Small-scale spatial pattern and dynamics of experimental plant communities

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Summary

Plant-plant interference is inherently local and seed dispersal generally limited. Both processes generate spatial and genetic structure within plant populations and communities that need to be better understood in order to predict dynamic community changes due for example to biodiversity loss or global change. There is increasingly strong theoretical evidence that spatial pattern is an essential factor controlling the species dynamics of many communities. In particular, one conclusion from spatial models is that intraspecific aggregation promotes coexistence by slowing down competitive exclusion. Whereas local interactions contribute to interspecific segregation, limited seed dispersal leads to aggregation at two hierarchical levels: i) species within communities and ii) genetically related individuals (e.g. siblings) within populations. However, especially for plant communities there is a need for experimental tests of the predictions generated from spatial models.

The principal goal of this thesis was to narrow the gap between theoretical and empirical investigations on the role of spatial pattern in plant communities and population dynamics. I focused on the effects of spatial pattern on the dynamics of experimental plant communities at the level of species as well as at the level of genotypes within species. In particular, I (i) manipulated the spatial pattern, i.e. the relative frequency of intra- vs. interspecific contacts and (ii) contrasted the performance of genetically related (half-sibs) vs. non-related individuals. The basic goal of the experiments was to investigate whether different spatial patterns (random vs. aggregated) and relatedness of neighbors had any effects on population dynamics within experimental plant communities.

The experiments provided interesting results and showed essential aspects of the role of intraspecific aggregation and sibling interference in regulating the dynamics of populations within experimental plant communities. I showed that weak competitors increased their fitness (e.g. biomass and seed production) when grown in neighborhoods of conspecifics compared to neighborhoods of heterospecifics, at least in the short run. The data further suggested that the advantages of intraspecific aggregation for weaker competitors might be independent of the species identity and that all other species are best avoided.

An additional aggregation at the level of genotypes (e.g. seed families) suggested species-specific effects linked with seed size. For instance, I found negative sibling competition effects for the small-seeded species (*Capsella*), while rather positive effects for the large-seeded species (*Stachys*). Negative effects of sibling competition were also observed among relatives of sunflower seed families. By contrast, genetically similar individuals of the

dimorphic species *Senecio jacobaea* increased their fitness (e.g. biomass) compared to genetically dissimilar individuals. However, also this species suggested seed traits specific relatedness effects (e.g. dispersal ability). Positive relatedness effects were more evident by seeds expected to aggregate more locally (without pappus) than by seeds expected to disperse wider (with pappus). Generally, I observed lower size variation (measured as coefficients of variation) among related compared to non-related individuals. This might be a consequence of more genetic uniformity and / or kin selection among relatives compared to non-relatives. Although, I could not provide strong evidence for sibling competition or kin selection, I believe that relatedness among plants, especially for species with highly localized dispersal, should play a considerable role in the regulation of local population dynamics. Similar to the species level, there must be subtle trade-offs (e.g. between neighbour relatedness and density) that determine the complicated local dynamics of plant communities. However, the question under which circumstances and to which extent relatedness effects are species-specific remains open and deserves further investigation.

At the level of species, effects of intraspecific aggregation on the dynamics of experimental plant communities were clear and consistent throughout my experiments. By contrast, at the level of genotypes, they were less clear and to some extent contrasting. This emphasized the importance for further investigations on population dynamics at levels below that of species.

From an applied point of view, findings of this thesis might help to give better information for management practices (e.g. restoring species rich communities). For example, by varying spatial pattern (random vs. intraspecifically aggregated) of selected species in wildflowers strips or fallows, the dominance of undesired species (e.g. *Dipsacus* sp.) and the exclusion of weaker species can be delayed.

Chapter 1

General introduction

An excursion in the tropical forest, hiking in the Alps or simply a visit to a botanical garden, gives a taste of the wonderful diversity of the plant worlds. Today there are approximately three hundred thousand flowering plant species (e.g. Scotland and Wortley 2003; Govaerts 2003), but each year their natural habitats shrink and are fragmented by human encroachment. As a result, a great number of plant species are presently at risk of extinction (e.g. Walter and Gillett 1998; IUCN Red List of Threatened Species 2006) and preventing these extinctions is an urgent task. However, understanding the forces structuring plant communities is required, to predict potential changes in community structure due to the extinction of species, introduction of alien species, changes in management practices, pollution and other anthropogenic factors threatening biodiversity and the services of ecosystems.

According to Darwin's theory of natural selection, individuals of species with favorable traits are more likely to survive and reproduce than those with unfavorable traits (Darwin 1859). Nevertheless, plant communities often display a remarkable richness of species – up to 300 tree species ha^{-1} can be found in some tropical forests and up to 40 herbaceous plant species m^{-2} in certain temperate grasslands (Silvertown and Law 1987). The questions that arise are: how than in a world threatened by the strongest ones, does such high diversity evolve? Or in other words, how can seemingly similar, competing species coexist with one another? Why are there not only few dominant species?

Plant diversity, whether in tropical forests or chalk grassland, is a puzzle. The paradox, that somehow similar species compete with one another and yet coexist, is the same for tropical forests as for chalk grassland and the possible solutions to the paradox are, at least in theory, very similar, if not the same. Much research has been devoted toward understanding how individuals of co-occurring plants species both affect and respond to one another and how these interactions influence structure, dynamics and evolution within plant communities (Harper 1977; Grime 1979; Schoener 1983; Grace and Tilman 1990; Bazzaz 1996; Keddy 2001). Elucidating, however, the many ways in which competing plant species manage to coexist remains one of the central issues in ecology (Hutchinson 1961; Silvertown and Charlesworth 2001).

