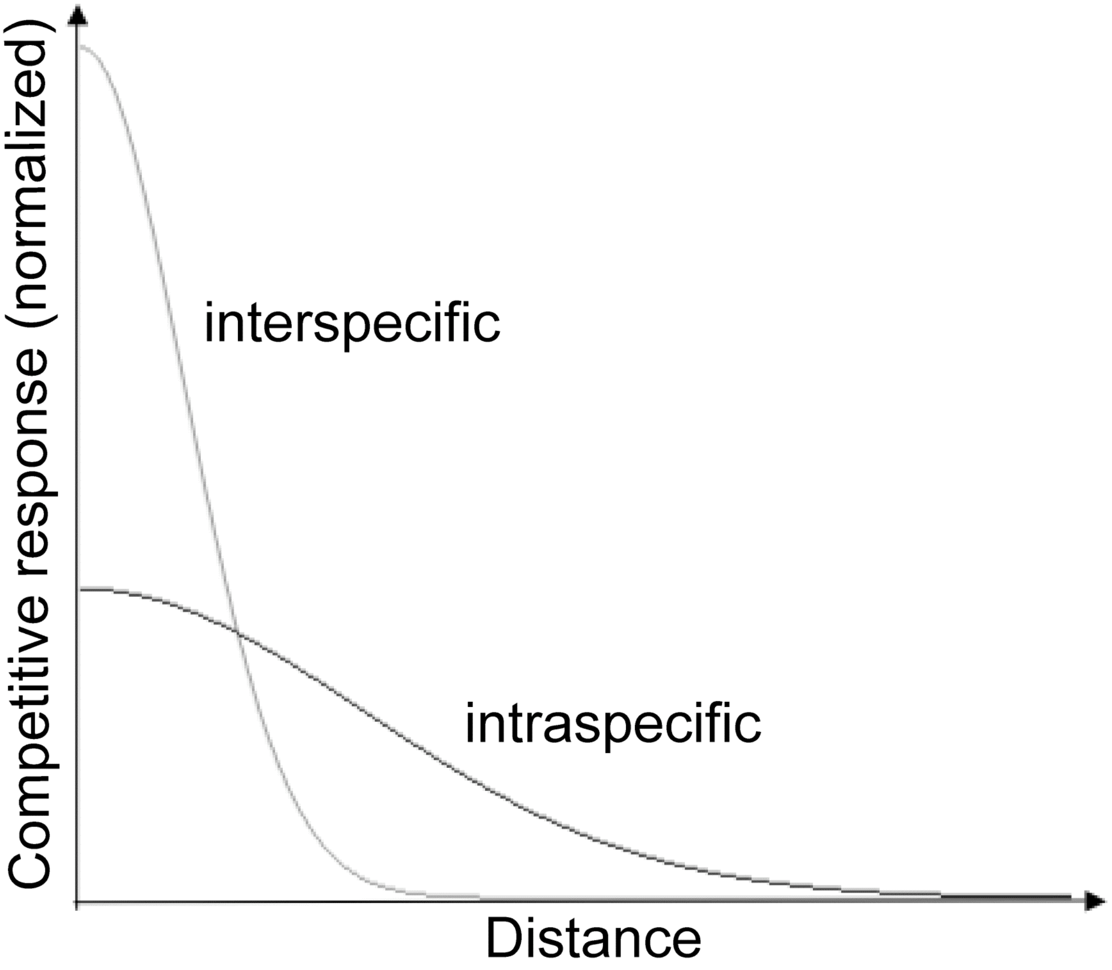

Figure 1: Two competition kernels for intra- and interspecific competition that lead to heteromyopia. A leptokurtic kernel results in a short interaction distance (interspecific competition), while a platikurtic kernel results in a large interaction distance (intraspecific competition). Since the kernels are normalized to sum to 1, i.e. the areas below the two curves are the same, the functions must cross.

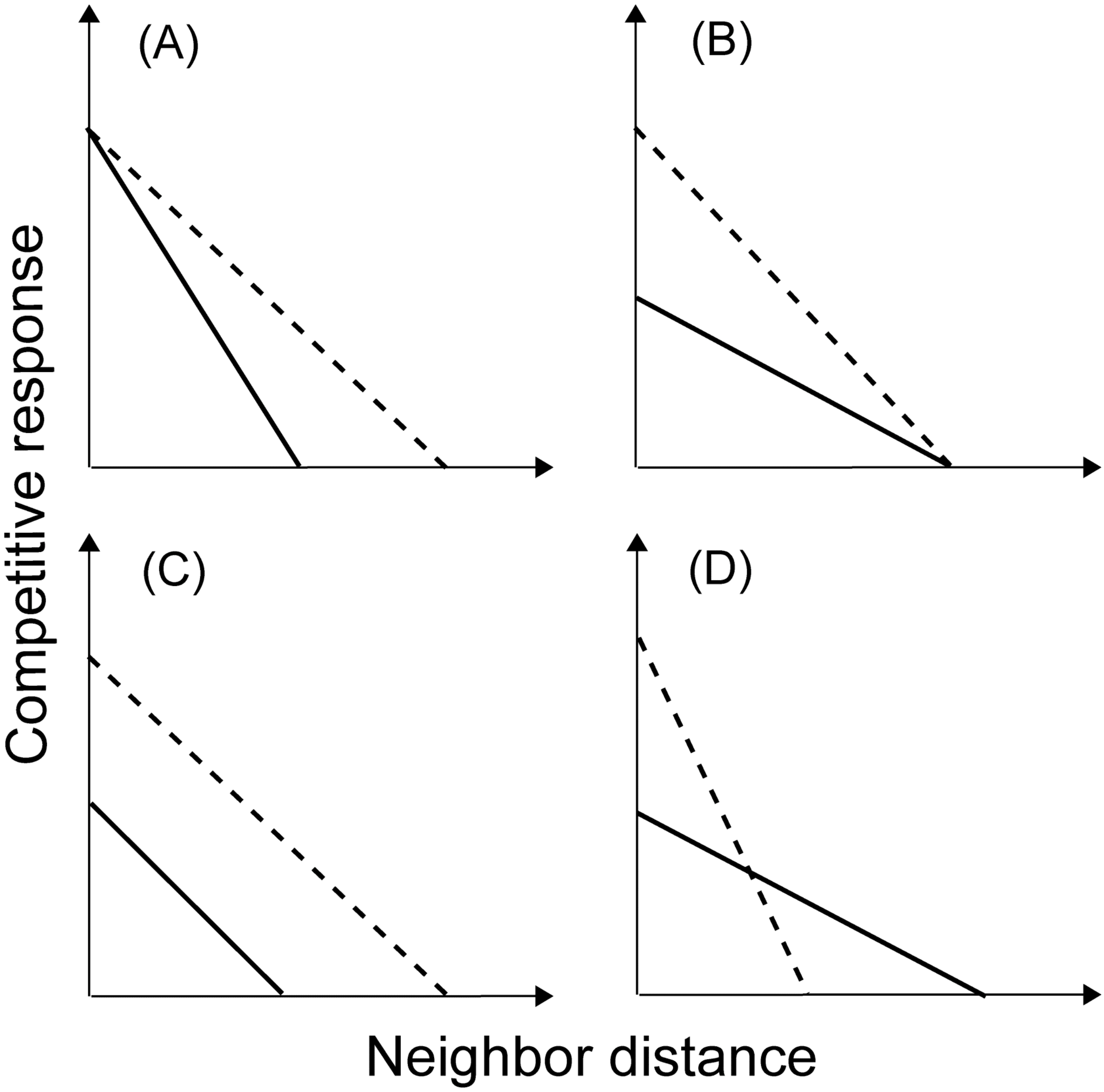

Figure 2: Hypothetical relationships between the slopes, describing how the competitive response to a neighbor declines with distance, and the total competitive response to a neighbor. Differences in slopes and total competitive response may or may not result in different interaction distances. The total competitive response to a neighbor, integrated over all distances, corresponds to the area below the lines (triangle). The different lines (straight and broken) may represent different target species, con- and heterospecific neighbors, or neighbors of different relative sizes. Assumptions are: (A) different slopes, different total competitive responses, resulting in different interaction distances; (B) different slopes, different total competitive responses, resulting in equal interaction distances; (C) equal slopes, different total competitive responses, resulting in different interaction distances; (D) different slopes, equal total competitive responses, resulting in different interaction distances.

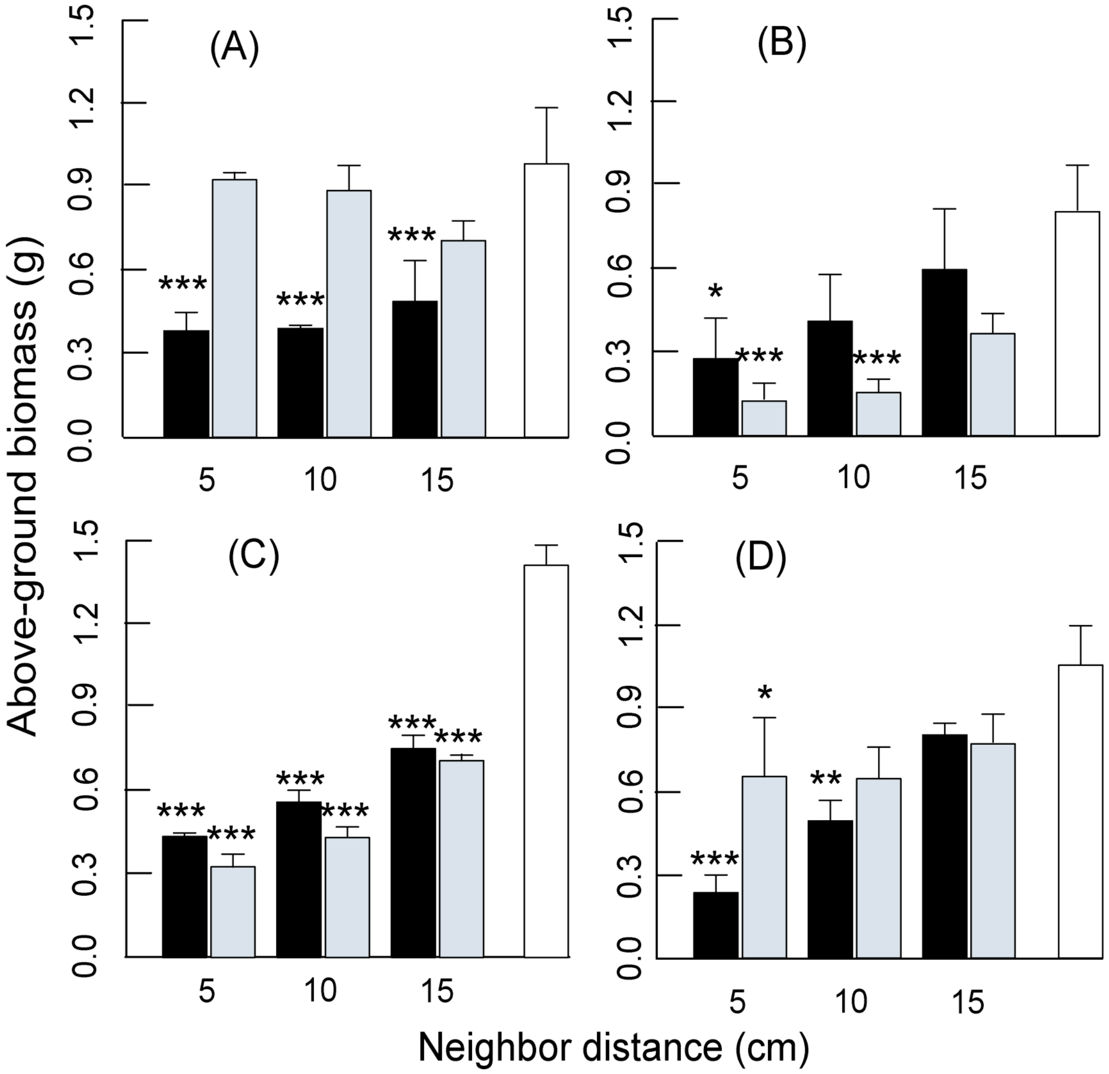

Figure 3: Mean above-ground biomass and estimated intra- and interspecific interaction distances of *Plantago lanceolata* (A), *Plantago media* (B), *Hieracium pilosella* (C) and *Prunella grandiflora* (D). Target individuals were grown with a conspecific neighbor (black bars) or with a heterospecific neighbor (grey bars) at different distances or without neighbor (control; white bars). Heterospecific neighbor species were: *P. lanceolata* for *P. media* and vice versa, *H. pilosella* for *P. grandiflora* and vice versa. Error bars show one standard error (n = 4; except for *P. media* with heterospecific neighbor at 10 cm and conspecific neighbor at 15 cm where n = 3). Asterisks above black and grey bars indicate significant differences between control and neighbor treatment based on per-species ANOVAs with treatment-contrasts. P-values are * < 0.05, ** < 0.01 and *** < 0.001.

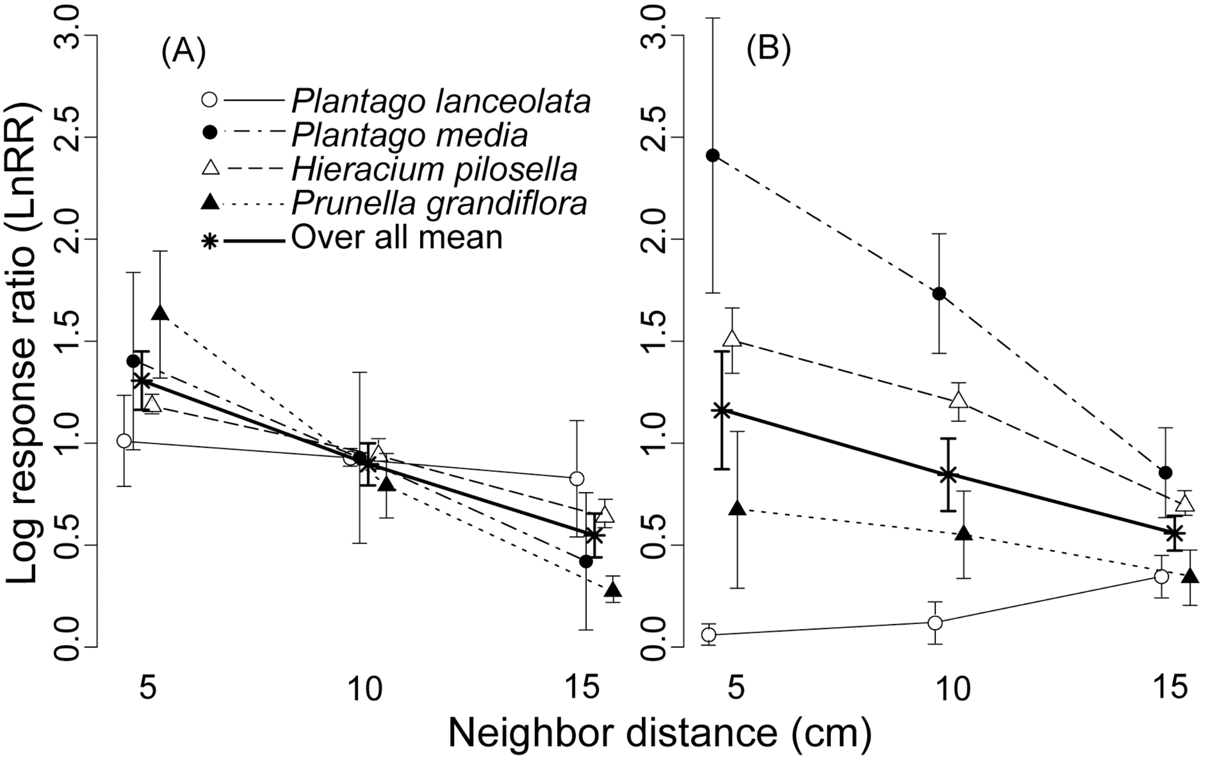

Figure 4: Decrease of mean log response ratio of target individuals of four perennial forbs from calcareous grasslands with distance of (A) conspecific neighbors or (B) heterospecific neighbors. Heterospecific neighbor species were: *P. lanceolata* for *P. media* and vice versa, *H. pilosella* for *P. grandiflora* and vice versa. Error bars show ± one standard error. Log response ratio was calculated as $\ln\mathrm{RR}_{ijd} = \ln\left(\overline{BM_i^c}/BM_{ijd}^t\right)$ where $\overline{BM_i^c}$ is the mean above-ground biomass of four control individuals of target species *i*, and BM_{ijd}^t is the above-ground biomass of a target individual of species *i* grown with a neighbor of species *j* (con- or heterospecific) at distance *d*.

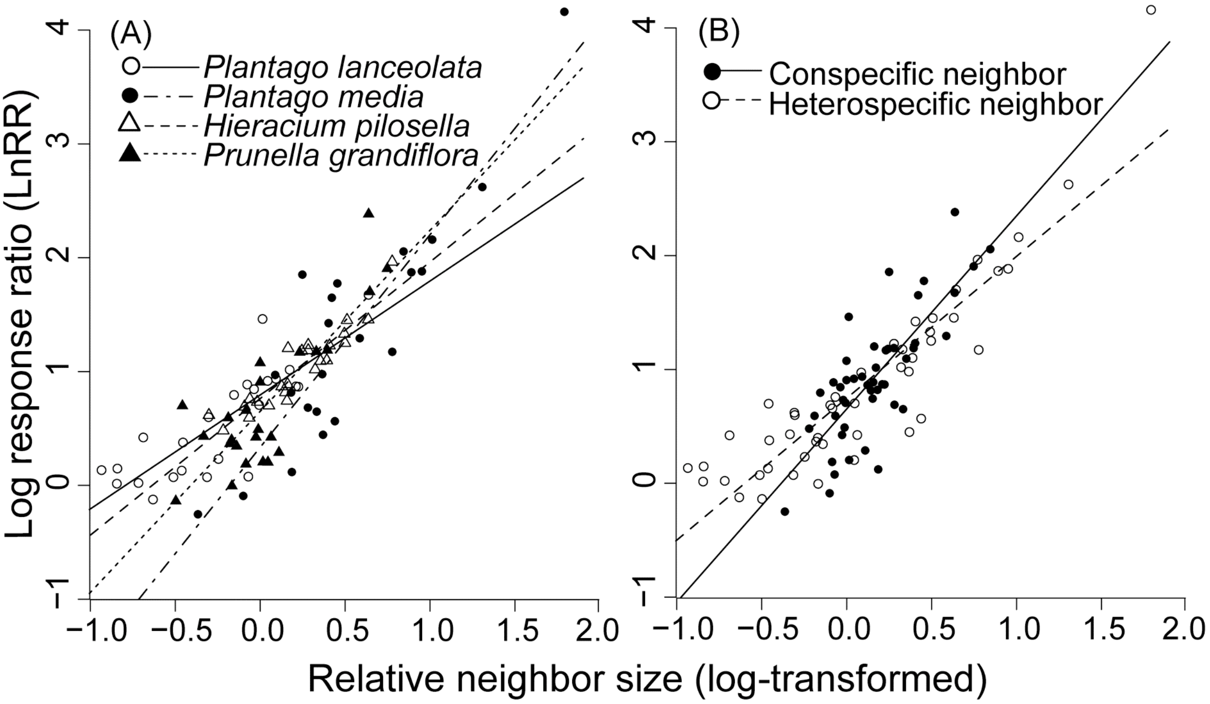

Figure 5: Log response ratio of target individuals versus relative size of neighbors (pooled over distances) of four perennial forbs from calcareous grasslands (A) by target species and (B) by neighbor identity. Linear regression lines are shown. Regressions differed significantly ($p < 0.05$) both between (A) target species and (B) neighbor identity, according to ANCOVA presented in table 1. Log response ratio was calculated as $\mathrm{lnRR}_{ijd} = \ln\left(\overline{BM_i^c} \big/ BM_{ijd}^t\right)$ where $\overline{BM_i^c}$ is the mean above-ground biomass of four control individuals of target species *i*, and BM_{ijd}^t is the above-ground biomass of a target individual of species *i* grown with a neighbor of species *j* (con- or heterospecific) at distance *d*. Relative neighbor size is total neighbor biomass divided by total target biomass.

Online Appendix A. Growth curves of control plants.

We estimated above-ground biomass during growth for control individuals using linear regressions between above-ground biomass and trait measurements (number of leaves, length and width of the three largest leaves) of all experimental plants at harvest. We found mean leaf length of the three largest leaves multiplied with the total number of leaves to be the best predictor for above-ground biomass ($p < 0.001$ for all species). Regression coefficients (r^2) between measured and estimated above-ground biomass at harvest were: 0.70 (*P. grandiflora*), 0.80 (*P. lanceolata*), 0.84 (*P. media*) and 0.95 (*H. pilosella*).

Based on estimated above-ground biomass (fig. A1), we fitted logistic growth functions. We use them as a description of intrinsic growth performance of the four target species, i.e. growth in the absence of competition. For the first two dates, biomass was underestimated (negative biomass) and was therefore set to zero. The paired species were tested for differences in point of inflection—i.e. the number of days, after which half of the asymptote was reached—, a measure for growth speed. *Plantago lanceolata* grew significantly faster than *P. media* ($t_6 = 2.65$, $p = 0.038$) and *H. pilosella* grew significantly faster than *P. grandiflora* ($t_6 = 2.49$, $p = 0.047$).

Within each of the two combined species pairs, one species turned out to be a stronger competitor than the other (namely *P. lanceolata* and *P. grandiflora*). Differences in early growth rates can result in size differences between species, leading to rapid resource depletion for a faster growing species. This may have been the case for the paired *Plantago* species. However, the growth curves in isolation could not describe the results for the interactions between *H. pilosella* and *P. grandiflora* since *H. pilosella* had a faster growth rate than *P. grandiflora* but *P. grandiflora* turned out to be the superior competitor. We speculate that above-ground and below-ground biomass are not linearly correlated with each other during growth, which means the growth curves based on above-ground biomass may have missed an important aspect of the “race-for below-ground resources”.

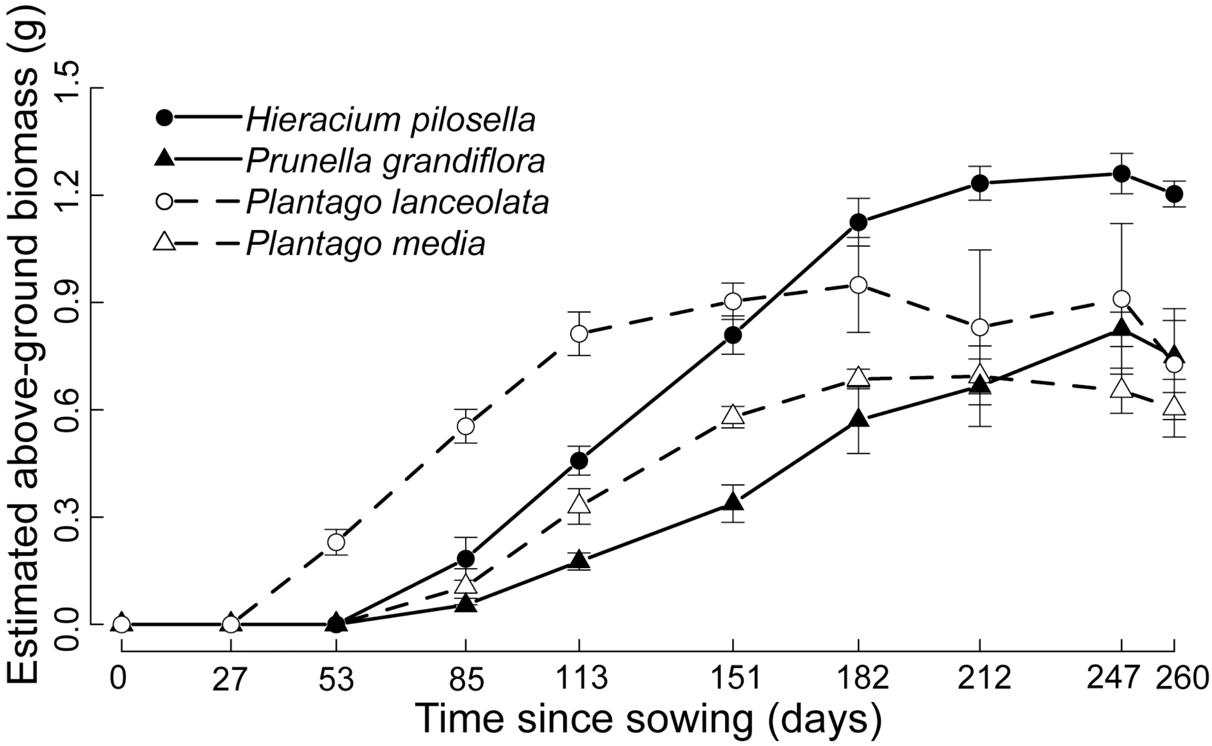

Figure A1: Growth curves based on estimated above-ground biomass of control individuals of four perennial forbs from calcareous grasslands grown without neighbors. Data points show mean values ± one standard error (n = 4).

Online Appendix B. Model selection using information criteria

We analyzed the competitive response of target individuals to their neighbors with an ANOVA testing for effects of target species, neighbor distance and neighbor identity and all second-order interactions. Since *P. lanceolata* showed no competitive response to its heterospecific neighbor (*P. media*), the analysis was performed with two data sets: Either including all four target species, or with *P. lanceolata* excluded. Neighbor species differed in mean biomass. To test whether target species-specific responses to neighbor identity were mainly due to such size differences, we explored six additional statistical models that included final neighbor size as covariate (ANCOVA models; table B1). We compared neighbor below-ground biomass and neighbor total biomass (sum of above-ground and below-ground biomass) as measures of neighbor size. Covariates were: Absolute neighbor size (neighbor biomass; models BelAbs and TotAbs in table B1), relative neighbor size (neighbor biomass divided by target biomass; BelRel and TotRel) and the logarithm of relative neighbor size (LogBelRel and LogTotRel). Hence, for each data set we compared a set of seven statistical models.

We used information criteria to select the best model, i.e. the one out of our seven candidate models that represents our data with the largest likelihood. When sample size is small with respect to the number of estimated parameters, which was the case in our analyses, it is recommended to use an AIC adjusted for small-sample bias (Burnham and Anderson 2002). We therefore calculated the second-order $\mathrm{AIC_c}$ after Hurvich and Tsai (1989) that includes a correction factor for the sample size and the number of estimated parameters and is given by

$$\mathrm{AIC}_c = \mathrm{AIC} + \frac{2K(K+1)}{n-K-1}$$

where n is sample size and K is the number of estimated model parameters. We calculated AIC_c differences between each model (i) and the model with the lowest AIC_c value (min)

$$\Delta_i = \mathrm{AIC}_{c\,i} - \mathrm{AIC}_{c\,min}$$

to estimate the level of empirical support for each model. The larger Δ_i is, the less plausible it is that model i is the best model for the given data. Models with $\Delta_i > 10$ have essentially no support, or, in other words, fail to explain substantial variation in the data (Burnham and Anderson 2002). We further calculated “Akaike weights”

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}$$

where the numerator is proportional to the likelihood of model *i* and the denominator is proportional to the sum of all model likelihoods of a set of *R* models. A given w_i is considered as the weight of evidence in favor of model *I* being the best model for the given data given that one of the *R* models must be the best model of that set of models (Burnham and Anderson 2002). Akaike weights thus represent the normalized relative likelihoods of all *R* models and sum up to 1.

Out of our seven candidate models, the model which included log relative neighbor size based on total biomass (LogTotRel) was by far the best model, irrespective of whether data included *P. lanceolata* or not (table B1). There was essentially no empirical support for any of the other six models ($\Delta_i > 10$). Moreover, the best model (LogTotRel) had a w_i of virtually 1. The ANOVA model, not taking neighbor size into account, obtained least empirical support of all candidate models. In general, we found less support for the models that used only below-ground neighbor biomass as size measure (BelAbs, BelRel, LogBelRel) compared to the corresponding models that included total neighbor biomass (TotAbs, TotRel, LogTotRel). Finally, the models that related neighbor size to target individual size (BelRel, LogBelRel, TotRel, LogTotRel) performed much better than those models that included absolute neighbor size (BelAbs, TotAbs).

From these findings we can derive three major conclusions: 1) Neighbor size is of crucial importance in pair-wise neighbor interactions. 2) Neighbor size both above and below ground should be taken into account to accurately describe the competitive response of a target individual to its neighbor. That is, processes related to above-ground and below-ground competition together shape the strength of neighborhood interactions. 3) It is the size of a neighbor *in relation* to the size of the target individual that determines the competitive response. Neighbor size therefore should be described from the “target plant’s view”.

Table B1: Comparison of statistical models analyzing the log response ratio of target individuals to their neighbors of four perennial forbs from calcareous grasslands. The best model, highlighted in bold, was selected using information criteria.

		All target species			*P. lanceolata* excluded		
Model	K	AIC$_c$	Δ_i	ω_i	AIC$_c$	Δ_i	ω_i
ANOVA	9	21.4	69.5	0.0000	29.9	57.8	0.0000
BelAbs	13	13.6	61.7	0.0000	20.3	48.2	0.0000
BelRel	13	-11.6	36.5	0.0000	4.9	32.8	0.0000
LogBelRel	13	-28.5	19.6	0.0001	-9.9	18.0	0.0001
TotAbs	13	13.2	61.3	0.0000	25.0	52.9	0.0000
TotRel	13	-20.0	28.1	0.0000	-1.7	26.2	0.0000
LogTotRel	**13**	**-48.1**	**0.0**	**0.9999**	**-27.9**	**0.0**	**0.9999**

Note: The number of model parameters (K), second-order AIC values (AIC$_c$), AIC$_c$ differences (Δ_i) and Akaike weights (ω_i) are shown. The ANOVA model included target species, neighbor distance and neighbor identity as explanatory variables; greenhouse chamber was included as random factor. The other six models were ANCOVA models consisting of the ANOVA model and one covariate incorporating neighbor size. BelAbs: Absolute below-ground neighbor size (neighbor below-ground biomass); BelRel: Relative below-ground neighbor size (neighbor below-ground biomass divided by target below-ground biomass); LogBelRel: Log of relative below-ground neighbor size; TotAbs: Absolute total neighbor size (total neighbor biomass); TotRel: Relative total neighbor size (total neighbor biomass divided by total target biomass); LogTotRel: Log of relative total neighbor size.

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Chapter 4: Arbuscular mycorrhizal fungi reduce effects of size differences between neighbouring plants

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Manuscript in preparation.

Abstract

Competitive interactions between plants usually occur over rather short distances. Theory has shown that the scale of these interaction distances may be crucial for plant population dynamics. In particular, stable coexistence can result if intraspecific interactions occur over larger distances than interspecific interactions (heteromyopia). Arbuscular mycorrhizal fungi (AMF) are well known to influence plant competition and have the potential to lengthen within and between species interaction distances. We examined how AMF influence intra- and interspecific competition over distance between species from calcareous grasslands. In a greenhouse experiment *Prunella grandiflora* and *Plantago lanceolata* target individuals were grown in isolation and with single con- or heterospecific neighbours at 5, 10 or 15 cm distance. Plants were either grown with or without AMF. Irrespective of mycorrhization level, significant competition was only found with *P. lanceolata* as neighbour, and competition did not decline with neighbour distance. The competitive response of target individuals increased with relative neighbour size. AMF significantly reduced the competitive response to a neighbour of a given size and resulted in more equally sized target and neighbour individuals. Our results suggest that AMF are unlikely to contribute to heteromyopia in our study system. However, AMF may promote coexistence by reducing size inequalities and the effects of size differences between neighbouring plants. This points out a potentially new aspect of AMF in plant–plant interactions.

Keywords: Common mycorrhizal network (CMN), coexistence, competition, heteromyopia, plant–plat interactions, spatial ecology, target–neighbour experiment.

Introduction

Explaining how large numbers of plant species are able to coexist in the light of strong resource competition remains one of the most challenging tasks in ecology. Since plants are sessile, their ecology is inherently spatial (Cousens *et al.*, 2008). Interactions between plants usually occur over rather short distances (e.g. Mack & Harper, 1977; Pacala & Silander, 1987; Purves & Law, 2002; Schneider *et al.*, 2006) and therefore, an individual's performance is mainly determined by its immediate neighbours (Antonovics & Levin, 1980; Stoll & Weiner, 2000; Murrell & Law, 2003). During the last three decades, theory has adopted this so-called "plant's-eye view" (Turkington & Harper, 1979). Classical ecological theory uses average population properties, such as population density, birth, death and growth rates. This so-called mean-field or population-level approach does not necessarily hold for plants. Spatial structure results from spatially limited dispersal and local interactions, and this can lead to individual neighbourhoods much different from mean population densities (Pacala & Levin, 1997; Stoll & Weiner, 2000; Murrell *et al.*, 2001). In contrast, individual-based ecology – a term proposed by Grimm and Railsback (2005) – explicitly focuses on the processes by which survival and growth of individuals are affected, and population and community dynamics emerge from these as a consequence. Individual-based models therefore have to make assumptions about the distances over which neighbourhood interactions occur and how these attenuate with distance (e.g. Bolker & Pacala, 1999; Murrell & Law, 2003; Snyder & Chesson, 2004).

Recent theory has shown that it is important to address the question whether intra- and interspecific neighbourhood interactions occur over different distances (Murrell *et al.*, 2002; Murrell & Law, 2003; Snyder & Chesson, 2004; Snyder, 2008). Most theory has so far assumed equal interaction distances within and between species with the consequence that spatial structure alone is often not sufficient to maintain (stable) coexistence. However, relaxing this assumption can have profound consequences for species coexistence (Murrell *et al.*, 2002; Murrell & Law, 2003). It has been shown theoretically that a competitively weaker species can invade a population of a superior species if the average distance at which conspecifics compete is longer than the average distance at which heterospecifics compete (Murrell & Law, 2003). The authors proposed the term "heteromyopia" for this mechanism, i.e. plant individuals are "short-sighted" in sensing neighbours of other species relative to their own. Under heteromyopia, intraspecific competition lowers the density of a more common species, creating small gaps that can be invaded by a rarer species, thereby facilitating coexistence (Amarasekare, 2003; Murrell & Law, 2003; Barot, 2004). Despite its potential implications for population and community dynamics, empirical evidence for heteromyopia is still outstanding (c.f. Vogt *et al.*, in press).

Most knowledge on the spatial scales of competition has been derived from neighbourhood analyses of forest systems. While some studies found no differences in con- and heterospecific neighbourhood sizes (Hubbell *et al.*, 2001; Uriarte *et al.*, 2004), other studies have shown that conspecific neighbours differ in interaction radii from heterospecific neighbours (Peters, 2003; Stoll & Newbery, 2005; Queenborough *et al.*, 2007). The spatial scales of competitive interactions in herbaceous species have been rarely investigated (but see Purves & Law, 2002; Schneider *et al.*, 2006; Milbau *et al.*, 2007), and we know of only two experimental studies that explicitly addressed the question whether intra- and interspecific competition occurs over different distances (Pacala & Silander, 1990; Vogt *et al.*, in press). Pacala and Silander (1990) found that the zones of influence for two competing weed species differed both within and between species. However, because of weak spatial aggregation and enormous plasticity, the authors concluded that a non-spatial model summarized the community dynamics sufficiently well. The first experimental test of heteromyopia examined competition between con- and heterospecific target–neighbour pairs grown at different distances (Vogt *et al.*, in press). This experiment has shown that species-specific size differences between neighbouring plants determine the strength and spatial scales of intra- and interspecific interactions. However, it revealed no evidence for heteromyopia, suggesting that heteromyopia is unlikely to result for resource competition and that additional mechanisms, indirectly affecting interaction distances, may be required. Such mechanisms may include Janzen–Connell effects (Janzen, 1970; Connell, 1971), allelopathy (Ridenour & Callaway, 2001; Gomez-Aparicio & Canham, 2008) or mycorrhizal fungi (Stoll & Newbery, 2005).