Numerous biological and physiological processes influence the presence of a plant species in a locality, its abundance and the number of other plant species with which it coexists. Abiotic and biotic factors may greatly affect plant dynamics and community structure. Competition both within and among species is one of the major forces determining the distribution and abundance of plant species and the biodiversity of plant communities.

Competition and evolution are tightly intermingled: species that form biodiversity are first created by evolution through speciation and conversely the structure of a plant community (and thus biodiversity) influence competition and thus evolutionary pressures.

Early non-spatial competition models (e.g. Lotka-Volterra competition model, Lotka 1925; Volterra 1926) assume infinitely large spatial scales of competition and dispersal distances. They predict that no more species can coexist than there are limiting resources and that coexistence can only occur if interspecific competition is less significant than intraspecific competition (Begon et al. 1990). These predictions are also known as the competitive exclusion principle (Gause 1934). This was later generalized to the statement that *n* species could not coexist on fewer than *n* resources or limiting factors (e.g. MacArthur and Levins 1964; Levins 1968). When a single resource was explicitly included in such a model, the species formed a competitive hierarchy, with poorer competitors displaced as the resource was depleted by superior competitors (Tilman 1982). The competitive exclusion principle immediately raised a paradox of diversity, however ('plankton-paradox', Hutchinson 1961). A given habitat, such as a grassland or lake, contains hundreds of species, but the number of limiting resources (e.g. nutrients, water, light) is relatively small. However, no community is truly the homogeneous, temporally invariant system described by simple Lotka-Volterra mathematics. Spatial aggregation is common in natural plant communities as there is substantial evidence that neither seeds nor individual plants are uniformly distributed in space (Thompson 1986; Rees et al. 1996; Tilman and Kareiva 1997; Maranon 1998). Hence, because plant-pant interference and seed dispersal are localized processes, Pacala (1997) and others argued that predictions from non-spatial models are unrealistic because classical competition models ignored these important small-scale spatial patterns. Consequently, quantification of the importance of coexistence mechanisms in determining species diversity and relative abundance require the use of spatially explicit models to capture the spatial structure of the habitat. Spatial models deal with the implication of spatial structure for major ecological phenomena such as stability, coexistence, biodiversity, invasions and pattern formation (Tilman and Kareiva 1997).

To persist in a community, a species must find moments when (time), and places (space) where it can send seeds that will be able to germinate and give birth to new individuals which in turn will find enough resources and space to survive and develop into new adults. It is now widely recognized that many species can coexist by partitioning space according to the heterogeneity of some traits of the physical environment (Chesson 2000). It is similarly recognized that plant species can coexist by partitioning time according to some variable traits of the environments (Chesson and Warner 1981). Very simply said, coexistence between species persists as long as inferior competitors can escape superior ones in time and / or space.

Many additional hypotheses have attempted to explain the coexistence of species with similar life histories (e.g. Shmida and Ellner 1984; Chesson 2000; Wright 2002; Shea et al 2004; Barot 2004; Silvertown 2004). Recently, Barot (2004) reviewed the mechanisms proved to foster coexistence, though often only theoretically. Here, I will mention only few of them. The classical competition theory based upon the Lotka-Volterra competition model leads to the expectation that stable coexistence between competing species requires that each species must specialize on its own 'private' part of the available resources. Thus, competition restricts the physiological to the ecological niche. In other words, species having the same ecological niche cannot coexist. While the niche hypothesis appears to explain coexistence in many animal communities remarkably well, it is difficult to see how it can work so easily for plants. The problem is that all plants require the same few essential resources (i.e. light, water, nutrients) and obtain them in a very limited variety of ways. Not only do most plants require the same resources and acquire them in similar ways, but it is also now clear from field experiments that interspecific competition for these resources is the norm in plant communities (Aarssen and Epp 1990; Goldberg and Barton 1992; Gurevitch et al. 1992). Moreover, plants that live together in the same community obviously tend to experience similar environmental conditions. Nevertheless, Silvertown (2004) reconsidered the role of niches in plant communities. He pointed out that although it is unlikely that niche separation along environmental axes is the only mechanism of coexistence in any species-rich community, there is nevertheless evidence suggesting that it plays a more significant role than has been previously appreciated. Indeed, if a study finds that species do not partition one particular niche axis, it cannot be rule out that there are other dimensions in which niche differentiation has taken place (Silvertown and Law 1987). Moreover, less is known about niche relationships among genotypes within species (Vellend 2006). Another classical mechanism is the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). This hypothesis suggests that the concentration of natural enemies around parent plants would subject their offspring growing nearby to heavy and fatal attack. Only the few offspring arising from seeds that had been dispersed a long way from the parent would escape. This would prevent local concentration of one species building up. Grubb (1977) emphasized the importance of the entire life cycle of an individual and its ability to become established as a part of the environment, which has recently became vacant (regeneration niches). A further mechanism explaining coexistence is based on the existence of a trade-off between colonization and competitive ability, i.e. good competitors are bad colonizers and *vice versa* (Tilman 1994; Levine and Rees 2002). In this case, weaker species can escape by colonizing newly created gaps, which are difficult to reach for stronger competitors. Empirical studies provide evidence for the importance of such trade-offs in communities of sand-dune annuals (Rees 1995; Turnbull et al. 1999, 2004). Such trade-offs are particularly important if disturbances remove strong competitors and create new gaps for colonization (Connell 1978; Huston 1979). Murrell and Law (2003) proposed a spatially explicit competition model that showed that if interspecific competition occurred over shorter distances than intraspecific competition, spatial segregation becomes strong enough to promote coexistence. However, this mechanism, known as heteromyopia, has not yet been experimentally tested. The most extreme approach explaining plant coexistence was proposed by Steve Hubbell in his Unified Neutral Theory (Hubbell 2001). He proposed that (i) species are competitively equivalent, (ii) niche differences are irrelevant, and (iii) species diversity is governed by the rate of random extinction and speciation events. However, in a recent study on species-specific neighborhood effects in the dipterocarpaceae of a Bornean rain forest, Stoll and Newbery (2005) provide empirical evidence that not all neighbors are equivalent, which disagrees with Hubbell's neutral model (2001).