Mycorrhizal fungi associate with about 90% of all terrestrial plant species to form mycorrhizae (Smith & Read, 1997). A mycorrhiza is a symbiotic association between fungal hyphae and plant roots, in which plant photosyntates are exchanged for mineral resources acquired by the fungus from the soil (Selosse *et al.*, 2006). About two-thirds of terrestrial plants associate with fungi from the phylum Glomeromycota, the arbuscular mycorrhizal fungi (AMF) (Fitter, 2005). AMF form finely branched hyphal structures within root cells, the so-called “arbuscules”, over which phosphate and, to a limited extend, also nitrogen, potassium and zinc is exchanged for carbon (Read, 2002). However, a mycorrhiza is a multifunctional symbiosis, and AMF can provide many other benefits to their hosts than improving their nutrient supply (Fitter, 2005). AMF seem to be involved at all levels of ecosystem complexity: they have been shown to play an important role for plant–plant interactions (Hartnett *et al.*, 1993; Facelli *et al.*, 1999; Ronsheim & Anderson, 2001; van der Heijden *et al.*, 2003; Ayres *et al.*, 2006), plant population dynamics (Allsopp & Stock, 1992; Koide & Dickie, 2002), plant–herbivore interactions (Goverde *et al.*, 2000; Kula *et al.*, 2005), plant diversity (van der Heijden *et al.*, 1998; Hartnett & Wilson, 1999), ecosystem properties and processes (van der Heijden *et al.*, 1998; Rillig, 2004; Fitter, 2005), and establishment of invasive plant species (Marler *et al.*, 1999; Callaway *et al.*, 2008).

Despite their obvious impact on plant species coexistence, the role of AMF in neighbourhood interactions is still under-explored. Experimental evidence suggests that the presence of AMF does not have a consistent effects on plant competition and coexistence, but this rather seems to depend on the biological and environmental context (Umbanhowar & McCann, 2005). If co-occuring species differ in their mycorrhizal dependency, AMF can facilitate or hinder plant coexistence by reversing or emphasising competitive dominance (Grime *et al.*, 1987; van der Heijden *et al.*, 1998; Marler *et al.*, 1999). For example, in a target–neighbour experiment with two species differing in mycorrhizal dependency strong competitive effects of the competitive dominant species disappeared in the absence of AMF (Hartnett *et al.*, 1993). However, the question whether AMF influence the distances over which competitive interactions occur has so far not been addressed.

AMF might play an important part in spatial plant ecology since they operate over relatively small spatial scales (Umbanhowar & McCann, 2005). If AMF could influence the interaction distances within and between species, they might contribute to heteromyopia. We can think of two ways how AMF might influence interaction distances: either by increasing the belowground zones of influence, or by increasing the distances over which neighbouring plants “sense” each other by connecting them via common mycorrhizal networks. There is increasing empirical evidence that different AMF species and genetically distinct strains differ in their efficiency of nutrient depletion and that the benefits provided to their hosts may differ between plant species (Koide & Mosse, 2004; Fitter, 2005). If neighbouring plants are colonised by AMF that differ in their efficiency to extract nutrients from the soil, or if plant species differ in their ability to become colonised, their belowground zones of influence (a zone corresponding to the root system with reduced nutrient availability) may differ in size due to the AMF associates. Common mycorrhizal networks (CMNs) are underground networks of mycorrhizal fungi linking roots of plants of the same or different species (Selosse *et al.*, 2006). If two plants from different species provide unequal amounts of carbon to a shared fungus, and/or acquire nutrients unequally from a fungus that they both support, one species will benefit from this association to the detriment of the other (Selosse *et al.*, 2006). Similarly, carbon and nutrients might flow from “source” to “sink” plants connected via CMNs, although there is much debate about the physiological and ecological relevance of this (Robinson & Fitter, 1999; Selosse *et al.*, 2006).

Our experiment aimed to shed some light on whether AMF influence the competitive interactions between con- and heterospecific neighbours and the distances over which these occur differently. In a previous experiment the effects of single con- or heterospecific neighbours on target individuals of four herbaceous grassland species over different distances were tested (Vogt *et al.*, in press). The present experiment carried this approach forward by additionally manipulating the level of mycorrhizal colonisation. We chose the two competitively stronger plant species of our previous experiment, *Prunella grandiflora* and *Plantago lanceolata*, as target species. Target individuals were grown with a con- or heterospecific neighbour at different distances with or without AMF. The performance of target individuals was compared to control individuals grown without neighbour under the same mycorrhizal conditions. We thereby tested for AMF as potential mechanism for heteromyopia. We expected that the presence of AMF would generally increase biomass production. We hypothesized that, if AMF promote coexistence, the competitive response of target individuals to their neighbours will be smaller under mycorrhizal than under non-mycorrhizal conditions. If AMF equalise resource availability between neighbours, target and neighbour plants should be of more similar size when grown with AMF than when grown without.

Material and methods

Plant species

We worked with four perennial plant species that often grow together on diverse calcareous grasslands: *Hieracium pilosella* L. (mouse-ear hawkweed, *Asteraceae*), *Plantago lanceolata* L. (ribwort plantain, *Plantaginaceae*), *Plantago media* L. (hoary plantain, *Plantaginaceae*) and *Prunella grandiflora* (L.) Schaller et Jacq. (big self-heal, *Lamiaceae*). They are native to Europe with dry and semi-dry grasslands on alkaline soils among their main habitats. All species show high levels of mycorrhizal dependency (Grime *et al.*, 1987; Streitwolf-Engel *et al.*, 1997; van der Heijden *et al.*, 1998).

Prunella grandiflora and *P. lanceolata* were chosen as target species. In a previous experiment (Vogt *et al.*, in press), both species proved to be relatively strong competitors with intraspecific competition being stronger and occurring over larger distances than interspecific competition. Besides conspecific neighbours, two heterospecific neighbour species were assigned to each target species, consisting of the other target species and the heterospecific neighbour species from our previous experiment. The resulting heterospecific neighbour species were: *P. lanceolata* and *H. pilosella* for *P. grandiflora*, and *P. grandiflora* and *P. media* for *P. lanceolata.*

Experimental set up and growth conditions

We established two parallel target-neighbour type competition experiments with either *P. grandiflora* or *P. lanceolata* as target species. The experiments were set up in separate greenhouse chambers at the Botanical Institute of the University of Basel between May 31st and June 7th 2007. Single target individuals were planted in rectangular plastic containers, measuring 22 x 11.5 x 9 cm, with either no neighbour (control) or one neighbour of three neighbour species (conspecific and two heterospecific species) at 5, 10 or 15 cm distance. Target and neighbour individuals were placed along the central longitudinal axis at equal distances from the centre (2.5, 5 or 7.5 cm, according to the distance treatment), so that the amount of available soil was the same for target and neighbour and was kept constant over all distances. Because the position of target individuals varied between the distance treatments, controls were established for each distance separately, in order to discriminate between effects of distance and position. Plants were either grown with or without AMF. Each treatment combination was repeated five times yielding a total of 240 containers (2 target species x 4 neighbour treatments x 3 distance treatments x 2 AMF treatments x 5 replicates).

Containers were filled with 1.2 l of a 8:3:1 (v:v:v) substrate-mixture consisting of TerraGreen (Oil Dri US-special, Maagtechnic, Duebendorf, Switzerland), soil inoculum and sieved (5 mm) loess and covered with an additional 2 dl of TerraGreen. TerraGreen and loess were autoclaved twice (120°C for 2 hours). As soil inoculum we used retained substrate from a previous experiment, where the same experimental species had been grown on a non-sterilised substrate-mixture consisting of quartz sand, loess and soil from a calcareous grassland (Vogt *et al.*, *in press*). Soil inoculum for plants of the non-mycorrhizal treatment was autoclaved as well. Each container additionally received 1 dl inoculum sieving (288 g / 2 dl inoculum per litre distilled water) to adjust for microorganisms, according to Koide and Li (1989).

Seeds were obtained from commercial Swiss ecotypes (fenaco, Winterthur, Switzerland) and directly sown into containers (five seeds per position). We used small transparent plastic tubes to prevent relocation of seeds and seedlings until the primary leaves had emerged. After 19 days, seedlings were reduced to one per position. A few individuals died during the subsequent weeks and were replaced by separately raised seedlings. *Plantago lanceolata* plants of the experiment with *P. lanceolata* as target species became infected by mildew and were therefore harvested after 119 days. This was not the case in the experiment with *P. grandiflora* as target species (different greenhouse chamber), which was harvested after 183 days. Within greenhouse chambers containers were randomly placed on separate benches per AMF treatments and re-randomized every 3 weeks. Plants were watered with distilled water as needed, several times a week.

Data collection

All plants were harvested, aboveground and belowground biomass separated and dry mass (48 hours at 65°C) determined afterwards. For each target and control individual we collected a fresh root sample (three subsamples from different locations of the root system) for estimation of fungal colonisation. Fresh weights of the root sample and the remaining root system of each plant were determined at the same time, and the dry weight of the root sample was estimated afterwards according to the ratio of fresh to dry mass of the remaining root system. Ripe fruits were collected continually during the experiment. However, since only a few individuals flowered, reproductive and vegetative biomass were combined to aboveground biomass.

Root samples were proceeded, according to the protocol of Vierheilig *et al.* (1998). Roots were cleared by boiling in 10% (wt/vol) KOH for 7 min and then rinsed several times with tap water. Cleared roots were boiled for 5 min in a 5% ink–vinegar solution with household cleaning vinegar (9% acetic acid) and black ink (Sheaffer Manufacturing Co., Ft. Madison, Iowa, USA). Roots were then destained by rinsing in tap water and kept in tap water at 4°C until further processing. We determined the percentage arbuscular, vesicular and total root colonisation, according to McGonigle *et al.* (1990). For each individual we checked 100 root intersections.

Mycorrhization of non-mycorrhizal plants

Estimation of root colonisation revealed that some plants of the non-mycorrhizal treatment were colonised by AMF. Eight out of 60 *P. grandiflora* target and control plants were colonised, and in the case of *P. lanceolata*, all target and control plants were colonised. However, average total root colonisation of plant from the non-mycorrhizal treatment was substantially smaller compared to plants from the mycorrhizal treatment (*P. grandiflora*: 2.8 ± 1.1% vs. 63.0 ± 1.5%, mean and standard error; *P. lanceolata*: 9.2 ± 1.1% vs. 46.8 ± 1.6%), and we found very few vesicles in roots of plants from the non-mycorrhizal treatment (average vesicular root colonisations, *P. grandiflora*: 0.4 ± 0.3% vs. 13.6 ± 1.1%; *P. lanceolata*: 0.3 ± 0.2% vs. 6.4 ± 0.8%). Vesicles are fungal lipid storage organs and develop only after the symbiosis is well established. We therefore assume that plants from the non-mycorrhizal treatment became infected at an advanced stage of our experiment.

For statistical analyses we assigned target and control plants of the two experiments to different mycorrhizal categories. Plants from the *P. grandiflora* experiment were categorised as either mycorrhizal (all plants from the original mycorrhizal treatment) or non-mycorrhizal (all plants from the original non-mycorrhizal treatment with a total root colonisation of 0%). Plants from the *P. lanceolata* experiment were categorised as either high-mycorrhizal (total root colonisation > 30%) or low-mycorrhizal (total root colonisation < 20%), irrespective of their original mycorrhizal treatment. In the case of *P. grandiflora* we excluded 8 replicates from data and in the case of *P. lanceolata* eleven replicates. As a consequence, the final replicate number per treatment combination varied between 3 and 5.

Statistical analyses

Biomass analyses were originally performed with aboveground, root and total biomass as dependent variable. However, since the resulting patterns did not differ substantially from each other, we show analyses of aboveground biomass only.

One aim of our experiment was to test whether the distances over which competitive interactions between neighbouring plants occur depend on target and neighbour species and the level of mycorrhization. We define interaction distance for species *x* on species *y* as the maximum distance at which the performance (average aboveground biomass) of target individuals of species *y* grown with a neighbour of species *x* was significantly worse compared to the performance of control individuals of species *y* grown at the corresponding position. We therefore performed ANOVAs for each target species and mycorrhizal treatment separately. We specified the contrast matrix so that each neighbour–distance combination was tested separately against the control corresponding to the distance treatment, resulting in nine planned treatment contrasts per analysis. As an example, mean aboveground biomass of *P. grandiflora* target individuals grown with *P. lanceolata* at 5 cm distance in the mycorrhizal treatment was tested for a significant difference to the mean aboveground biomass of *P. grandiflora* control individuals in the mycorrhizal treatment placed at the same position as the target individuals.

In order to compare the performance of plants over the different distance and mycorrhizal treatments, we calculated the log response ratio of each target individual based on aboveground biomass:

$$\ln\mathrm{RR}_{ijd} = \ln\left(\overline{BM_{id}^{c}} \Big/ BM_{ijd}^{t}\right)$$

where $\overline{BM_{id}^{c}}$ is the mean above-ground biomass of all control individuals of target species *i* at distance *d*, and BM_{ijd}^{t} is the above-ground biomass of a target individual of species *i* grown with a neighbour of species *j* at distance *d*. The log response ratio is a measure for the competitive response, i.e. how much a target individual suffered due to its neighbour (c.f. Goldberg *et al.*, 1999; Weigelt & Jolliffe, 2003), and is therefore a more appropriate measure of relative performance than absolute biomass. In a previous experiment (Vogt *et al.*, in press), relative neighbour size turned out to be an extremely important factor influencing the competitive response to a neighbour and was therefore also included as covariate in our analyses of lnRR. We calculated relative neighbour size by dividing neighbour aboveground biomass by target aboveground biomass.

Control plants of *P. grandiflora* in the non-mycorrhizal treatment were exceptionally small at the 15 cm distance treatment (see fig. 1). However, no such pattern was observed for the corresponding target individuals, irrespective of neighbour species. We therefore believe that this resulted from a positional effect. It seems that, when grown alone and without AMF, *P. grandiflora* suffered from root growth limitation due to being fairly close to one container edge (3.5 cm) and could not compensate for this by increasing root growth towards the opposite container edge. As a consequence, lnRR values of the non-mycorrhizal treatment at 15 cm distance were extremely low and strongly influenced the results of the analyses. We therefore show the results of lnRR analyses with two data sets for *P. grandiflora*: either including all three experimental distances, or with 15 cm distance excluded.

We further calculated the coefficient of variation (CV) per container based on target and neighbour aboveground biomass to test whether size inequality between different neighbour combinations changed with neighbour distance or level of mycorrhization.

The root–shoot ratio was calculated by dividing root biomass by aboveground biomass. Since the allocation to aboveground and belowground biomass has been shown to change with a plant's size (Muller *et al.*, 2000), we included total biomass as covariate in our analyses of the root–shoot ratio.

Statistical analyses consisted of ANOVAs and ANCOVAs of linear models. Data were transformed as necessary to meet the requirements of a normal distribution: aboveground biomass of *P. grandiflora* (Box–Cox transformed, $\lambda = 0.1$), lnRR of *P. lanceolata* (square root transformed, after addition of 0.5 since some values were negative), root–shoot ratio of *P. grandiflora* (Box–Cox transformed, $\lambda = - 0.5$) and *P. lanceolata* (Box–Cox transformed, $\lambda = 0.35$). All statistical analyses were performed with the statistical program R, version 2.9.1 (R Development Core Team, 2009).

Results

Aboveground biomass production

Prunella grandiflora produced four times more aboveground biomass when grown with AMF than without (ANOVA: $F_{1/107} = 72.1$, $p < 0.001$; figs. 1 (a) and (b)). In contrast, we found no difference in aboveground biomass of *P. lanceolata* when grown under high-mycorrhizal or low-mycorrhizal conditions (ANOVA: $F_{1/105} = 0.1$, $p = 0.737$; figs. 1 (c) and (d)). However, when *P. lanceolata* was grown as neighbour of *P. grandiflora*, it produced twice as much aboveground biomass under mycorrhizal than non-mycorrhizal conditions (ANOVA: $F_{1/28} = 50.9$, $p < 0.001$). Aboveground biomass of control individuals of both target species grown with AMF (i.e. non-mycorrhizal *P. grandiflora* control plants excluded) was not correlated to the percentage total, arbuscular or vesicular mycorrhizal colonisation (results not shown). Aboveground biomass of all control individuals did not change between the distance treatments, with the remarkable exception of *P. grandiflora* when grown without AMF: at 15 cm distance control individuals were exceptionally small and we found a tendency for aboveground biomass to decline with distance (ANOVA: $F_{1/11} = 3.8$, $p = 0.076$).