Intraspecific aggregation is still another mechanism that has been theoretically shown to foster coexistence. Although seeds have evolved many adaptations to increase dispersal (e.g. Ellner 1986), the majority of seeds are dispersed over very short distances (Willson 1993; Cain et al. 2000). Consequently, most plant species create aggregations of conspecifics, thereby increasing the importance of intraspecific competition relative to interspecific competition (spatial segregation theory, Pacala 1997), which should promote coexistence. Therefore, the spatial pattern of individuals within and among species is central in ecological theory (Huston et al. 1988; Pacala 1997; Dieckmann et al. 2000). It means that the frequency with which individuals have other individuals of the same or different species as neighbors depends less on the relative abundance than on the particular spatial pattern. Thus, survivorship and fecundity are affected more by local population density than by the average density of the population (Pacala and Silander 1985; Pacala 1997; Stoll and Weiner 2000; Murrell et al. 2001).

Intraspecific spatial aggregation and interspecific spatial segregation are very common in plant communities and are expected to slow down the competitive exclusion of weaker competitors. It decreases the contacts between heterospecific individuals and thus diminishes the chances of stronger competitors to invade local patches occupied by poorer competitors. Yet, at the cluster edges the species with the better competitive ability should be able to invade the cluster of the weaker competitor (Chesson and Neuhauser 2002). Thus, clusters of dominant species should slowly exclude clusters of less competitive species. Sooner or later, weaker competitors have to escape the stronger ones. Otherwise, they will go extinct.

A host of theoretical work underlines the importance of spatial pattern for ecological phenomena, such as coexistence and maintenance of biodiversity (Kareiva 1990; Bergelson 1990; Coomes et al. 2002; Bolker et al. 2003; Levine and Murrell 2003), ecosystem function (Pacala and Deutschman 1995; Simioni et al. 2003) and the spread of invasive species (Travis and Park 2004). However, this theoretical work also highlighted that the effects of spatial structure can be complex, depending on the relative magnitude and spatial scales of competition, environmental heterogeneity and dispersal (see Murrell and Law 2003; Snyder and Chesson 2003, 2004). Thus, the effects of spatial pattern depend on the details, suggesting that if general statements about the role of space are possible, they will need to be based on empirical work in natural communities (Amarasekare 2003; Bolker et al. 2003). Unfortunately, progress on the empirical front has been comparatively slow and an experimental validation of spatial ecology is still largely missing (e.g. Law and Watkinson 1989; Rejmánek 2002; Amarasekare 2003; Bolker et al. 2003). The lack of empirical studies, particularly with plants, results in part from the complexity of spatial structure itself (Bolker et al. 2003). Nevertheless, there is some empirical evidence that spatial pattern affects plant community dynamics in such a way that weak competitors might increase their fitness within neighborhoods of conspecifics compared to neighborhoods of heterospecifics. For example, an early experimental study with two clonal perennials showed that after three years, interspecific competition was reduced and coexistence of competitors facilitated, in intraspecifically aggregated populations of *Solidago canadensis* and *Urtica dioica* (Schmidt 1981). Bergelson (1990) in an experiment with *Capsella bursa-pastoris* and *Senecio vulgaris* showed that the performance of *Capsella* and *Senecio* was much higher when grown in a patchy matrix of *Poa annua* than in a matrix of randomly distributed *Poa*. Stoll and Prati (2001) tested the prediction from spatial competition models, that aggregation may promote coexistence by slowing down competitive exclusion and thus maintain biodiversity. Using an experimental plant community composed of four annual species, they showed that the spatial pattern of individuals altered the competitive interactions in plant communities and facilitated coexistence at least in the short-term. In particular, they found that weaker competitors increased the above ground biomass when intraspecifically aggregated, especially at high density where competition was greater than at low density. On the other hand, competitively superior species produced lower biomass in the aggregated pattern than in the random pattern at high density. Although, other studies showed similar pattern effects on population dynamics (Harper et al. 1961; Brophy and Mundt 1991; Stauber et al. 1991; Norris et al. 2001) there are still controversial views over what permits competitors to coexist in the absence of obvious niche differentiation, conspicuous life history trade-offs (e.g. competition / colonization trade-off; Rees 1995; Turnbull et al. 1999, 2004) or evident disturbance (Connell 1978) (e.g. Neuhauser and Pacala 1999; Wright 2002; Levine and Murrell 2003; Amarasekare 2003; Barot 2004; Silvertown 2004). Even if spatial processes do promote coexistence, there remains a question as to how important these processes are relative to other non-spatial ones (Adler and Mosquera 2000; Chesson and Neuhauser 2002).

Much of community ecology is predicated on the notion that the fitness of individual organisms depends on their own identity rather than on the identities and abundances of other community members. Extensive emphasis has been placed on species as the fundamental unit of observation. However, genetic differences among individuals within species may have important consequences for community level phenomena such as consumer-resource dynamics (Neuhauser et al. 2003) and competitive interaction (Pimentel 1968; Levin 1971; Aarssen 1989). Therefore individual fitness may depend not only on the species identity of other community members, but on their genotypic identity as well (Aarssen 1989).