Total aboveground biomass per container (i.e. sum of target and neighbour aboveground biomass), was strongly reduced under non-mycorrhizal and low-mycorrhizal conditions compared to mycorrhizal and high-mycorrhizal conditions (table 1). In the case of *P. lanceolata* as target species, this effect resulted from *P. grandiflora* neighbours that produced significantly less aboveground biomass under low-mycorrhizal than high-mycorrhizal conditions (ANOVA: $F_{1/28} = 34.6$, $p < 0.001$), while other neighbour species (*P. lanceolata* and *P. media*) were not affected. The performance of conspecific and heterospecific pairs differed between the two target species (table 1). With *P. grandiflora* as target species, conspecific pairs produced more aboveground biomass than heterospecific pairs, and this difference was stronger under mycorrhizal than under non-mycorrhizal conditions (mean ± 1 standard error: mycorrhizal: conspecific = 2.63 ± 0.20 g, heterospecific = 1.82 ± 0.13 g; non-mycorrhizal: conspecific = 0.78 ± 0.16 g, heterospecific = 0.50 ± 0.06 g). However, with *P. lanceolata* as target species, conspecific pairs produced less aboveground biomass than heterospecific pairs, but only under high-mycorrhizal conditions (mycorrhizal: conspecific = 1.63 ± 0.13 g, heterospecific = 1.94 ± 0.07 g; non-mycorrhizal: conspecific = 1.48 ± 0.15 g, heterospecific = 1.54 ± 0.05 g).

Interaction distances

We found no clear picture for interaction distances. Although most target individuals were smaller than the corresponding control individuals, these differences were statistically significant only with *P. lanceolata* as neighbour species (fig. 1). *Plantago lanceolata* neighbours strongly reduced aboveground biomass of both target species over all three experimental distances, irrespective of the level of mycorrhization. *Plantago lanceolata* target plants grew even larger with a heterospecific neighbour than without neighbour in two cases (*P. media* at 5 cm distance and *P. grandiflora* at 15 cm distance; figs. 1 (c) and (d)). Irrespective of target or neighbour species, aboveground biomass of target individuals did not change over distance. In other words, negative neighbour effects did not decline with distance. Based on our definition of interaction distance, these results suggest interaction distances are larger than 15 cm with *P. lanceolata* as neighbour and smaller than 5 cm with the other three neighbour species.

Competitive response to neighbours

The log response ratio (lnRR) was strongly influenced by relative neighbour size that explained up to 73% of total variance (table 2). When data of all neighbour distances of *P. grandiflora* were included for analysis, we found strong effects of neighbour distance and a highly significant interaction of mycorrhization with distance (table 2, left part). These effects were, however, solely due to control individuals in the non-mycorrhizal treatment being exceptionally small at 15 cm distance (fig. 1 (b)) and vanished when the 15 cm distance treatment was excluded (table 2, middle part). The average lnRR of both target species differed considerably between the mycorrhization levels (*P. grandiflora* 15 cm treatment excluded). Log response ratio increased clearly with relative neighbour size, and was larger under non-mycorrhizal and low-mycorrhizal conditions than under mycorrhizal and high-mycorrhizal conditions for a given relative neighbour size (fig. 2). This indicates that AMF reduced the effects of neighbour size. After correction for neighbour size and mycorrhization level, neighbour species only slightly affected lnRR in the case of *P. lanceolata* (table 2, right part). This resulted from generally large competitive responses to conspecifics and very low responses to heterospecifics.

Coefficient of variation

We tested the coefficient of variation (CV) of target and neighbour aboveground biomass for effects of neighbour species, neighbour distance and mycorrhization level. Effects of neighbour distance were, however, non-significant (main effects and interactions) and neighbour distance treatments were therefore pooled. Since target and neighbour species differed in average aboveground biomass, CV differed accordingly between neighbour combinations (table 3). The CV was significantly larger under non-mycorrhizal and low-mycorrhizal conditions compared to mycorrhizal and high-mycorrhizal conditions (table 3 and fig.3). This was mainly caused by heterospecific neighbour pairs including *P. lanceolata*. Of all four experimental species, *P. lanceolata* aboveground biomass responded least strongly to the level of mycorrhization. CV was largest when *P. grandiflora* and *P. lanceolata* were grown together under non-mycorrhizal or low-mycorrhizal conditions (fig. 3 (b) and (d)). This was further reflected in the significant interaction between neighbour species and mycorrhization level (table 3).

Root-shoot ratio

The root–shoot ratio of both target species varied significantly with a target individual's size (table 4). However, while the root–shoot ratio decreased with size in the case of *P. grandiflora*, it increased with size in the case of *P. lanceolata.* After correction for size, the root–shoot ratio of *P. grandiflora* was larger when grown with than without AMF, while for *P. lanceolata* there was no difference between low- and high-mycorrhization. For both target species the root–shoot ratios were lowest for control individuals (mean and standard error: *P. grandiflora*: 1.05 ± 0.11; *P. lanceolata*: 1.07 ± 0.07) and largest when grown with *P. lanceolata* as neighbour (*P. grandiflora*: 2.71 ± 0.38; *P. lanceolata*: 1.38± 0.08). Neighbour effects further interacted with size and mycorrhization in the case of *P. grandiflora* (table 4).

The significant three-way interactions of both target species between size, mycorrhization and neighbour species emphasize the plasticity of the root–shoot ratio.

Discussion

Although AMF have been shown to influence competition within and between species (e.g. Allsopp & Stock, 1992; Hartnett *et al.*, 1993; Facelli *et al.*, 1999; Ayres *et al.*, 2006), their impact on pair-wise target–neighbour interactions and whether they add a spatial component to these is not known. The aim of our study was to examine the role of AMF in intra- and interspecific plant–plant interactions over different distances. Specifically, we tested whether intraspecific interactions occur over larger distances than interspecific interactions (heteromyopia) and whether these were influenced by AMF. More generally, we wanted to evaluate how AMF affect the competitive outcome of con- and heterospecific pairs of neighbours. Our study yielded two main results: (1) that there were no distance effects and consequently no evidence for heteromyopia, irrespective of the mycorrhization level, and (2) that AMF considerably reduced the impact of size differences between neighbouring plants and may thereby facilitate coexistence.

General effects of AMF on aboveground biomass

Plants in our experiment grew generally larger with AMF and with higher mycorrhization levels than without AMF or with lower mycorrhization levels. The two target species, however differed in their mycorrhizal responsiveness. Both species produced significantly more aboveground biomass whith AMF than without (*P. grandiflora* as target species and *P. lanceolata* as neighbour species), but the difference between mycorrhizal and non-mycorrhizal plants was twice as large for *P. grandiflora* compared to *P. lanceolata*. *Prunella grandiflora* further responded to a difference in the quantity of mycorrhization: plants grew significantly smaller under low-mycorrhizal compared to high-mycorrhizal conditions, while *P. lanceolata* did not respond (*P. grandiflora* as neighbour species and *P. lanceolata* as target species). Taken together, *P. grandiflora* showed a higher level of mycorrhizal dependency than *P. lanceolata* under our experimental conditions. This difference had consequences for the outcome of pair-wise competitive interactions (see *AMF buffer neighbour effects*).

The productivity of a community is expected to increase with number of species and functional groups due to niche complementarity (Hector *et al.*, 1999). If this would also hold for neighbour pairs, heterospecific neighbour pairs should have produced more aboveground biomass than conspecific neighbour pairs. Our results, however, revealed no clear evidence for this. With *P. lanceolata* as target species, heterospecific neighbour pairs produced more aboveground biomass than conspecific neighbour pairs, but the opposite was found with *P. grandiflora* as target species. Presence of AMF and high level of mycorrhization intensified these differences. However, since our “mixed-cultures” only consisted of two species and of only one individual each, this results are not surprising. Potential patterns of complementarity will become more easily visible in multi-species communities consisting of more than two species. Increased ecosystem productivity under increased plant diversity as a consequence of increased AMF species richness has been shown by van der Heijden *et al.* (1998).

Lack of distance effects

We found no distance effects, that is, competitive response to a neighbour did not decline with distance, and this was not affected by the level of mycorrhization. We had defined interaction distances as the maximum distance at which the performance of target individuals was significantly worse compared to the control individuals. In our experiment, target individuals of both target species either performed worse than the control individuals over all three experimental distances (with *P. lanceolata* as neighbour) or their performance was not significantly decreased at either distance (with all other neighbour species). These results do not allow us to draw a clear conclusion on the spatial scales of competitive interactions. AMF did not influence the distances over which competition occurred or the strength of the competitive response over distance. Consequently we could not provide evidence for heteromyopia.

The lack of distance effects stands in contrast to several experimental studies, where neighbour effects clearly declined with distance (Pacala & Silander, 1990; Purves & Law, 2002; Schneider *et al.*, 2006; Vogt *et al.*, in press). The key to understanding our results may be the positioning of target and neighbour individuals within containers. In a previous experiment of Vogt *et al.* (in press), target and control individuals were always placed at the same position within containers, while the position of neighbours varied with distance. Consequently, the amount of soil available for the target individual increased with neighbour distance while that for the neighbour decreased. In our present experiment we wanted to eliminate this disparity in order to separate distance and “volume” effects. Therefore, target and neighbour positions varied accordingly with distance treatment, so that the amount of available soil was the same for target and neighbour and was kept constant over all distances.

It now seems that, under this experimental set up, belowground limitation via neighbouring roots at one side was compensated by neighbour-free space at the opposite side. Both neighbour distance and soil volume may significantly affect the outcome of pair-wise interactions. In target–neighbour pairs, distance and available soil volume are linked. A conceptually, but not necessarily analytically, easier experimental set up might consist of multi-individual stands (e.g. Schneider *et al.*, 2006). Neighbourhood effects could then be integrated over all plants occurring within a certain radius of each individual. However, the dilemma is that all neighbouring individuals mutually affect each other and pair-wise interactions cannot be extracted, while theory, i.e. individual-based models, are based on such pair-wise interactions.

AMF buffer neighbour effects

Mycorrhizal and high-mycorrhizal plants were less affected by neighbours. We could show that AMF reduced the competitive response to neighbours of a given size and lowered the coefficient of variation of target and neighbour aboveground biomass. The competitive response to neighbours increased strongly with relative neighbour size. That is, the larger the neighbour was in relation to the target individual, the smaller was the target individual in relation to an average control individual. This reflects previous results, where relative neighbour size accounted for 70% of the variation in competitive response (Vogt *et al.*, in press). Both studies point out that size differences between neighbouring plants are likely to be a key determinant of competitive interactions and must be incorporated into theory.

Varying the level of mycorrhization furthermore revealed that AMF reduce the competitive response to neighbours of a given size. With a neighbour of a given size, mycorrhizal and high-mycorrhizal plants grew significantly larger than non-mycorrhizal or low-mycorrhizal plants. AMF thus enabled target individuals to tolerate larger neighbours, presumably by improving nutrient supply and thus reducing the strength of root competition. To our knowledge, the question how AMF influence the competitive response in relation to neighbour size has not been investigated before. Our results point thus towards a potential novel coexistence mechanism. However, in our study, we assessed the effects of single neighbours, and there is evidence that, as plant density increases, the beneficial effects of AMF decline (e.g. Allsopp & Stock, 1992; Hartnett *et al.*, 1993; Facelli *et al.*, 1999). Possible mechanisms may include increasing overlap of nutrient depletion zones, a reduction in mycorrhization level or an increase of the cost–benefit ratio of AMF colonisation (for references see review of Koide & Dickie, 2002). Further experiments that vary neighbour density are therefore needed before we can draw generalising conclusions from our results. If it should however frequently be found that AMF buffer the effects of relative size differences between neighbouring plants, this might provide a new coexistence mechanism facilitating seedling establishment and maintaining diversity of differently sized competitors.

AMF further lowered the coefficient of variation of target and neighbour aboveground biomass, which means that target and neighbour were of more equal sizes with AMF than without and under high- versus low-mycorrhizal conditions. However, this effect resulted only from heterospecific pairs including *P. lanceolata*, the species least affected by the level of mycorrhization. In our experiment, AMF decreased size inequalities within heterospecific pairs by increasing aboveground biomass of otherwise smaller species. To our knowledge, size-equalising effects of AMF have not been reported so far. Competition experiments detected either no change or an increase in size inequalities of mycorrhizal compared to non-mycorrhizal plants (Allsopp & Stock, 1992; Moora & Zobel, 1998; Facelli *et al.*, 1999; Ronsheim & Anderson, 2001; Ayres *et al.*, 2006). The reason for this discrepancy might be simple: all these studies focussed on intraspecific competition, and we found decreased size inequalities due to AMF only within heterospecific pairs (including *P. lanceolata*). Our results thus suggest that AMF may reduce size inequalities between heterospecific neighbours. A possible mechanism therefore could be common mycorrhizal networks (CMNs).

Grime et al. (1987) have hypothesized that AMF equalise nutrient availability between co-occurring plant species by moving assimilates from larger plants of one species to smaller plant of another species via a CMN (resource sharing hypothesis). Two decades later, experimental evidence both for and against exchange of carbon, nitrogen and phosphorus via CMNs has accumulated (reviewed e.g. by Robinson & Fitter, 1999; Selosse *et al.*, 2006). There is controversy as to whether received nutrients remain in fungal hyphae (Robinson & Fitter, 1999; Pfeffer *et al.*, 2004) or migrate into the metabolism of the receiving plant (Lerat *et al.*, 2002), and whether the magnitude and rate of nutrient transfer are large enough to affect the receiving plants (Johansen & Jensen, 1996). CMNs can also mediate interactions between plants other than nutrient transfer (Selosse *et al.*, 2006). For example, negative soil feedbacks mediated by AMF of dominant species can decrease their performance compared with inferior co-occurring species and thereby maintain community diversity (Bever, 2002; Castelli & Casper, 2003; Hart *et al.*, 2003; Umbanhowar & McCann, 2005). In summary, the potential exists that plant species diversity might be facilitated if CMNs equalise the size of neighbouring plants. The physiological and ecological importance of this, however, remains under debate.

Conclusions

Our experiment revealed no evidence that negative neighbour effects decline with distance and suggests that AMF are unlikely to be involved in heteromyopia in herbaceous species from grasslands. However, our findings emphasize the importance of relative neighbour size in pair-wise interactions. Moreover, they suggest that AMF may promote competitive coexistence by reducing size inequalities and the effects of size differences between neighbouring plants. This points out a potential new aspect of the role of AMF in plant–plant interactions.

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Table 1: Results of ANOVA testing for effects of mycorrhization (% root colonisation) and neighbour identity on total above ground biomass per container (sum of target and neighbour aboveground biomass) of *Prunella grandiflora* and *Plantago lanceolata* plants grown with single con- or heterospecific neighbours. Effects of neighbour distance were non-significant and are therefore ommited.

	Prunella grandiflora				*Plantago lanceolata*			
Source	d.f.	SSQ	F	p	d.f.	SSQ	F	p
Mycorrhization (M)[a]	1	43.76	117.9	< 0.001	1	2.06	13.2	< 0.001
Neighbour identity (ID)[b]	1	5.67	15.3	< 0.001	1	0.62	4.0	0.050
M x ID	1	1.27	3.4	0.068	1	0.24	1.6	0.207
Residuals	77	28.59			76	11.92		

[a] *P. grandiflora*: mycorrhizal vs. non-mycorrhizal; *P. lanceolata*: high-mycorrhizal vs. low-mycorrhizal.

[b] Con- vs. heterospecific.

Table 2: Results of ANCOVA testing for effects of relative neighbour size (covariate), mycorrhization (% root colonisation), neighbour species and neighbour distance on the log response ratio of *Prunella grandiflora* and *Plantago lanceolata* plants grown with single con- or heterospecific neighbours. Interactions with the covariate were non-significant and are therefore omitted.

	P. grandiflora[a]								*P. lanceolata*			
	all neighbour distances				5 and 10 cm distance							
Source	d.f.	SSQ	F	p	d.f.	SSQ	F	p	d.f.	SSQ	F	p
Relative neighbour size[b]	1	112.0	257.0	< 0.001	1	87.6	172.3	< 0.001	1	2.37	130.3	< 0.001
Mycorrhization (M)[c]	1	0.3	0.8	0.388	1	6.5	12.8	< 0.001	1	0.16	8.9	0.004
Neighbour species (N)	2	0.7	0.8	0.445	2	1.1	1.1	0.335	2	0.09	2.6	0.086
Neighbour distance (D)	2	172	19.7	< 0.001	1	0.7	1.4	0.237	2	0.04	1.2	0.322
M x N	2	1.3	1.5	0.237	2	0.0	0.0	0.965	2	0.01	0.4	0.671
M x D	2	26.0	29.8	< 0.001	1	0.0	0.0	0.929	2	0.06	1.5	0.222
N x D	4	0.7	0.4	0.794	2	0.6	0.6	0.545	4	0.13	1.9	0.131
Residuals	66	28.8			43	21.9			65	1.18		

[a] Log response ratios at 15 cm distance were extremely low under non-mycorrhizal conditions due to very little aboveground biomass of control individuals. Since data suggest that this resulted from a position rather than distance effect, analyses of data both including all three experimental distances and with 15 cm distance excluded are shown.

[b] Aboveground biomass of neighbour divided by aboveground biomass of target individual.

[c] *P. grandiflora*: mycorrhizal vs. non-mycorrhizal; *P. lanceolata*: high-mycorrhizal vs. low-mycorrhizal.

Table 3: Results of ANOVA testing for effects of mycorrhization (% root colonisation) and neighbour species on the coefficient of variation of above ground biomass of *Prunella grandiflora* and *Plantago lanceolata* plants grown with single con- or heterospecific neighbours. Effects of neighbour distance were non-significant and are therefore ommited.

	Prunella grandiflora				*Plantago lanceolata*			
Source	d.f.	SSQ	F	p	d.f.	SSQ	F	p
Neighbour species (N)	2	1.214	4.1	0.020	2	3.255	18.9	< 0.001
Mycorrhization (M)[a]	1	1.301	8.8	0.004	1	0.692	8.0	0.006
N x M	2	1.032	3.5	0.036	2	1.600	9.3	< 0.001
Residuals	75	11.085			74	6.388		

[a] *P. grandiflora*: mycorrhizal vs. non-mycorrhizal; *P. lanceolata*: high-mycorrhizal vs. low-mycorrhizal.