The evolutionary consequences of neighbor interaction depend on the spatial genetic structure of a population. Because of limited seed and pollen dispersal, many plant populations exhibit a high degree of spatial genetic structure (Govindaraju 1988; Levin 1988), with the consequence that neighboring conspecifics are often relatives (half- or full-sibs). In other words, when the prevailing pattern of dispersal results in relatives being aggregated in space and interacting primarily with one another, then local competition may become sibling competition (Cheplick 1992, 1993a,b; Kelly 1996). Therefore, in plant species with spatially limited dispersal the effects of spatial pattern should not only operate at the level of species but also at the level of genotypes within species (Schmid 1990; Vuorisalo et al. 1997; Wilson and Nisbet 1997).

It is well accepted that the intensity of competition should increase with genetic similarity of the competitors and that parental fitness is lowered if there is severe competition between their descendants (Maynard Smith 1978). According to the resource-partitioning hypothesis (Young 1981; Argyres and Schmitt 1992), genetically variable offspring will experience less severe competition than genetically similar or identical offspring. This is because of the greater ability to partition available resources. Hence, especially in plant species with relatively short dispersal distances, mature individuals that produce a large number of offspring are at greater risk of fitness losses due to sibling competition. Thus, competition among sibling affects the microevolution of populations, leading to life-history attributes that counteract the phenomenon. For example, it has been suggested that adaptation favoring seed dispersal (Schoen and Lloyd 1984; Venable and Brown 1988, 1993; Willson 1992; Cheplick 1993b) or seed dormancy (Ellner 1986; Silvertown 1988; Venable and Brown 1988; Nilsson et al. 1994) may be more strongly selected when sibling competition is significant.

Alternatively, individuals may behave more altruistically and less competitively toward their relatives, because of their common genes. Consequently, helping a relative to reproduce, an individual can contribute to its genes to the next generation. The kin selection theory shows how individuals gain inclusive fitness indirectly by increasing the reproduction of related individuals as well as directly through their own reproduction (Hamilton 1964; Maynard Smith 1964). In its simplest form, Hamilton's rule states that altruistic behavior is favored when $rb-c > 0$; where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary and r is their genetic relatedness. In other words, an individual may reduce its own fitness (for example being less competitive toward their relatives) if the costs are compensated with increased fitness of its relative. From the very beginning, two distinct means of benefiting relatives have been distinguished (Hamilton 1964). First, individuals might distinguish relatives from other individuals that are encountered. For plants, this might be of less importance as for mobile organisms. Indeed, the sessile-life style and limited dispersal results almost automatically in nearest neighbors being relatives. Nonetheless, there is some evidence of self / non-self discrimination in roots (Falik et al. 2003) and that roots are able to detect and avoid the presence of neighboring roots of the same individual (Krannitz and Caldwell 1995). Second, highly localized dispersal (population viscosity) was proposed to increase the probability that positive interactions among group members will benefit relatives as opposed to unrelated individuals and thereby promoted the evolution of altruistic behavior (Hamilton 1964; Wilson 1987). However, Taylor (1992) showed theoretically that, in viscous populations, competition can exactly counteract the advantage of being in a group with altruistic relatives such that limited dispersal ultimately does not influence the probability of the evolution of altruism (Queller 1992, 1994; Taylor 1992; Wilson et al. 1992; West et al. 2001). Unfortunately, empirical tests of theory that determine the relative importance of increases in both relatedness and competition between relatives, have been hindered because both factors are influenced by dispersal, and so their effects are usually confounded (Queller 1992,1994; Frank 1998; Kelly 1994).

Inherited differences in the ability to grow and reproduce under competitive conditions can produce differences in the degree of suppression and dominance among neighbors as a function of the relatedness among those neighbors. This relatedness among competitors can affect their abilities to reproduce in such a way as to favor neighbors that are more closely related. Hence, especially for plant species with frequent sibling interactions (e.g. heavy, locally dispersed seeds) the possibility that kin selection might be selected to restrain competition, to promote altruism and to regulate parent-offspring behavior should not be excluded (Nakamura 1980; Cheplick 1993b; Kelly 1996; Griffin and West 2002).

Despite the straightforward predictions from sibling competition and kin selection hypotheses, empirical work on plants still lags behind and the current knowledge is scanty and equivocal.

Only few studies could show that plants competing with genetic relatives outperformed those competing with unrelated individuals (Willson et al. 1987; Tonsor 1989; Andalo et al. 2001; Donohue 2003). In an experiment comparing genotypes at two CO_2 concentrations (ambient vs. elevated), Andalo et al. (2001) found that at ambient CO_2 concentration, the fitness of a genotype was greater when surrounded by the same genotype than when surrounded by individuals of different genotypes. Tonsor (1989) showed that the number of *Plantago lanceolata* flowering per pot increased with an increase in genetic relatedness from non-sibs to half-sibs to full-sibs and Willson et al. (1987) observed that *Phytolacca americana* plants growing with their siblings showed a transient enhancement of size compared to plants growing with non-siblings. Noteworthy, Donohue (2003) in a field experiment with the annual dune species *Cakile edentula* provided solid evidence that higher reproductive success occurred when individuals grew with siblings compared with non-sibling, in support of the kin selection hypothesis. However, such positive sibling competition effects are rather unusual, as most studies that were designed to detect effects of neighbor relatedness on fitness did either detect only slight effects or none at all (e.g. Willson et al. 1987; Schmitt and Ehrhardt 1987; McCall et al. 1989; Kelley 1989; Argyres and Schmitt 1992; Cheplick 1992; Karron & Marshall 1993; Delesalle and Mazer 2002; Cheplick and Kane 2004).

Whether genetically similar individuals might ‘cooperate’ in some ways and / or kin selection may work as selective agent in plant communities is not yet known. This information would be valuable first in order to establish the ecological and evolutionary importance of sibling competition and second to better describe the dynamics of local competition in plant populations and communities.

Focus of this thesis

The basic goal of this thesis was to narrow the gap between theoretical and empirical investigations on the role of spatial pattern in plant communities and population dynamics.