Table 4: Results of ANCOVA testing for effects of size (covariate), mycorrhization (% root colonisation) and neighbour species on the root–shoot ratio of *Prunella grandiflora* and *Plantago lanceolata* plants grown with single con- or heterospecific neighbours. Effects of neighbour distance were non-significant and are therefore ommited.

	P. grandiflora				*P. lanceolata*			
Source	d.f.	SSQ	F	p	d.f.	SSQ	F	p
Size (S)	1	0.502	14.6	< 0.001	1	0.068	6.7	0.012
Mycorrhization (M)[a]	1	0.718	20.9	< 0.001	1	0.003	0.3	0.574
Neighbour species (N)	2	0.178	2.6	0.083	2	0.185	9.0	< 0.001
S x M	1	0.025	0.7	0.399	1	0.000	0.0	0.844
S x N	2	0.310	4.5	0.015	2	0.047	2.3	0.108
M x N	2	0.174	2.5	0.087	2	0.019	0.9	0.401
S x M x N	2	0.228	3.3	0.042	2	0.080	3.9	0.025
Residuals	69	2.372			68	0.697		

[a] *P. grandiflora*: mycorrhizal vs. non-mycorrhizal; *P. lanceolata*: high-mycorrhizal vs. low-mycorrhizal.

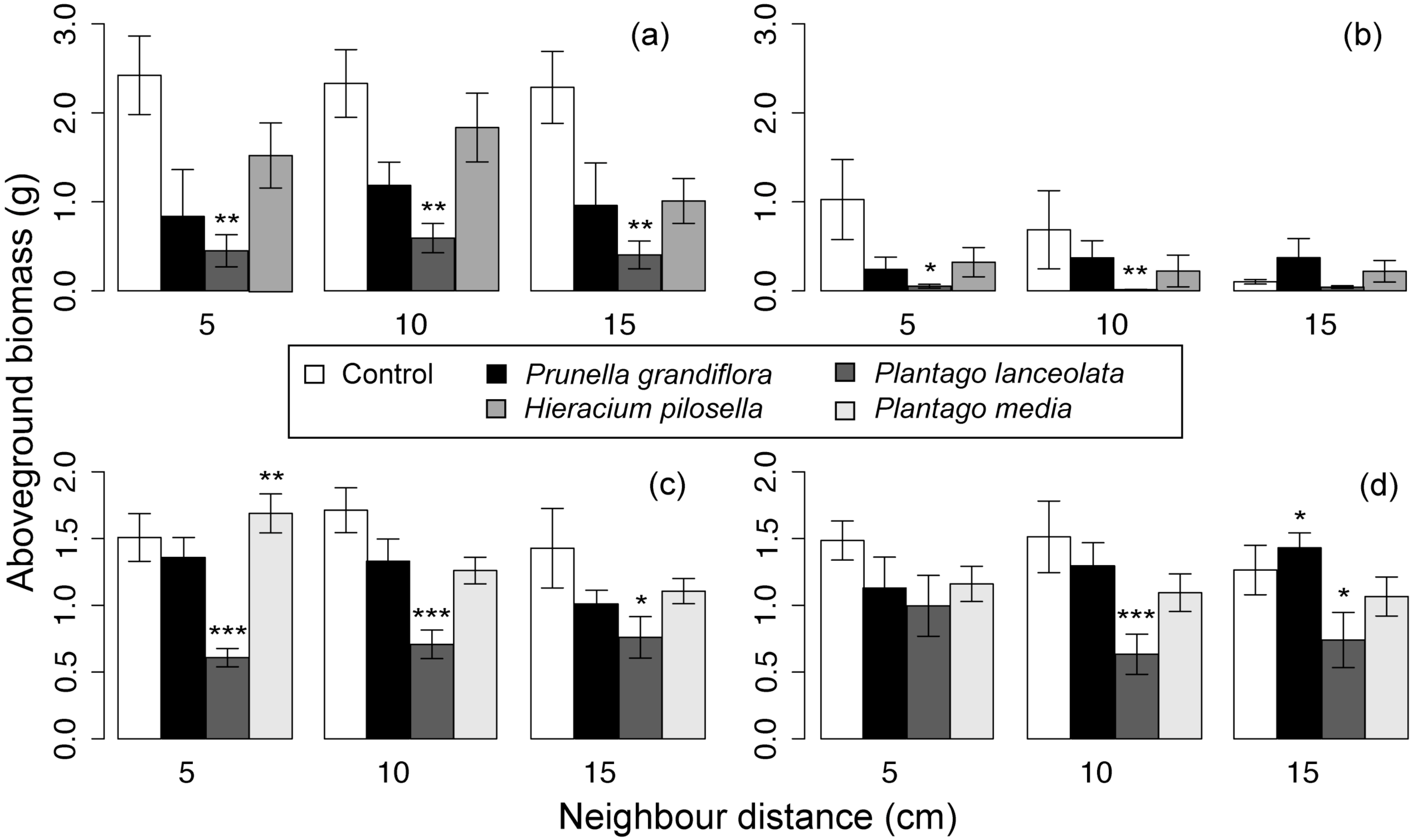

Figure 1: Aboveground biomass of *Prunella grandiflora*, (a) and (b), and *Plantago lanceolata*, (c) and (d), plants grown alone (control) or with a single neighbour at different distances under mycorrhizal (a) and non-mycorrhizal (b), respectively high-mycorrhizal (c) and low-mycorrhizal (d) conditions. Mean values ± one standard error are shown. Asterisks above bars indicate significant differences between target plants grown with neighbours and the corresponding control plants (p-values: * < 0.05, ** < 0.01, *** < 0.001).

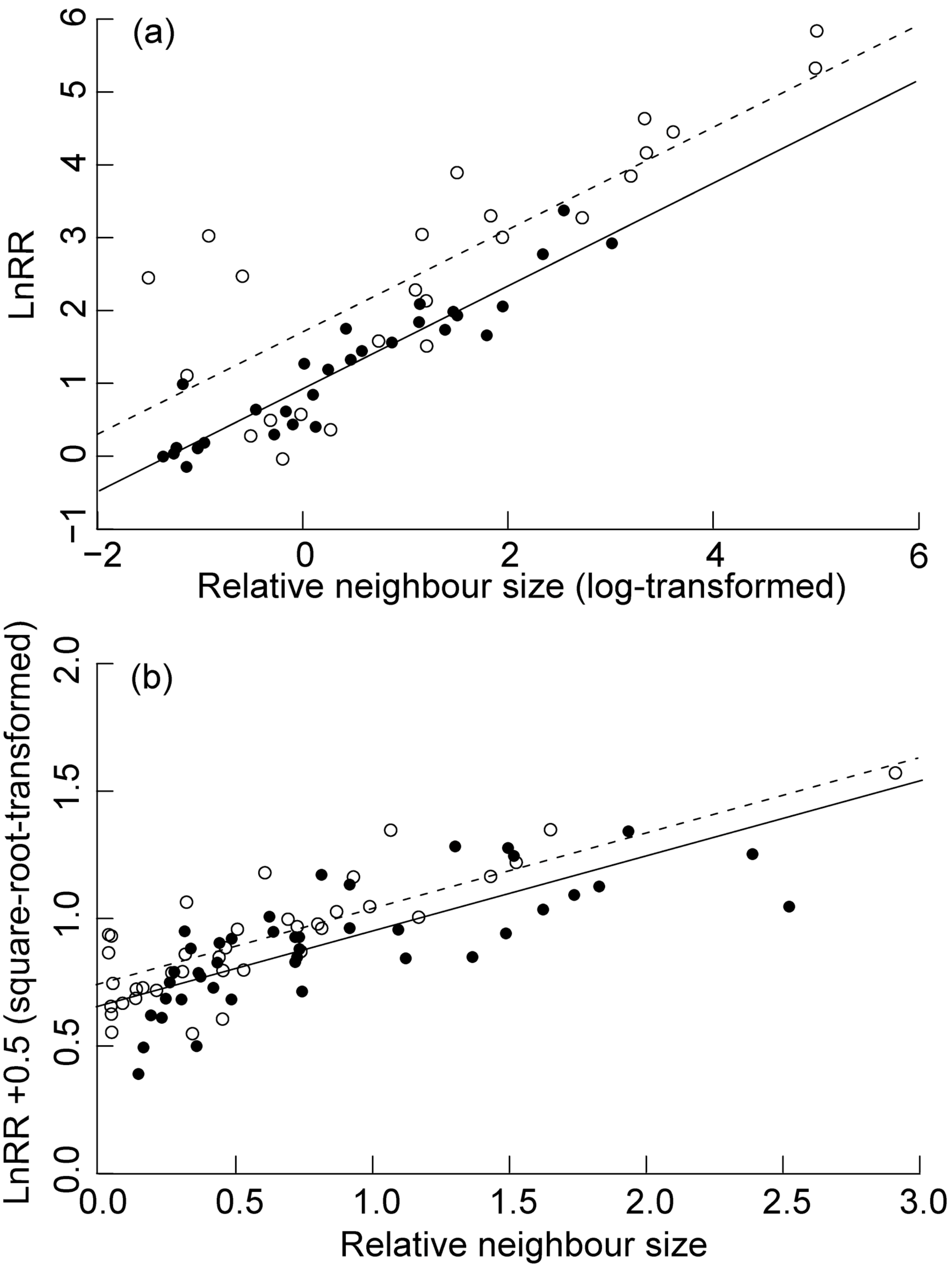

Figure 2: Log response ratio in relation to relative neighbour size of *Prunella grandiflora* (a) and *Plantago lanceolata* (b) plants grown with a single neighbour under different mycorrhization levels. Filled circles and lines represent mycorrhizal (a) and high-mycorrhizal (b) conditions, open circles and dashed lines represent non-mycorrhizal (a) and low-mycorrhizal (b) conditions. Data are pooled for neighbour species and neighbour distances (*P. grandiflora*: 5 and 10 cm; *P. lanceolata*: 5, 10 and 15 cm).

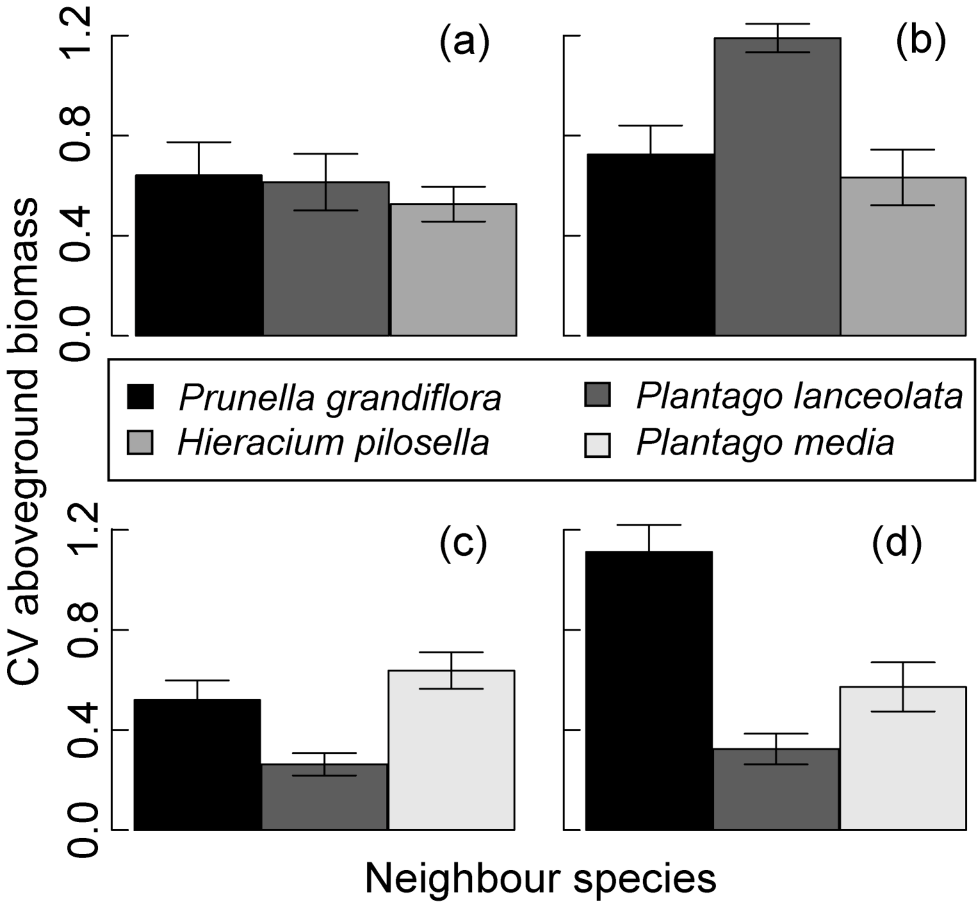

Figure 3: Coefficient of variation of target and neighbour aboveground biomass of *Prunella grandiflora*, (a) and (b), and *Plantago lanceolata*, (c) and (d), plants grown with a single con- or heterospecific neighbour under mycorrhizal (a) and non-mycorrhizal (b), respectively high-mycorrhizal (c) and low-mycorrhizal (d) conditions. Mean values ± one standard error are shown. Data are pooled over neighbour distances.

Chapter 5: Species-specific response of host plants to within-population genetic variability of arbuscular mycorrhizal fungi

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Manuscript in preparation.

Abstract

Different species of arbuscular mycorrhizal fungi (AMF) alter plant growth and affect plant diversity and ecosystem productivity. Much less is known about how genetic variability and functional diversity within AMF species affects plant and fungal performance. I performed a greenhouse experiment in which single plants of four perennial forbs from calcareous grasslands (*Hieracium pilosella, Plantago lanceolata, Plantago media* and *Prunella grandiflora*) were either grown without AMF or inoculated with one of five genetically different *Glomus intraradices* isolates originating from one AMF population. The different isolates significantly altered plant biomass and differed in their efficiency to colonise plant roots. Moreover, the strength of the response to isolates varied substantially between plant species. This indicates that plant species may differ in their susceptibility to genetic variability within species of AMF. Small-scale functional diversity within AMF populations could have profound consequences for plant population and community dynamics and hint at a novel facet of spatial plant ecology.

Keywords: Functional variability, genetic diversity, *Glomus intraradices*, growth response, host-specificity, symbiosis.

Introduction

Arbuscular mycorrhizal fungi (AMF; class Zygomycetes, order Glomales) are extremely successful fungi that colonise the roots of approximately two-thirds of terrestrial plant species (Smith & Read, 1997). These obligate symbionts supply inorganic nutrients to plants in exchange of photosynthates (Munkvold *et al.*, 2004). However, the benefits plants gain from AMF go far beyond improved nutrient acquisition and include enhanced stress, pathogen and herbivore tolerance (Newsham *et al.*, 1995; Smith & Read, 1997; Kula *et al.*, 2005). Arbuscular mycorrhizal fungi have long been considered to show no host-specificity because of their broad host range, the small number of about 150 described species, and the unpredictability in the distribution of species assemblages (Sanders, 2002). However, this view has changed dramatically since different AMF species have been shown to induce differential plant growth response (Streitwolf-Engel *et al.*, 1997; van der Heijden *et al.*, 1998a; van der Heijden *et al.*, 2003), and AMF species composition has been shown to affect plant diversity and ecosystem productivity (van der Heijden *et al.*, 1998b). Similarly, AMF performance has been shown to depend on plant species identity (Helgason *et al.*, 2002).

Moreover, there is recent evidence accumulating that also functional diversity within AMF species causes significant variation in plant and fungal growth performance. Gamper *et al.* (2005) tested isolates of two AMF species from field plots of ambient and elevated CO_2 partial pressure on *Trifolium repens*. The authors found that root colonisation and nitrogen assimilation differed within and between AMF species and also between isolates from the two CO_2 environments. Munkvold *et al.* (2004) compared isolates of four AMF species originating from a broad geographical range and reported large intraspecific diversity for fungal growth and plant phosphorous uptake. Koch *et al.* (2004) found that *Glomus intraradices* isolates, originating from one population from an agricultural field (Jansa *et al.*, 2002) showed a high genetic variability, and this genetic variability has been shown to significantly alter growth of *Brachpodium pinnatum* and *Prunella vulgaris* (Koch *et al.*, 2006). Further, fitness traits of these AMF isolates have been shown to depend on host plant species and on the level of available phosphorous (Ehinger *et al.*, in press). These studies provide evidence that the outcome of the mycorrhizal symbiosis depends on both plant and fungal genotypes and changes with environmental conditions. Such functional diversity in plant–AMF interactions may be crucial from an ecosystem perspective, since differences in individual performance can affect plant population and community dynamics.

The present experiment aimed to evaluate how within-population genetic variability of an AMF species affects growth performance of co-occurring plant species. I performed a greenhouse experiment in which single plants of four perennial forbs from calcareous grasslands (*Hieracium pilosella, Plantago lanceolata, P. media* and *Prunella grandiflora*) were either inoculated with one of five different *Glomus intraradices* isolates or grown without AMF. Plant biomass and root colonisation under the different isolate treatments were compared within and among plant species.

Material and methods

Plant and fungal material

I chose four perennial plant species that are common and co-occurring on calcareous grasslands: *Hieracium pilosella* L. (mouse-ear hawkweed, *Asteraceae*), *Plantago lanceolata* L. (ribwort plantain, *Plantaginaceae*), *Plantago media* L. (hoary plantain, *Plantaginaceae*) and *Prunella grandiflora* (L.) Schaller et Jacq. (big self-heal, *Lamiaceae*). All species show high levels of mycorrhizal dependency (Grime *et al.*, 1987; Streitwolf-Engel *et al.*, 1997; van der Heijden *et al.*, 1998b). Plant seeds were obtained from cultivated Swiss ecotypes (Fenaco, Winterthur, Switzerland). Fungal material was provided by the group of Ian Sanders, University of Lausanne, Switzerland. I used five different isolates of the AMF species *Glomus intraradices* Schenk & Smith. The single-spore isolates (A4, B3, C2, C3 and D1) originate from four different plots (A–D) from one agricultural field in Tänikon, Switzerland (Jansa *et al.*, 2002) and have previously been shown to differ phenotypically and genotypically (Koch *et al.*, 2004; Koch *et al.*, 2006). Isolate cultures were kept under identical conditions for several years to eliminate any maternal effects (Koch *et al.*, 2004). The spores used as inoculum in the present experiment were previously grown for 22 weeks with Ri T-DNA transformed carrot roots on split plates.

Experimental Design

I performed a greenhouse experiment where plants of the four host species were grown singly in pots, either without AMF (NM) or inoculated with one of the five isolates. Each plant–isolate treatment was replicated nine times yielding a total of 216 pots (4 plant species x 6 isolate treatments x 9 replicates). Pots were filled with 550 ml of a 1:1 (vol:vol) mixture of TerraGreen (Oil Dri US-special, Maagtechnic, Duebendorf, Switzerland) and nutrient poor soil (Topferde 140, Ricoter, Switzerland). The soil mixture was steam autoclaved twice at

120°C three weeks before planting. Seeds were sown on autoclaved TerraGreen. Twenty-two days after sowing, seedlings of similar size were transferred to the pots. Each seedling was either inoculated with 0.26 ml spore suspension that contained 50 spores of one of the five isolates or received 0.26 ml tap water (NM plants). Pots were randomly placed on separate greenhouse benches per isolate treatment and re-randomized every two weeks. Plants were watered with distilled water as needed, several times a week. Greenhouse temperature ranged from 10–33°C. Six individuals died during the experiment, reducing the final number of pots to 210.

Data collection

Plantago lanceolata individuals became infected by mildew during the first months of the experiment. Therefore, above ground biomass of all plants was cut at 5 cm above ground after 76 days (harvest 1). One hundred eighty four days after harvest 1 (260 days after transferring), whole plants were harvested (harvest 2) and biomass separated into aboveground and belowground biomass. Aboveground biomass at harvest 1 was further separated into vegetative (shoots) and reproductive (inflorescences and seeds) biomass. Biomass of both harvests was dried at 70°C for 48 hours and dry mass determined.

At harvest 2 I collected fresh root samples (three subsamples from different locations of the root system) from five randomly selected individuals per plant–isolate treatment for estimation of the percentage root colonisation. Fresh weights of the root sample and the remaining root system of each plant were determined at the same time, and the dry weight of the root sample was estimated afterwards, according to the ratio of fresh to dry mass of the remaining root system. Root samples were proceeded, according to the protocol of Vierheilig *et al.* (1998). Roots were stained by boiling for 5 min in a 5% ink–vinegar solution with household cleaning vinegar (9% acetic acid) and black ink (Sheaffer Manufacturing Co., Ft. Madison, Iowa, USA) and kept in tap water at 4°C until further processing. I determined the percentage arbuscular, vesicular and total (hyphae, arbuscules and vesicules) root colonisation, according to McGonigle *et al.* (1990). For each individual I checked 100 root intersections. One sample each was missing for *P. lanceolata* (isolate D1) and *P. media* (isolate A4).

Statistical analyses

I tested whether plant biomass (aboveground biomass at harvest 1 and 2, root biomass and total biomass), root–shoot ratio and percentage root colonisation (total, arbuscular and vesicular) differed between plant species and AMF isolates. Total biomass was calculated as the sum of aboveground biomass at harvests 1 and 2 and root biomass. Root–shoot ratio was calculated by dividing aboveground biomass at harvest 2 (regrown for 184 days from harvest 1 to harvest 2) by root biomass (grown for the whole duration of the experiment, thus 260 days). Data were analysed with crossed two-way ANOVAs with plant species and isolate as fixed factors. In order to test whether NM plants differed from mycorrhizal plants, all isolates were pooled. To test for a general effect of AMF isolates, NM plants were omitted. Species were analysed separately for differences between isolate treatments, using Tukey's HSD test (NM plants included). Reproductive biomass (harvest 1) could only be analysed for *H. pilosella* because too few individuals of the other species flowered. Data were Box–Cox transformed if necessary to meet the requirements of a normal distribution. All statistical analyses were performed with the statistical program R, version 2.9.1 (R Development Core Team, 2009).

Results

Biomass

Plant species differed significantly in aboveground biomass at harvest 1 (fig. 1A) and harvest 2 (fig. 1B), root biomass, total biomass and root–shoot ratio (fig. 1C) (all: table 1). The two *Plantago* species showed less regrowth of aboveground biomass (harvest 2) than the other two species (fig. 1B). *Hieracium pilosella* and *P. grandiflora* produced less belowground than aboveground biomass (root–shoot ratio), while the opposite was found for the two *Plantago* species (fig. 1C).

Inoculated plants did not differ significantly from NM plants in aboveground biomass at both harvests, root biomass or root-shoot ratio (fig. 1). However, NM plants produced significantly more total biomass than inoculated plants (3.75 ± 0.16 g vs. 3.47± 0.05 g (mean and standard error); $F_{1/202} = 5.1$, $p = 0.025$).

All species pooled, plants inoculated with different isolates differed in aboveground biomass at harvest 1, root biomass and root–shoot ratio (table 1). Plants inoculated with isolate C2 produced more aboveground biomass at harvest 1 than with isolate D1 (Tukey's HSD test, $p < 0.05$; fig. 1A). Plants inoculated with isolate B3 produced slightly less root biomass than with isolate A4 (Tukey's HSD test, $p < 0.1$) and had a lower root–shoot ratio compared to plants inoculated with isolates A4 and C2 (Tukey's HSD test, $p < 0.05$; fig. 1C). I found no significant effects of isolates on aboveground biomass at harvest 2 and total biomass. Further, no significant plant–isolate interaction was found for any of the measured biomass parameters (table 1).

When testing species separately for effects of isolate treatments, *H. pilosella* proved to be the most sensitive species. *Hieracium pilosella* NM plants produced significantly more aboveground biomass at harvest 2 than plants inoculated with isolates A4, C2 or D1 (fig. 1B), and NM plants had a smaller root–shoot ratio than plants inoculated with isolate C2 (fig. 1C). *Plantago media* produced significantly less aboveground biomass at harvest 1 when inoculated with isolate D_1 than when inoculated with isolates A4, C2 or compared to NM plants (fig. 1A). I found no significant effects of isolate treatments on *P. grandiflora* and *P. lanceolata*.

Reproductive biomass of *H. pilosella* did not differ between inoculated and NM plants or between AMF isolates (data not shown).

Root colonisation

The percentage total, arbuscular and vesicular root colonisation of inoculated plants ranged between 2–85%, 0–52% and 0–33% respectively. Roots of NM plants were not colonised.

All species pooled, the percentage total, arbuscular and vesicular root colonisation differed strongly between plant species and isolates, but I found no significant plant–isolate interaction (table 2). Plants inoculated with isolate C2 showed a significantly higher total root colonisation than plants inoculated with any other isolate (Tukey’s HSD test, $p < 0.05$; fig. 2A). Arbuscular root colonisation was further slightly higher with isolate C2 compared to isolate A4 (Tukey’s HSD test, $p < 0.1$; fig. 2B) and vesicular root colonisation was significantly larger with isolates C2 and C3 compared to isolate D1 (Tukey’s HSD test, $p < 0.05$; fig. 2C).

On average, *H. pilosella* showed the highest and *P. lanceolata* the lowest percentage root colonisation (fig. 2). *Hieracium pilosella* and *P. grandiflora* showed the highest percentage total root colonisation with isolate C2 and the lowest with isolate D1 (*H. pilosella*) and C3 (*P. grandiflora*) (fig. 2A). The percentage vesicular root colonisation of the two species further differed between AMF isolates. For *P. grandiflora* percentage vesicular root colonisation was again highest with isolate C2 but lowest with isolate D1 (fig. 2C). *Hieracium pilosella* showed significantly higher levels of vesicular root colonisation with isolate C3 than with isolates B3 and D1. Root colonisation did not differ between isolate treatments in the cases of the two *Plantago* species (fig. 2).

Discussion

My results show that genetically different isolates of *G. intraradices*, originating from one field population, alter plant biomass and differ in their efficiency to colonise plant roots. This confirms previous findings, where the same AMF isolates were found to significantly affect growth of one grass and one forb species (Koch *et al.*, 2006). In my experiment, however, these isolates were tested on four forb species, and I could show in addition that plant species differed substantially in how strong they responded to such genetic variability. This is further evidence that ecologically relevant (genetically-based) functional diversity in the AMF symbiosis can exist over relatively small spatial scales.

My experiment revealed no beneficiary effects of AMF, i.e. growth performance of inoculated plants was not enhanced compared to NM plants. Rather, inoculated plants produced less total biomass than NM plants. The most likely reason for this seems that plants were grown under beneficiary greenhouse conditions: plants were watered as needed, and nutrients seem not to have been limited. Koch *et al.* (2006) found that these isolates enhanced plant growth only under dry growth conditions but not under wet growth conditions. The mycorrhizal association has been shown to broadly range from mutualism to parasitism and the net benefit a host plant gains from a certain AMF species often depends on environmental conditions (Johnson *et al.*, 1997). Further there is evidence that AMF from fertilized soils are less mutualistic (Johnson, 1993). Still, the findings of Koch *et al.* (2006) show that the isolates used in my experiment maintained functions, which can be beneficiary to their hosts. I therefore assume that the experimental conditions in the present study were not harsh enough to results in mutualistic AMF symbioses.

However, plants inoculated with different AMF isolates differed significantly in biomass, both above and below ground. All species pooled, I found isolate effects on aboveground biomass at harvest 1 (76 days after inoculation) but not at harvest 2 (260 days after inoculation). Aboveground biomass at harvest 2 can be viewed as the “regrowth potential” after a disturbance event (e.g. hay cut or consumption by cattle) under a well-established mycorrhiza symbiosis. Cutting of aboveground biomass at harvest 1 drastically reduced the plants’ photosynthetic capability, while the amount of carbohydrates required by the fungi stayed large. As a consequence, the net costs for the plants must have increased (c.f. Johnson *et al.*, 1997). Therefore, one might expect stronger negative effects of AMF on aboveground biomass at harvest 2 compared to harvest 1. Evidence for this was provided by *H. pilosella*, where aboveground biomass at harvest 2 was significantly suppressed by three isolates compared to NM plants. This finding, however, was not repeated when species were analysed together, which may suggest that potential effects of genetically different AMF isolates diminish after disturbances.

I furthermore found that isolates differently affected root biomass. Especially, plants inoculated with isolate B3 produced less root biomass than with isolate A4, and, since aboveground biomass at harvest 2 did not differ between isolates, this was also reflected in the root–shoot ratio (all species pooled). From these results I cannot draw direct conclusions about how the different isolates affected biomass allocation, since root biomass had been grown for 260 days and aboveground biomass at harvest 2 only for 194 days. However, these results indicate that the amount of roots needed to regrow a certain amount of aboveground biomass differed between isolates, which was smallest with isolate B3 and largest with isolate A4.

Besides affecting plant biomass, isolates also differed in their efficiency to colonise plant roots: the percentage total, arbuscular and vesicular root colonisation differed significantly between plants species and isolates. Isolate C2 thereby proved to be a relatively good coloniser and isolate D2 to be a relatively bad coloniser. However, I found no direct link between an isolate’s colonisation efficiency and its effect on plant biomass. Further, isolate effects were stronger for vesicular than for arbuscular root colonisation. Bearing in mind that arbuscules are the organs by which AMF provide their hosts with nutrients and that vesicules are fungal storage structures (Johnson, 1993), I conclude that the observed differences in root colonisation efficiency are likely to be of more importance for the fungus than for the plant. Recent evidence for this also comes from an experiment in which isolates B3, C2 and C3 have been grown on axenic root cultures of three different host plants (Ehinger *et al.,* in press). The authors found that fitness traits differed significantly between AMF isolates and were strongly affect by host identity.

The fact that I found no significant plant–isolate interactions in my experiment indicates that the response of the four plant species did not differ according to which isolate they had been inoculated with. That is, I found no isolate that one plant species grew especially well with and another plant species especially bad with. This is congruent with the findings of Koch *et al.* (2006). It thus seems likely – though not surprising – that genetic diversity within AMF species will result in less host-specificity than genetic diversity between AMF species. Nevertheless, I found that the four plant species tested in my experiment differed substantially in their susceptibility to different AMF isolates. *Hieracium pilosella* was the most sensitive species with significant isolate effects on aboveground biomass at harvest 2, root–shoot ratio and percentage total and vesicular root colonisation. In contrast, I found no significant isolate effects for *P. lanceolata*. Interestingly, *H. pilosella* also showed the highest and *P. lanceolata* the lowest levels of percentage root colonisation. It could thus be that plant species differ in their response to genetic variability within an AMF species according to their infectability. However, my experiment and similar studies either focussed on one AMF species (Koch *et al.*, 2006; Ehinger *et al.,* in press) or one plant species (Munkvold *et al.*, 2004; Gamper *et al.*, 2005) at a time and used only AMF species of the genus *Glomus*. Further experiments, explicitly addressing this issue, are therefore needed before general conclusions can be drawn.

There is accumulating evidence that AMF show more host-specificity than has previously been considered (c.f. Sanders, 2002; Fitter, 2005). Recent research further showed that also functional variability within certain AMF species can alter the performance of plant and fungal partners (Munkvold *et al.*, 2004; Gamper *et al.*, 2005; Koch *et al.*, 2006; Ehinger *et al.,* in press). My experiment now adds yet another layer of complexity to the mycorrhizal symbiosis in that plant species differed in their susceptibility to such functional variability within species of AMF. Genetically based heterogeneity in the benefits provided by an AMF species may further interact with small-scale environmental heterogeneity in the field. The outcome of such complex interactions on individual plant performance is difficult to predict without further investigation. Still, spatial variation in benefits provided by AMF could have profound consequences for plant population and community dynamics and may hint at a novel facet of plant ecology.

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Table 1: Results of ANOVA testing for effects of AMF isolate, plant species and their interaction on biomass and root–shoot ratio of single *Hieracium pilosella, Plantago lanceolata, P. media* and *Prunella grandiflora* plants grown with one of five AMF isolates of *Glomus intraradices*.

		Biomass														
		aboveground harvest 1[a]			aboveground harvest 2[b]			root[c]			total[d]			Root–shoot ratio[e]		
Source	d.f	SSQ	F	p	SSQ	F	p	SSQ	F	p	SSQ	F	p	SSQ	F	p
Isolate (I)	4	3.23	2.7	0.031	0.25	1.2	0.305	0.24	2.49	0.046	2.64	1.6	0.171	1.45	4.7	0.001
Plant species (S)	3	8.84	10.0	< 0.001	11.17	74.1	< 0.001	2.50	34.8	< 0.001	6.55	5.4	0.002	36.49	159.0	< 0.001
I x S	12	4.15	1.2	0.307	0.75	1.3	0.256	0.17	0.6	0.851	3.58	0.7	0.717	0.75	0.8	0.637
Residuals	155	45.67			7.80			3.74			63.08			11.86		

[a] Harvested after 76 days.

[b] Regrown biomass, harvested 184 days after harvest 1.

[c] Harvested at harvest 2, grown for 260 days.

[d] Sum of aboveground biomass at harvests 1 and 2 and root biomass.

[e] Root biomass divided by aboveground biomass at harvest 2.

Table 2: Results of ANOVA testing for effects of AMF isolate, plant species and their interaction on the percentage mycorrhizal root colonisation of single *Hieracium pilosella, Plantago lanceolata, P. media* and *Prunella grandiflora* plants grown with one of five AMF isolates of *Glomus intraradices*.