With four experiments, I tested the effects of spatial pattern on the dynamics of experimental plant communities at the level of species as well as at the level of genotypes within species. In particular, I (i) manipulated the spatial patterns, i.e. the relative frequency of intra- vs. interspecific contacts and (ii) contrasted the performance of genetically related vs. non-related individuals.

Specifically, I asked:

1. Does spatial pattern (i.e. random vs. aggregated) of species influence the dynamics of experimental plant communities?
2. Whether an additional aggregation at the level of genotypes within species had any negative or positive effects on individual performance, which may be interpret as sibling competition or kin selection.
3. Does the individual growth and reproduction depend on the relatedness of neighbors? If yes, do genetically variable individuals have greater potential to partition limiting resources than genetically similar individuals? Do related individuals, mainly because of similar growth, show more equal (symmetric) resources share compared to non-related individuals?
4. Does seed dimorphism (e.g. seeds with pappus vs. seeds without pappus) affect individual growth and reproduction of genetically related and non-related individuals differently? Specifically, do the effects of growing among relatives differ among individuals grow from seeds expected to aggregated more locally (seeds without pappus) than among individuals grown from seeds expected to disperse more wider (seeds with pappus)?

In the experiments described in **Chapter 2 and Chapter 3** I investigated the effects of spatial pattern and density on the relative importance of intra- and interspecific competition. I set up two similar field experiments using the annual species *Capsella bursa-pastoris*, *Stachys annua*, *Stellaria media* and *Poa annua*. I hypothesized that weak competitors increased biomass and seed production within neighborhoods of conspecifics, while stronger competitors would show increased biomass and seed production within neighborhoods of heterospecifics. Results of both experiments confirmed that spatial patterns affect growth and reproduction of plant species in such a way that weak competitors increased their fitness when grown in neighborhoods of conspecifics compared to neighborhoods of heterospecifics.

Data of the first spatial pattern experiment (**Chapter 2**) further suggested that for the weakest competitors the species identity is not important and all other species are best avoided through intraspecific aggregation. They, further draw attention to the complexity of community dynamics and the balance between spatial and non-spatial factors. The second spatial pattern experiment (**Chapter 3**) extended the first one and aimed to evaluate effects of intraspecific aggregation not only at the level of species, but also at the level genotypes (e.g. seed families) within species. Specifically, I collected seed families of *Capsella* and *Stachys* (seeds were at least half-sibs), which allowed me to assess not only effects of intraspecific aggregation but also effects of intrafamily aggregation on the growth and fitness of individuals. Although I could not provide strong evidence for sibling competition or kin selection, the results suggested that competition among relatives was more severe for *Capsella* (lighter seeds) compared to *Stachys* (heavier seeds).

Chapter 4 and **Chapter 5** describe two different experiments (a greenhouse and a field experiment) with the same goal to contrast the performance of genetically related with non-related individuals. Additionally, I compared the size variation (measured as coefficient of variation) and hence indirectly the competition mode (asymmetric vs. symmetric) of individuals competing with genetically related versus non-related individuals. In both experiments different degrees of relatedness were realized by collecting seeds from individual mother plants. Seeds within such seed families were at least half-sibs. Depending on how resources are partitioned among individuals it is possible to distinguish between two modes of competition. If the resources are divided disproportional to the size of the competitors, competition is called 'size-asymmetric' competition. By contrast, when resources are divided equally or proportionally to the size of competing individuals, competition is called 'size-symmetric'. Because of the genetic similarity it might be argued that related individuals would share the resources more equally compared to non-related individuals. Therefore, it might be expected that competition would be more symmetric in populations composed of genetically related and more asymmetric in populations of non-related individuals. In the greenhouse experiment (**Chapter 4**) I used seeds collected from maternal plants of *Senecio jacobaea* (Asteraceae). *Senecio* is a dimorphic species and produces two kinds of achenes with different morphologies and ecological behavior (McEvoy and Cox 1987). Seeds produced in the centre of the flower head are small and bear a pappus that aid wind dispersal, while seeds produced on the edge of the flower head are heavy and do not have a pappus

(Harper and Wood 1957). Therefore, *Senecio* provided an excellent opportunity to study the interactions between related and non-related individuals with different dispersal abilities. Results of this experiment showed that (i) related individuals had lower coefficients of variation compared to non-related individuals, indicating less asymmetric competition and (ii) related individuals produced more biomass than non-related individuals. Additionally, positive effects of growing among relatives were more evident among individuals grown from seeds expected to aggregated more locally (seeds without pappus) than among individuals grown from seeds expected to disperse more widely (seeds with pappus). Therefore, taken together these results did not support the sibling competition hypothesis, but provide at least some support for the kin selection hypothesis.

The experiment described in **Chapter 5** investigated similar questions as the greenhouse experiment, but differs in three main points: (i) it was conducted under more natural conditions, (ii) it used another plant species and (iii) it used a different experimental design. In this experiment I used seeds collected from six maternal plants of *Helianthus annuus* (Asteraceae). Individuals were sown either in groups of related (i.e. seeds from the same seed family) or in groups of non-related individuals (i.e. seeds from different seed families). The findings showed that groups of non-related individuals produced more vegetative and reproductive biomass than groups of related individuals. Moreover, I found slightly lower size variation (coefficient of variation) among groups of related compared to groups of non-related individuals. This indicated a more symmetrical resource sharing among related compared to non-related individuals. Results of this experiment suggested that groups of non-related individuals had greater potential to partition limiting resources (below- and aboveground) compared to groups of related individuals, according to the resource-partitioning hypothesis. Therefore, aboveground biomass data of this experiment were in opposition to the aboveground biomass data obtained in the greenhouse experiment. Remarkably, even though the results on biomass production were completely different, related individuals showed lower coefficients of variation than non-related individuals in both experiments. To keep in mind, however, is that the two experiments described in Chapter 4 and Chapter 5 used different plant species and different experimental designs.