		% root colonisation								
		total			arbuscular			vesicular		
Source	d.f	SSQ	F	p	SSQ	F	p	SSQ	F	p
Isolate (I)	4	51.6	6.4	< 0.001	18.1	2.7	0.038	8.7	3.0	0.025
Plant species (S)	3	176.5	29.2	< 0.001	121.0	23.8	< 0.001	31.1	14.1	< 0.001
I x S	12	20.1	0.8	0.617	13.4	0.7	0.786	13.2	1.5	0.145
Residuals	78	157.0			132.2			57.3		

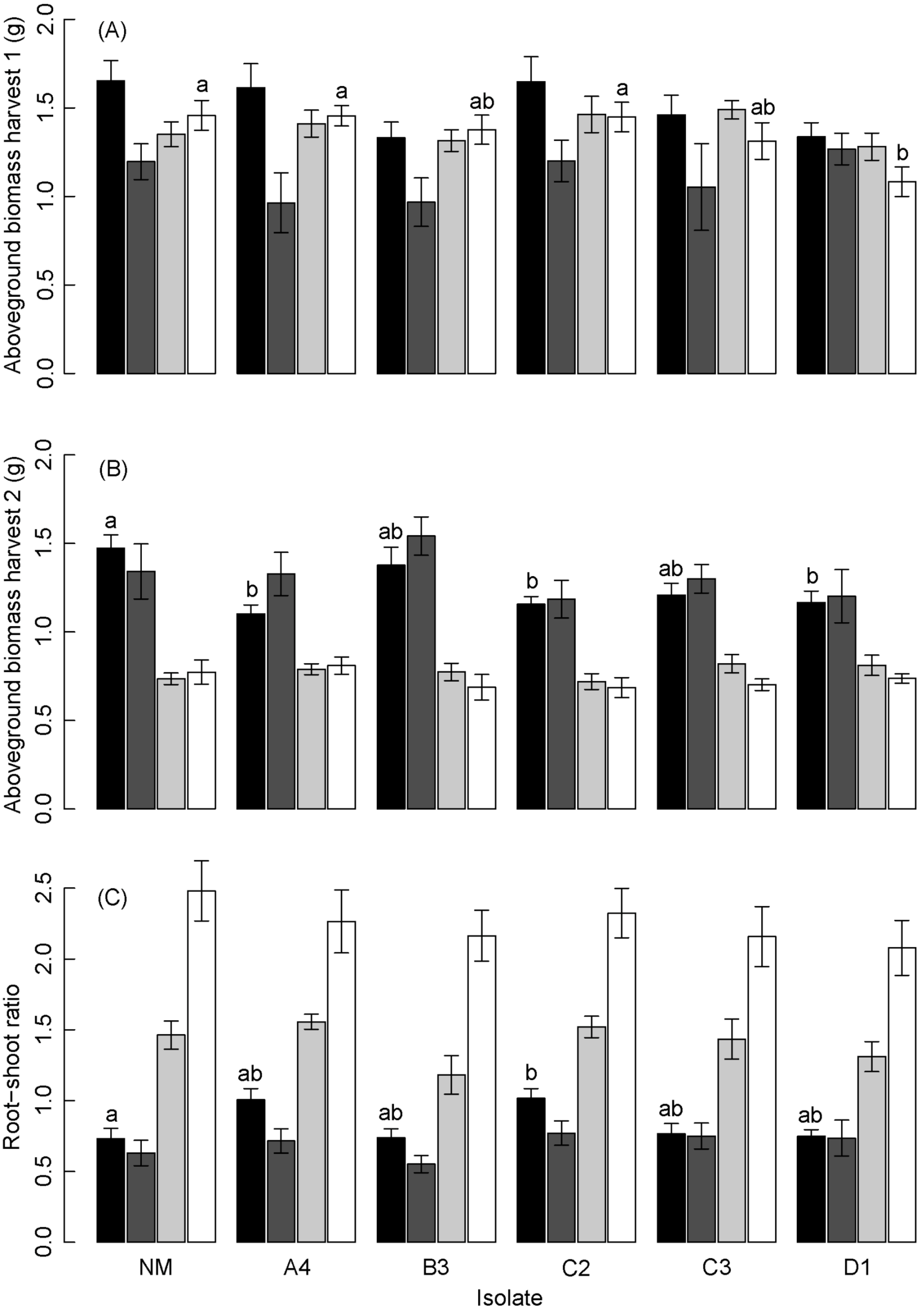

Fig. 1: Mean aboveground biomass at harvest 1 (A) and harvest 2 (B) and mean root–shoot ratio (C) of *Hieracium pilosella* (black), *Prunella grandiflora* (dark grey), *Plantago lanceolata* (light grey) and *Plantago media* (white) plants grown singly without AMF (NM) or with one of five isolates of *Glomus intraradices*. Error bars represent ± one standard error. Different letters above bars of the same plant species indicate a significant difference according to Tukey's HSD test ($p < 0.05$).

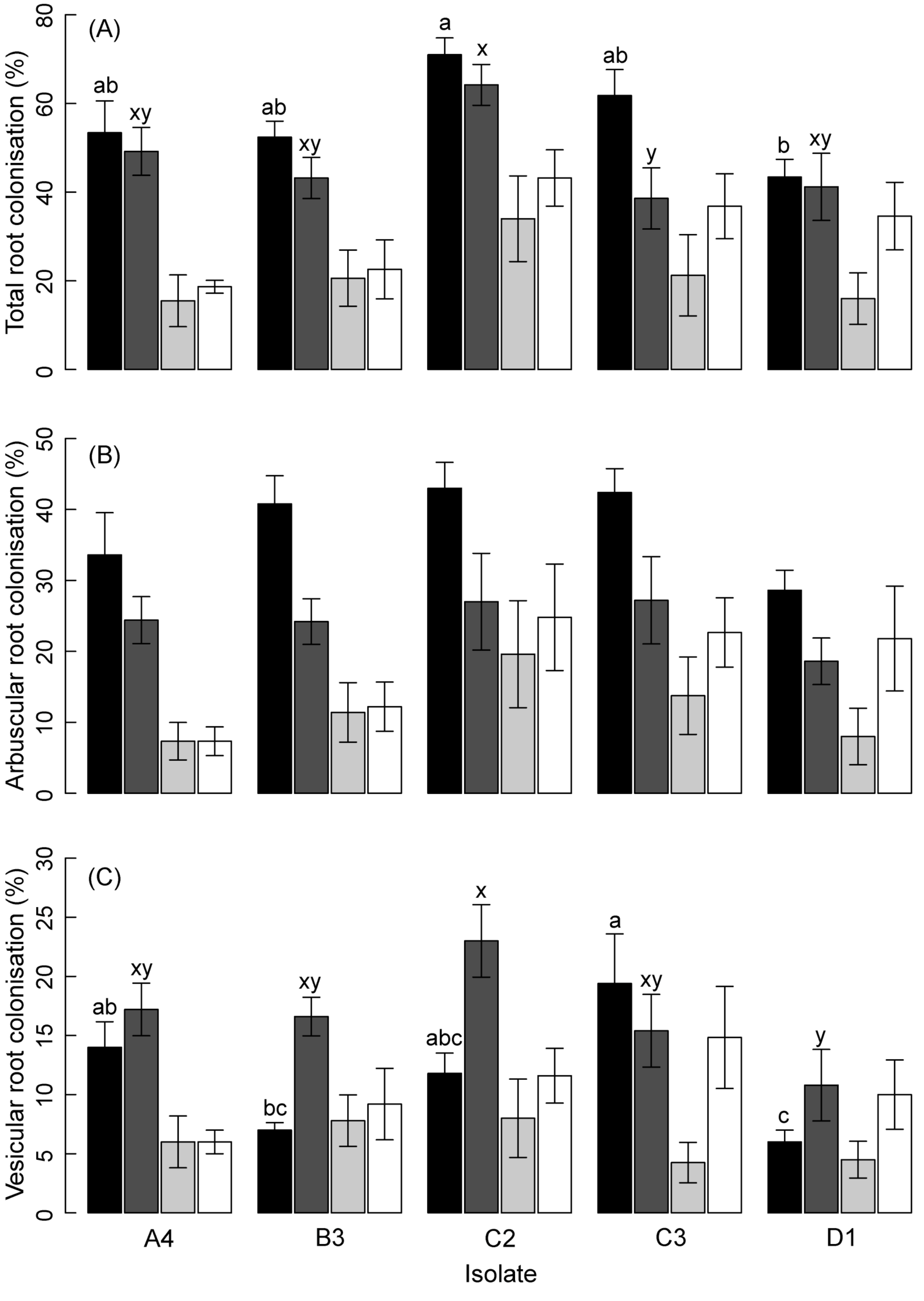

Fig. 2: Mean percentage total (A), arbuscular (B) and vesicular (C) root colonisation of *Hieracium pilosella* (black), *Prunella grandiflora* (dark grey), *Plantago lanceolata* (light grey) and *Plantago media* (white) plants grown singly with one of five isolates of *Glomus intraradices*. Error bars represent ± one standard error. Different letters above bars of the same plant species indicate a significant difference according to Tukey's HSD test ($p < 0.05$).

Chapter 6: General discussion

The general aim of my thesis was to investigate the role of dispersal and competition for plant coexistence. My approach was to experimentally test basic model assumptions and theoretically derived hypotheses from spatial plant ecology. On the one hand, I examined the consequences of altered seed dispersal distance under field conditions and compared them with predictions from theory (chapter 2). On the other hand, I explored the distances of intra- and interspecific competitive interactions and how these attenuate with distance (chapters 3 and 4). Special attention was paid to the role of arbuscular mycorrhizal fungi (AMF) therein (chapter 4). I focussed on pair-wise interactions – basic elements of individual-based models – by combining target plants with single neighbours. These experiments also provide the first experimental tests of heteromyopia. I further tested for within-population host-specificity of AMF (chapter 5). The results of this last experiment may serve as basis for future experiments, exploring the role of AMF in neighbourhood interactions and heteromyopia.

The role of dispersal for plant population dynamics

Theory suggests that seed dispersal may contribute substantially to population dynamics and plant coexistence (Tilman & Kareiva, 1997; Levine & Murrell, 2003; Cousens *et al.*, 2008). However, in natural communities, additional processes besides seed dispersal affect the spatial structure of plant communities (Peart, 1989; Schupp & Fuentes, 1995; Houle, 1998; Nathan & Muller-Landau, 2000). The seed dispersal pattern depends on the abundance, spatial distribution and fecundity of reproductive plants and on landscape structures that may act as seed traps. Interactions between neighbouring plants and processes related to environmental conditions affect the survival and fitness of established individuals. Therefore, the consequences of seed dispersal distance for community patterns are not clear *a priori*. The majority of dispersal studies have focussed on long-distance dispersal, and the importance of small scale seed dispersal on the local abundance, distribution and coexistence of plant species is still under-explored (Schupp & Fuentes, 1995). Theoretical papers strongly advocate experiments that directly manipulate dispersal patterns. Rather than providing extra seeds, experimental studies should manipulate the spatial distribution of seeds by first collecting all seeds produced in a plot and then dispersing them randomly or locally (Bolker & Pacala, 1999; Levine & Murrell, 2003). The resulting abundance, distribution and coexistence of species within such replicate plots should then be compared to that in unmanipulated control plots.

The experiment described in chapter 2 pursued this approach and focussed on dispersal from a local, individual to population level perspective. The aim was to test whether variation in the seed dispersal distance – with all other community processes unaffected – leads to a significant change in the abundance and spatial distribution of plants, using the perennial forb *Prunella grandiflora* as model species. As the experiment revealed, the spatial pattern and the abundance of vegetative individuals were clearly affected, while reproductive individuals showed no significant response to seed dispersal manipulation. Increasing dispersal distance increased the abundance of vegetative individuals, and decreasing dispersal distance resulted in a more aggregated spatial distribution of these. In synthesis, this study provides experimental evidence that dispersal indeed plays an important role in local population dynamics of natural plant communities, as has been claimed by theory.

However, the results of this experiment also indicate that the population response to dispersal takes some time to establish and may be further obscured by initial spatial structure and stochastic and density-dependent processes. That I found no effects of dispersal manipulation on the reproductive stage seems most likely due to a time-lag in response. The initial spatial distribution and abundance sets a template from which the new patterns result from manipulated dispersal. Many of the initial individuals will have survived until the end of the experiment, thereby "echoing" the initial spatial pattern. Effects of dispersal distance should, however, primarily evolve from individuals emerging from experimentally dispersed seeds. In a perennial species like *P. grandiflora* it takes time to override the original signature, thus reproductive individuals could be expected to react slower than vegetative individuals. Therefore, I assume that my study was too short to capture the response of the reproductive stage.

As a consequence, I cannot draw direct conclusions about the influence of dispersal distance on reproductive population dynamics. Although it seems intuitively very likely that an alteration in abundance and spatial distribution of the vegetative stage will eventually be reflected by the reproductive stage, experimental proof is needed. Running this experiment over a period of three years or even longer could have provided clarity. However, due to the time limits of a PhD thesis, this was not feasible. Alternatively, I could have followed the individual fates of experimentally distributed seeds or of seedlings germinating in spring in order estimate average germination, survival and reproduction rates. Field-parameterised simulation models could then have been developed with these additional data. Choosing an annual plant species might have been another option. However, annuals are largely missing in calcareous grasslands such as our study site, which was chosen because *P.*

grandiflora used in the other experiments occurred with sufficient abundance. Moreover, calcareous grasslands in the Swiss Jura region harbour a large plant diversity, and testing theories for plant coexistence is especially exciting in species rich communities.

Despite these caveats, this experiment has shown that seed dispersal scale significantly affects the spatial distribution and local population dynamics of the recruiting stage – at least in the short run. However, it still remains to be demonstrated into what direction long-term population dynamics under manipulated seed dispersal would go and whether short time advantages would persist. An interesting further step would be to manipulate the dispersal scales of co-occurring strong and week competitors simultaneously and to test for theoretically derived dispersal strategies (c.f. Bolker & Pacala, 1999).

Competitive interactions between neighbouring plants

Competition in nature results from a complex interplay of components, such as neighbour number, size, identity and distance. To advance our understanding of local competition, one has to reduce this complexity to its components and to vary these experimentally (Purves & Law, 2002; Ramseier & Weiner, 2006). Theory has to make assumptions about the distances over which individuals interact (e.g. Bolker & Pacala, 1999; Murrell & Law, 2003; Snyder & Chesson, 2004). Despite a large body of competition studies in herbaceous systems (see e.g. Goldberg & Barton, 1992; Gurevitch *et al.*, 1992), the spatial scales of interactions in these communities have been rarely investigated. It has been shown theoretically that a competitively weaker species can invade a population of a superior species if the average distance at which conspecifics compete is longer than the average distance at which heterospecifics compete (“heteromyopia” Murrell & Law, 2003). The two defining features of this proposed coexistence mechanism are (1) that intraspecific competition occurs over longer distances than interspecific competition; and (2) that interspecific interactions are more intense than intraspecific interactions at short distances, whereas at longer distances, this relationship is reversed. Despite its potential implications for population and community dynamics, empirical evidence for heteromyopia is still outstanding. Greenhouse experiments allow to control for environmental heterogeneity and to isolate the actual effects of the components in focus from natural complexity. In two experiments (chapters 3 and 4), I examined the most basic elements of individual-based models by studying pair-wise interactions. The aim of both experiments was to evaluate potential differences in within- and between-species interaction distances and thereby to test for heteromyopia.

No evidence for heteromyopia

In the first target–neighbour experiment (chapter 3) the distances over which intra- and interspecific competition could be detected varied substantially. However, no general pattern, e.g. intraspecific interaction distances being larger than interspecific interaction distances, was revealed. I found larger intra- than interspecific interaction distances for the stronger competitors within each species pair but no evidence for a reversal of the relative importance of intra- and interspecific competition at larger distances. These findings provided no evidence for heteromyopia. I assume that direct belowground competition accounted for most neighbour interactions in this experiment, and I therefore conclude that if heteromyopia should prove to be a general coexistence mechanism, it probably does not result from resource competition.

It has been hypothesized that heteromyopia might be aided by mechanisms that indirectly shape the competition kernels (Murrell & Law, 2003), such as specialist pathogens, herbivores or seed predators (Janzen, 1970; Connell, 1971), host-specific mycorrhizal fungi (Stoll & Newbery, 2005) or allelopathy. The second target–neighbour experiment (chapter 4) additionally explored the question whether AMF influence interaction distances by letting plants grow with or without fungi. In contrast to the first target-neighbour experiment (chapter 3), I found no distance effects. That is, competition did not decline with distance, and this was not affected by the level of mycorrhization. Target individuals either performed worse than the control individuals over all three experimental distances or their performance was not significantly decreased at either distance. Arbuscular mycorrhizal fungi neither influenced the distances over which competition occurred nor how the strength of competition declined over distance. These findings suggest that AMF are unlikely to be involved in heteromyopia in herbaceous species from grasslands.

Taken together, these two experiments suggest that resource competition and – at least for forbs from calcareous grasslands – also AMF can be ruled out as potential mechanisms for heteromyopia. It has been hypothesized that host-specific mycorrhizal fungi lead to strong conspecific neighborhood effects in tropical trees (Stoll & Newbery, 2005). This would act to increase intraspecific interaction distances, which might contribute to heteromyopia. The vast majority of tropical tree species associate with mycorrhizal fungi and most of them with AMF (e.g. Onguene & Kuyper, 2001). Although, I found no indications that AMF may influence interaction distances, their potential for doing so in tropical trees remains an open question. Heteromyopia might also include host-specific vectors, such as specialist pathogens, herbivores or seed predators (Janzen, 1970; Connell, 1971) that could indirectly lengthen the distance over which conspecifics affect each other (Murrell & Law, 2003). Moreover, a recent example showed that Janzen–Connell effects mediated by soil pathogens may have been underestimated as drivers of plant diversity in temperate ecosystems such as grasslands (Petermann *et al.*, 2008), but the wealth of evidence is for tropical communities (see e.g. Wright, 2002; Freckleton & Lewis, 2006). Allelopathy might yet be another mechanism resulting in heteromyopia. Some plant species are known to produce chemicals that inhibit the establishment and growth of heterospecifics (e.g. Ridenour & Callaway, 2001), and this effect may decay very rapidly with distance (Sharma *et al.*, 2000; Gomez-Aparicio & Canham, 2008). However, allelopathic compounds have also been shown to inhibit conspecific seedling establishment (Perry *et al.*, 2005; Arteaga *et al.*, 2006), and the frequency and importance of allelopathy in plant-plant interactions is so far still widely unknown.

Considering the proposed mechanisms that involve host-specific vectors, it seems that heteromyopia should most likely be found in diverse communities, under rather homogenous environments, and should include long-lived species; under these conditions, host-specificity is likely to evolve (c.f. HilleRisLambers *et al*., 2002). Diverse tropical forests are therefore perhaps the most likely candidate systems for heteromyopia but diverse temperate systems, such as calcareous grasslands, should not be ruled out *a priori* (c.f. Petermann *et al.*, 2008).

The role of neighbour identity and relative neighbour size

The intensity of competitive interactions in both experiments (chapters 3 and 4) was primarily determined by the relative size differences between target and neighbour plants, irrespective of whether they were con- or heterospecifics. Species differed in their average final sizes. This seems most likely related to species-specific life–history traits, and I therefore consider size as a species-specific attribute. In conclusion, species-specific relative size differences between neighbouring plants are likely to be key factor determining the intensity of competitive interactions and must be incorporated into theory. It is interesting to note that the size of the neighbour relative to the target individual, rather than the absolute size of the neighbour explained most variation in the results. This emphasizes the importance of taking on the "plant's eye view" (Turkington & Harper, 1979) when examining and modelling plant–plant interactions. Discovering the various life-history traits that are associated with large or small neighborhood ranges is an important next step in uncovering the crucial processes that determine plant community structure and dynamics.