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Chapter 2

Spatial patterns and species performances in experimental plant communities

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Abstract

Amongst the various hypotheses that challenged to explain the coexistence of species with similar life-histories, theoretical and empirical studies suggest that spatial processes may slow down competitive exclusion and hence promote coexistence even in the absence of evident trade-offs and frequent disturbances. We investigated the effects of spatial pattern and density on the relative importance of intra- and interspecific competition in a field experiment. We hypothesized that weak competitors increased biomass and seed production within neighborhoods of conspecifics, while stronger competitors would show increased biomass and seed production within neighborhoods of heterospecifics. Seeds of four annual plant species (*Capsella bursa-pastoris*, *Stachys annua*, *Stellaria media*, *Poa annua*) were sown in two spatial patterns (aggregated vs. random) and at two densities (low vs. high) in three different species combinations (monocultures, three and four species mixtures). There was a hierarchy in biomass production among the four species and *Capsella bursa-pastoris* and *Stellaria media* were among the weak competitors. *Capsella* and *Stellaria* showed increased biomass production and had more individuals in the aggregated compared to the random pattern, especially when both superior competitors (*Stachys annua, Poa annua*) were present. For *Poa annua* we observed considerable differences among species combinations and unexpected pattern effects. Our findings support the hypothesis that weak competitors increase their fitness when grown in the neighborhood of conspecifics, and suggested that for the weakest competitors the species identity is not important and all other species are best avoided through intraspecific aggregation. In addition, our data suggest that the importance of spatial pattern for the other competitors might not only depend on the position within the hierarchy but also on the identity of neighbor species, species characteristics, below ground interactions, and other non-spatial factors.

Key-words: annual species, coexistence, intra- and interspecific competition, population dynamics

Introduction

Competition both within and among species is one of the major forces determining the distribution and abundance of plant species and the biodiversity of plant communities (Tilman 2000). Although most plants compete for the same resources (light, water and nutrients) we observe large numbers of coexisting species in many plant communities (Silvertown and Charlesworth 2001). One of the central issues in ecology remains to explain how large numbers of species are able to coexist in natural communities. Many hypotheses have attempted to explain the coexistence of species with similar life-histories (see e.g. Chesson 2000; Wright 2002; Shea et al. 2004; Barot et al. 2004). Intuitively, spatial heterogeneity of resources used by plants is probably one of the most powerful promoters of niche separation and coexistence between plants. However, niche separation alone cannot explain the more species-rich communities. Grubb (1977) emphasized the importance of the entire life cycle of an individual and its ability to become established as part of the environment, which has recently become vacant (regeneration niches). Another classical mechanism explaining coexistence is based on the existence of a trade-off between colonization and competitive ability: good competitors must be poor colonizers and *vice versa* (Tilman 1994; Levine and Rees 2002). In that case coexistence occurs because species with sufficiently high dispersal rates persist in sites not occupied by superior competitors. Recent, studies provided empirical evidence for the importance of such trade-offs in communities of sand-dune annuals (Rees 1995; Turnbull et al.1999, 2004). Moreover, such trade-offs are particularly important if disturbances remove strong competitors and create new gaps for colonization (Connell 1978, Huston 1979). However, explaining species coexistence in the absence of conspicuous life-history trade-offs and in relatively homogeneous environments remains challenging and controversial (see e.g. Amarasekare 2003; Barot 2004). As a consequence of the limited seed dispersal and/or clonal growth, most plant species create aggregations of conspecifics, thereby increasing the importance of intraspecific competition relative to interspecific competition (spatial segregation hypothesis, Pacala 1997). This is particularly relevant to plant communities, because most of the ecological and genetic interactions between individual plants are with their immediate neighbors. Therefore, survivorship and fecundity are affected more by local population density than by the average density of the population (Pacala and Silander 1985; Pacala 1997; Stoll and Weiner 2000; Murrell et al. 2001). There is a large body of theories that underlines the importance of spatial pattern for ecological phenomena, for example coexistence and maintenance of biodiversity (Kareiva 1990; Bergelson 1990; Rees 1995, Rees et al.1996; Murrell et al. 2001; Coomes et al. 2002; Bolker et al. 2003;

Levine and Murrell 2003). Indeed, one proposed mechanism promoting coexistence is that intraspecific aggregation caused by limited seeds dispersal and local interactions might slow down competitive exclusion. Although spatial theory has made great strides in advancing the understanding of coexistence in patchy environments, progress on the empirical front has been comparatively slow and an experimental validation of spatial ecology is still largely missing (see e.g. Rejmánek 2002; Amarasekare 2003; Bolker et al. 2003). Nevertheless, an early experimental study (Schmidt 1981) with two clonal perennials showed that after three years, interspecific competition was reduced and coexistence of competitors facilitated, in intraspecifically aggregated populations. Bergelson (1990) in an experiment with *Capsella bursa-pastoris* and *Senecio vulgaris,* showed that the performance of *Capsella* and *Senecio* was much higher when grown in a patchy matrix of *Poa annua* than in a matrix of randomly distributed *Poa*. Recently, Stoll and Prati (2001) tested the prediction, made from spatial competition models, that aggregation may promote coexistence by slowing down competitive exclusion and thus maintain biodiversity. Using an experimental plant community composed of four annual species, they showed that the spatial pattern of individuals altered the competitive interactions in plant communities and facilitated coexistence at least in the short-term. In particular, they found that weaker competitors increased the above ground biomass when intraspecifically aggregated, especially at high density where competition was greater than at low density. On the other hand, competitively superior species produced lower biomass in the aggregated pattern than in the random pattern at high density. Other studies showed similar pattern effects on plant population dynamics (Harper et al. 1961; Brophy and Mundt 1991; Stauber et al. 1991; Norris et al. 2001). Nevertheless, there are still controversial views over what permits competitors to coexist in the absence of conspicuous life-history trade-offs and frequent disturbances (e.g. Neuhauser and Pacala 1999; Wright 2002; Levin and Murrell 2003; Amarasekare 2003; Barot 2004). Moreover, because empirical and experimental evidence of effects of intraspecific aggregation on species interactions is still poor, the question whether or not intraspecific aggregation of species prevents or promotes coexistence remains open (Chesson 1991; Chesson and Neuhauser 2002; Murrell et al. 2002; Bolker et al. 2003). Indeed, the simplistic view of aggregation as a mechanism of coexistence of plant species proposed by some studies (e.g. Pacala1997; Pacala and Levin 1997; Murrell et al. 2001, 2002) has been criticized and the importance of trade-offs between life-history parameters (Bolker and Pacala 1999) in the explanation of plant species coexistence has been stressed (Chesson and Neuhauser 2002). In response to Chesson and Neuhauser (2002), Murrell et al. (2002), gave an example in which the spatial extension of a non-spatial model allowed coexistence of two species even without trade-offs. Furthermore, Murrell and Law (2003) using an explicitly spatial versions of the Lokta-Volterra model showed that weaker competitors were able to coexist with their stronger rivals when interspecific interaction occurred over shorter distances than intraspecific interactions (heteromyiopia). Thus, as the authors suggested, it is most likely that there are some conditions under which spatial structure promotes coexistence and others under which it does not.

The goal of the present experiment was to investigate the effects of spatial pattern and density on the relative importance of intra- and interspecific competition on plant dynamics. This experiment expands the pilot experiment of Stoll and Prati (2001) and differs in three ways: i) it relies on more natural conditions (not stem sterilized soil and less weeding), ii) plants grew on a heavy soil with high clay content, and iii) substitutes a common annual species (*Cardamine hirsuta*) with a rare annual species (*Stachys annua*). In both experiments the four plant species were annuals with different morphologies. Based on the pilot experiment we hypothesized that spatial pattern may affect the growth and the fitness of plant species in such a way that weaker competitors may benefit (i.e. would show increased biomass and seed production) in an aggregated compared to a random pattern, while stronger competitors would show increased fitness in random compared to aggregated patterns. Furthermore, because overall density of plants generally affects the intensity of competition, we expect the effect of intraspecific aggregation to be more evident at higher densities.

Materials & Methods

We investigated the effects of spatial pattern and density on plant performance and community dynamics in a field experiment (at the Research Institute of Organic Agriculture (FiBL), Frick, Switzerland) using four annual plant species with different morphologies. *Capsella bursa-pastoris* L. (Brassicaceae) is a rosette-forming plant with a multi-flowered erect stem up to 40 cm high. *Poa annua* L. (Poaceae) has adventitious roots at the first nodes and tillers up to 30 cm high. *Stellaria media* L. (Caryophyllaceae) is prostrate to ascending, with high adventitious rooting and a height of up to 40 cm. *Stellaria* and *Poa* are widely distributed, cosmopolitan annuals of disturbed habitats. *Stachys annua* L. (Lamiaceae) has a multi-flowered erect stem up to 40 cm high. Compared to the other three species, *Stachys annua* is quite rare in most parts of Europe. Moreover, members of the Brassicaceae (e.g. *Capsella*) and Caryophyllaceae (e.g. *Stellaria*) are usually considered non-mycorrhizal, while members of the Poaceae (e.g. *Poa*) and Lamiaceae (e.g. *Stachys*) are generally mycorrizal (Harley and Harley 1987; Smith and Read 1997).

The experiment was designed as a split-plot and contained 2 blocks (0.6 x 8 m, separated by 0.5 m), established between May 20 and 24 and harvested in the fall of 2002. Each block was subdivided into an upper- and lower subblock (Fig.1). During the first two months the 2 blocks were covered with a plastic tunnel (200 holes/m^2, GVZ-Bolltec AG, Zürich, Switzerland) to protect the seedlings from adverse weather and full sunlight. Each block contained eight main plots (0.6 x 0.6 m, separated by 0.3 m). Spatial pattern and density were used as plot-level treatments and each treatment was replicated twice per block and randomly assigned to plots (Fig.1). The plots were sown between May 30 and June 4 and watered each evening until May 6; thereafter, an automatic irrigation system (Gardena AG, Bachenbülach, Switzerland) was installed. The system was programmed to give rain cycles lasting 1 minute (i.e. 1 liter water) starting at 5:15 a.m., 6:15 a.m., 7:15 a.m., and 7:15 p.m., 8:15 p.m., and 9:15 p.m. The duration of the 8:15 p.m. rain cycle was changed from 1 to 2 minutes on June 25.

The combinations of mixtures of species (see below) and monocultures were used as within-plot treatments. The plots were subdivided into nine subplots (0.2 x 0.2 m), each of which contained either one of the four species in monoculture, one of the four possible three-species mixtures, or the four-species mixture (Fig.1). In the random pattern, seeds of each species were sown over the subplots so that in the mixtures, the individuals experienced inter- and intraspecific encounters at the same frequency. In the aggregated pattern, the subplots were further subdivided into 16 cells (5 x 5 cm), and each cell contained only one of the species in such a way that individuals experienced more intra- than interspecific encounters (Fig.1). The species were randomly allocated to the cells. In the four-species mixture, each species occupied four cells, whereas in the three-species mixtures, each species occupied five cells and one third of the sixteenth cell. At low density, we sowed 10 seeds per cell (4000 seeds/m^2) whereas at high density we sowed 100 seeds per cell (40000 seeds/ m^2). After sowing, in order to increase germination, the seeds were covered by a layer (2 cm) of commercial garden soil, instead of the heavy soil (high clay content), and pressed down slightly to prevent the seeds from being washed away. The seeds were obtained from a commercial supplier (Herbiseed, Wokingham, Berkshire, UK) and counted using a mechanical seed counter (Elmor). 100 seeds for each species were weighted to determine the mean seed weight.