The experiment described in chapter 3 further revealed that a conspecific neighbour may be more important than a heterospecific neighbour but only as the neighbour becomes very large compared to the target individual. A nearby neighbour that is much larger will have a negative effect on an individual, regardless of its' species identity. However, my results suggest that there might be a general interaction between neighbour size and identity: the competitive response of a target individual was independent of neighbour identity, as long as the neighbour was of equal size or only slightly larger, but with increasing size differences, individuals became more sensitive towards conspecific neighbours. If such a size–identity interaction should be frequently found in empirical data, this could have important implications for community dynamics. For example, it may well affect seedling establishment, making establishment near a heterospecific of a given size more likely than establishment near a conspecific. It has been shown repeatedly for tropical trees that seedling establishment near heterospecifics is often more likely compared to establishment near conspecifics (e.g. Harms *et al.*, 2000). Moreover, my data suggest that such a size–identity interaction could further influence the performance of individuals at later stages. Both processes may promote coexistence and help maintain community diversity. Specific target–neighbour experiments, combining seedlings and adult plants, would be needed to test this hypothesis.

The role of arbuscular mycorrhizal fungi

While I found no effects of AMF on the spatial scales of competitive interactions, my second target–neighbour experiment (chapter 4) revealed that, on average, mycorrhizal and high-mycorrhizal plants were less affected by neighbours. On the one hand, AMF reduced the competitive response to neighbours of a given size and thus enabled target individuals to tolerate larger neighbours, presumably by improving nutrient supply and reducing the strength of root competition. As far as I know, the question how AMF influence the competitive response in relation to neighbour size has not been investigated before. My results are interesting because they point towards a potential novel coexistence mechanism: if it should be generally found that AMF buffer the effects of relative size differences between neighbouring plants, they could play an important role in seedling establishment and in the coexistence of differently sized plant species.

I further found that AMF lowered the coefficient of variation of target and neighbour aboveground biomass. This means that target and neighbour were of more equal sizes under mycorrhizal and high-mycorrhizal conditions than under non-mycorrhizal and low-mycorrhizal conditions. Interestingly, this effect resulted only from heterospecific pairs that included *Plantago lanceolata*, the species least affected by the level of mycorrhization. Thus, AMF decreased size inequalities within heterospecific pairs mainly by increasing aboveground biomass of otherwise smaller species. To my knowledge, size-equalising effects of AMF have not been reported so far. Competition experiments detected either no change or an increase in size inequalities of mycorrhizal compared to non-mycorrhizal plants (Allsopp & Stock, 1992; Moora & Zobel, 1998; Facelli *et al.*, 1999; Ronsheim & Anderson, 2001; Ayres *et al.*, 2006). However, all these studies focussed on intraspecific competition, and I found decreased size inequalities due to AMF only within heterospecific pairs (including *P. lanceolata*). Although *P. lanceolata* has shown a large sensitivity to AMF in other studies (van der Heijden, 2002), in my experiments (chapters 4 and 5) it was the species that least responded to AMF. It would therefore be interesting – and relatively easy – to test whether size-equalising effects of AMF vary between neighbours with different mycorrhizal dependencies.

Taken together, these findings point out a potentially new aspect of AMF in plant–plant interactions. I therefrom hypothesise that AMF may promote coexistence by reducing size inequalities and effects of size differences between neighbouring plants. However, I assessed the effects of single neighbours, and there is evidence that, as plant density increases, the beneficial effects of AMF decline (e.g. Allsopp & Stock, 1992; Hartnett *et al.*, 1993; Facelli *et al.*, 1999). Possible mechanisms may include increasing overlap of nutrient depletion zones, a reduction in mycorrhization level or an increase of the cost–benefit ratio of AMF colonisation (for references see review of Koide & Dickie, 2002). Therefore, further experiments that vary neighbour density are needed to test the proposed hypothesis.

Comparison of the two target–neighbour experiments

The two target–neighbor experiments (chapters 3 and 4) addressed the same main question: does intra- and interspecific competition differ in how it declines over distance? While the first experiment (chapter 3) revealed clear effects of neighbour distance, i.e. neighbour effects declined with distance, I found no such effects in the second experiment (chapter 4). At the first glance, this seems contradictive. However, the reason therefore is likely lying within the slightly different experimental set ups.

In the first experiment (chapter 3), target individuals were always placed at the same position within the containers (3.5 cm distance from one container end) and the neighbour's position was changed according to the distance treatment. As a consequence, the amount of soil volume available to the target individual was small when the neighbour was placed very close (5cm distance) and increased with neighbour distance. Thus, under this set up, effects of neighbour distance and available soil volume were correlated. For the second target–neighbour experiment (chapter 4), I therefore decided to change the experimental set up. Both target and neighbour position changed according to the distance treatments: target and neighbour individuals were placed along the central longitudinal axis at equal distances from the centre, so that the amount of available soil was the same for target and neighbour and was kept constant over all distances. Moreover, the substrates used in the two experiments differed. In the first experiment, I used a substrate mixture consisting of quartz sand, soil from a calcareous grassland (the field site described in chapter 2) and loess. For the second experiment, it was not possible to re-establish the same substrate mixture because it would have been unsustainable to remove the needed amount of soil from the calcareous grassland. The compromise was to use a mixture consisting of the retained substrate from the first experiment (serving as AMF soil inoculum), TerraGreen and loess. In this mixture, plants grew noticeably larger than in the first experiment (approximately twice as much aboveground biomass).

The lack of distance effects in the second experiment may thus be the result of 1) constant amounts of soil available to the target individuals and 2) larger plants and consequently generally larger interaction distances. I believe that the second point is rather unlikely because, even if larger plants do result in larger interaction distances, I should still have found a difference in the effects between neighbours growing at 5 cm and 15 cm distance. It therefore seems more plausible that in the second experiment, belowground limitation via neighbouring roots at one side was compensated for by neighbour-free space at the opposite side, as target and neighbour positions changed.

Was it therefore a mistake to change the experimental set up between the two target–neighbour experiments? In my opinion it was not. Although the findings of the first experiment (strong distance effects) could not be reproduced in the second experiment, this discrepancy provided some useful insights concerning the set up of target–neighbour experiments. My results suggest that effects of neighbour distance are mainly effects of available soil volume. In natural communities, distance and available soil volume between neighbouring plants are linked (unless in the rare situation of two neighbouring plants growing without any other neighbours). Therefore, I recommend that target–neighbour experiments assessing the effects of neighbour distance also vary the amount of available soil. Concretely, this means that if I was to repeat such a target–neighbour competition experiment, I would go for the set up used in the first experiment (chapter 3). A conceptually, but not necessarily analytically, easier experimental set up might consist of multi-individual stands (e.g. Schneider *et al.*, 2006). Neighbourhood effects could then be integrated over all plants occurring within a certain radius of each individual. However, the dilemma would be that all neighbouring individuals mutually affect each other and pair-wise interactions cannot be extracted, while individual-based models are based on pair-wise interactions.

Consequences of functional variability within populations of arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi have long been considered to show no host-specificity. However, this view has changed dramatically since different AMF species have been shown to differ in their effects on plant growth, diversity and ecosystem productivity (e.g. Streitwolf-Engel *et al.*, 1997; van der Heijden *et al.*, 1998a; van der Heijden *et al.*, 1998b; van der Heijden *et al.*, 2003). Similarly, AMF performance has been shown to depend on plant species identity (Helgason *et al.*, 2002). Moreover, there is recent evidence accumulating that also functional diversity within AMF species causes significant variation in plant and fungal growth performance (Koch *et al.*, 2004; Munkvold *et al.*, 2004; Gamper *et al.*, 2005; Koch *et al.*, 2006; Ehinger *et al.*, in press). Functional diversity in mycorrhiza may be crucial from an ecosystem perspective since differences in individual performance can affect plant population and community dynamics.

In the greenhouse experiment described in chapter 5, I combined the *Glomus intraradices* isolates used by Koch *et al.* (2004; 2006) and Ehinger *et al.* (in press) with single plants of the four target species used in my target–neighbour experiments (chapters 3 and 4). This experiment aimed to evaluate how within-population genetic variability of an AMF species affects the performance of co-occurring plant species. I found that the different AMF isolates altered plant biomass and differed in their efficiency to colonise plant roots. This confirms previous findings (Koch *et al.*, 2006). However, my experiment showed in addition that plant species differed substantially in their susceptibility to different functional differences between these isolates. Interestingly, the most sensitive species, *Hieracium pilosella*, also showed the highest levels of percentage root colonisation and the least sensitive species, *Plantago lanceolata*, the lowest levels. It could thus be that plant species differ in their response to genetic variability within or between AMF species according to their infectability. However, my experiment and similar studies either focussed on one AMF species (Koch *et al*, 2006; Ehinger *et al., in press*) or one plant species (Munkvold *et al.*, 2004; Gamper *et al.*, 2005) at a time. Further experiments, combining plant species that differ in AMF infectability and/or dependency with different AMF isolates and species, are therefore needed before general conclusions can be drawn.

Host-specificity of AMF species or isolates might play an important role in plant neighbourhood interactions, including heteromyopia. On the one hand, if neighbouring plants are colonised by AMF that differ in their efficiency to extract nutrients from the soil, or if plant species differ in their ability to become colonised, their belowground zones of influence may differ in size due to the AMF associates. On the other hand, AMF can connect the roots of many plant individuals (con- and heterospecifics) via common mycorrhizal networks (CMN). If two plants from different species provide unequal amounts of carbon to a shared fungus, and/or acquire nutrients unequally from a fungus that they both support, one species will benefit from this association to the detriment of the other (Selosse *et al.*, 2006). Similarly, carbon and nutrients might flow from “source” to “sink” plants connected via CMNs, although there is much debate about the physiological and ecological relevance of this (Robinson & Fitter, 1999; Selosse *et al.*, 2006). My experiment was originally planned as a pilot study to search for specific plant–isolate pairs. I was hoping to find one or several isolate(s) that one plant species performed well and another plant species bad with. This would have required statistically significant plant–isolate interactions, which I, however, did not find. Also Koch *et al.* (2006) reported no significant plant–isolate interactions. It thus seems that genetic diversity within AMF species has less potential for host-specificity than genetic diversity between AMF species.

Spatial variation in the benefits provided by AMF could have profound consequences for plant population and community dynamics and may hint at a novel facet of plant ecology. My experiment revealed that plant species differed in their susceptibility to within-population functional variability of an AMF species. Genetically-based heterogeneity in the benefits provided by an AMF species may further interact with small-scale environmental heterogeneity in the field. The possible outcomes of such complex interactions on individual plant performance are manifold but difficult to predict without further investigation.

Closing remarks

In this last section, I wish to briefly discuss a few “side-effects” of my experiments. All these unforeseen events involved AMF. At the moment, I consider mycorrhizal fungi as very fascinating, important belowground agents that, however, are a little difficult to handle.

My first target–neighbour experiment (chapter 3) originally consisted of twice as many containers as described in the final manuscript and included presence and absence of AMF as additional treatment. Half of the containers were treated with the fungicide Carben (Carbendazim 60 SC, Sintagro AG, Härkingen, Switzerland) in order to get non-mycorrhizal conditions. Carben contains the same active ingredients as Benomyl, a standard fungicide, very frequently used to get mycorrhiza-free controls (c.f. Kahiluoto & Vestberg, 2000). Unexpectedly, most of the plants in the non-mycorrhizal treatment grew so poorly that 113 days after sowing, about half of them had died. Therefore, it was decided to continue this experiment with the mycorrhizal plants only and to focus on the role of AMF in target–neighbour interactions in a second experiment (chapter 4). It is not clear whether Carben-treated plants performed so badly due to unknown, harmful effects of the fungicide or whether plants were not able to grow and survive without AMF in the substrate mixture I used. For any experiment that plans the use of fungicides in order to get non-mycorrhizal soil conditions, I consequently strongly recommend performing a pilot study to test whether plants are able to survive in fungicide-treated substrate.

My second target-neighbour experiment (chapter 4) therefore included presence and absence of AMF as treatment. This time, I sterilised the substrate and inoculated plants from the mycorrhizal treatment by adding non-sterile soil that contained AMF spores and hyphen. As it turned out, in the end, also plants from the non-mycorrhizal treatment were colonised by AMF. Average total root colonisation of plants from the non-mycorrhizal treatment was substantially smaller compared to plants from the mycorrhizal treatment, and I also found very few vesicles in roots of plants from the non-mycorrhizal treatment. I therefore assume that the substrate was sterilised successfully but that plants from the non-mycorrhizal treatment became infected at an advanced stage of the experiment. Contamination via dust containing AMF spores seems very likely and could probably have been avoided under more sterile greenhouse conditions.

Another idea was to work with mycorrhiza-defective mutants for target–neighbour experiments. I planned to work with *Petunia hybrida* line W 138 (provided by the research group of Didier Reinhardt, University of Fribourg, CH) as model organism. In *P.*

hybrida there exist several mutant lines that cannot successfully establish a mycorrhiza. By using the wild type (WT) and a mycorrhiza defective mutant (MUT), mycorrhizal and non-mycorrhizal conditions would have been regulated at the level of plant individuals rather than substrate, which would have superseded fungicides and soil sterilisation. Combining WT and MUT plants in pairs could for example have simulated extremely host-specific AMF species (thus, one plant would have been mycorrhizal and the other one not). However, the mutant lines proved not to be genetically stable yet, and this idea was abandoned in favour of the other experiments.

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Curriculum vitae

Personal Data

Name	Deborah Ruth Vogt (nee Renz)
Born	09 April 1979
Nationality	Swiss
Place of origin	Basel
Marital Status	Married

Education

2006 – 2009	University of Basel. PhD in Botany. PhD thesis: “Spatial mechanisms promoting plant coexistence: the role of dispersal and competition.” Advisor: PD Dr. Peter Stoll
1998 – 2004	University of Basel. Diploma Biology I (Master in Integrative Biology). Diploma thesis: “Spatial patterns in old fields: new approaches to conserve biodiversity” Supervisor: PD Dr. Peter Stoll Subsidiary Subjects: Ecophysiology and System Ecology, Population Biology, Vertebrate Biology Elective Subjects: Geosciences, Sustainable Development
1990 – 1998	Gymnasium Bäumlihof, Basel. Matura Type B.

During my studies I attended lectures by:

Barnett P., Baur B., Berger U., Boller T., Clausen M., Ebert D., Erhardt A., Fabbro T., Gehring W.J., Ghazoul J., Grimm V., Grossniklaus U., Gurevitch J., Hauri H.-P., Hector A., Kaden T., Kawecki T., Klein A., Körner C., Kraft P., Lüdin E., Meyer C., Oelhafen J., Oetiker J., Railsback S., Rasplus J.-Y., Rodewald R., Rusterholz H.P., Schneider H., Senn D., Siegel H., Stearns S.C., Stöcklin J., Stoll P., Tanner M., Trevelyan R., Weiss N., Wiemken A., Wurtz M., Zschokke S.

Working experience

Feb 2006 – March 2006	ecos consulting, Basel (CH): exhibition and congress evaluation.
Aug 2004 – July 2005	Federal Office for Agriculture, Section Ecology, Bern (CH): practical.
Sept 2001 – July 2004	University of Basel, Department of Environmental Sciences, Section Conservation Biology (CH): research assistant.

Publications

Vogt, D.R., D.J. Murrell and P. Stoll (in press) Testing spatial theories of plant coexistence: No consistent differences in intra- and interspecific interaction distances. *American Naturalist*.

Armbruster, G.F.J., **D. Renz** and M. Schweizer (2005) Eine dreijährige Feldstudie zum sichtbaren Frühjahrszug am Bodensee (Süddeutschland). *Vogelwarte* 43: 171-178

University Training Courses

June 2009	Sommer school course on individual- and agent-based modelling, Bad Schandau, Germany; Prof. Uta Berger, TUD Dresden
July 2008	Field course on conservation management, Beinn Eighe National Nature Reserve, Scotland; Prof. Jaboury Ghazoul, ETH Zürich
July 2008	Training course in meta-analysis, ETH Zürich; Dr. Jessica Gurevitch, University of New York
June 2008	Statistical course on multiple regression model selection using information criteria and multi-model averaging in R, ETH Zürich; Prof. Andy Hector, University of Zurich
Oct 2006	Course on advanced statistics using R; Dr. Thomas Fabbro, University of Basel
Nov 2002	Field course on tropical ecology and conservation, Kirindy Forest, Madagascar; Tropical Biology Association (TBA)
July 2001	Field course on plant ecology, Engelberg, Switzerland; Prof. Christian Körner, University of Basel
June 2001	European workshop in population biology, Guarda, Switzerland; Prof. Dieter Ebert, University of Basel

Conference Contributions

May 2009	Oral presentation at the Plant Population Biology Working Group Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Bern (CH)
Sept 2008	Poster at the Annual Meeting of the British Ecological Society, London (UK)
May 2008	Oral presentation at the Plant Population Biology Working Group Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Luxembourg (L)
Feb 2008	Oral presentation at the biology'08 (Annual Meeting of the Swiss Zoological, Botanic, Mycological and Systematic Societies), Lausanne (CH)
Sept 2007	Oral presentation at the Annual Meeting of the British Ecological Society, Glasgow (UK)

Invited talks

June 2009	Institute of Environmental Sciences, University of Zürich (CH): "Where to be and who to be there with: competitive coexistence in plants."
Oct 2007	Agroecology, Georg-August-Universität, Göttingen (D): "Competitive coexistence in plant species: do intra- and interspecific interaction distances differ?"

Awards

May 2009	Best oral presentation, Plant Population Biology Working Group Meeting GfÖ 2009
Sept 2008	Runner up poster prize, Annual Meeting of the British Ecological Society 2008
Feb 2008	Best oral presentation, biology'08