A snail fence enclosed the entire experimental field and slug pellets were regularly used to curtail herbivory.

The above ground biomass was harvested between August 20 and September 29, and the total number of individuals per species was counted. For *Poa* we counted ramets rather than genets. When the total number of individuals per species exceeded 10, we randomly selected 10 individuals, measured their height, and separated vegetative from reproductive parts. We only separated vegetative from reproductive biomass for the remaining plants. Almost all individuals of *Stellaria, Capsella* and *Stachys* produced flowers, while only few *Poa* flowered. The harvested biomass was dried at 60° C for 48 h in Frick and then stored. Before it was weighed the biomass was dried again for 17 h at 60° C.

Since the fixed automatic irrigation system might have affected the above ground biomass production we tested i) the correlation between the amount of water supplied by the fixed automatic irrigation system and total biomass of all fours species produced at the subplot level, and ii) the effects of both factors by using an analysis of covariance. Because no correlation was found and since the total biomass of all four species produced at the subplot level showed a significant covariate effect, we decided to use the total biomass as indirect measure to quantify the effects of the fixed irrigation system and other unknown factors. Since the main treatments (pattern and density) varied at the plot rather than at the subplot level, the covariate should not be confounded with the main treatments.

The data were analyzed with multifactorial analysis of covariance (ANCOVA). The main effects (pattern, density) and their interaction were tested against the plot-level residual mean square. When the effect of the species mixtures combinations was significant, we used linear contrasts to separate them into i) the difference between monoculture and mixtures and ii) difference between the three- and four-species mixtures.

In the cases where the design became unbalanced because of missing values (i.e. subplot where plants did not growth) we used regression analysis or performed the analysis, either without the corresponding subplots, or restricted the analysis to the high density. In the particular case for *Capsella* and *Stellaria* when the analysis was restricted to the species combinations with *Stachys* and *Poa*, there were at the low-density two missing values: four species mixture/random pattern and four species mixture/aggregated pattern. Because the results of the analysis changed significantly depending on whether we considered those missing values as 'true zero' or left them out, we decided to present both results. Generally we did the analysis without the factor 'subblock' because it was not significant. However, for *Poa* we integrated it in the analysis for the vegetative biomass, number of individuals, and the coefficient of variation (CV) in length because it had a significant effect. Using the 10 selected individuals, the CV in length, vegetative and reproductive biomass was evaluated to assess the mode of competition (i.e. symmetric vs. asymmetric).

The data were calculated as grams per square meter and log-transformed to obtain normal distribution of the residuals and homogeneity of variances. Back transformed means and standard errors from the analysis are presented throughout.
All analyses were conducted using the program GENSTAT 5 (Payne et al.1987).

Results

Stachys annua had the heaviest seeds, followed by *Stellaria media, Poa annua,* and *Capsella bursa-pastoris* with the lightest seeds. *Stachys* produced the highest biomass, followed by *Poa*, *Capsella* and *Stellaria (*Table 1).

The spatial pattern affected the growth and the fitness of *Capsella,* and to some extent, *Stellaria*, in such a way that there was an increase in biomass, seed production, and number of individuals in the aggregated compared to the random pattern.

The analysis for *Capsella* excluding the monoculture, showed higher biomass in the aggregated (vegetative = 167.11 g/m^2; reproductive = 19.86 g/m^2) compared to the random pattern (vegetative = 100.23 g/m^2; reproductive = 9.46 g/m^2) (Table 2a). In addition, the total number of individuals was significantly higher in the aggregated (851.14 ind/m^2) compared to the random pattern (527.23 ind/m^2) (Table 2a). These spatial pattern effects were only marginally significant for both vegetative and reproductive biomass, yet they were more pronounced in the species mixtures with *Stachys* and *Poa* (Table 2b, Fig. 2). In this case, vegetative biomass of *Capsella* increased by 186% and reproductive biomass by 126% within neighborhoods of the same species, which corresponded to an increase of about roughly 10'000 seeds/m^2 (Fig.2).

Capsella in the species combinations together with *Stachys* and *Poa* at the high-density treatment showed significantly higher coefficient of variation (CV) for length in the aggregated (81%) compared to the random pattern (63.9%) ($F_{1,4}$ = 13.85, p = 0.020).

For *Stellaria* the positive effects of aggregation occurred only in those mixtures where *Stachys* and *Poa* were present (Table 3, Fig.3). *Stellaria* increased the vegetative biomass by 288% and the reproductive biomass by 280% in the aggregated compared to the random pattern (Fig.2). *Stellaria* did not show any significant differences in size variation between patterns.

The analysis for *Poa annua* including all combinations, showed significantly higher vegetative biomass in the aggregated compared to the random pattern (Table 4). In addition, we found highly significant differences among the species combinations (Table 4). The linear contrasts indicated that this effect was due to the differences between the four species mixture and the three species mixtures ($F_{1,4}$ = 6.27; p = 0.016). Moreover, they showed significant differences among three species mixtures with *Stachys* and without *Stachys* ($F_{1,4}$ = 10.58; p = 0.002) (Fig.3).

The total number of individuals of *Poa* differed significantly among species combinations (Table 4). The calculated linear contrasts showed that the differences were again due to the differences between the species mixture and the monoculture ($F_{1,4}$ = 9.09; p = 0.004) and among three species mixtures with *Stachys* and without *Stachys* ($F_{1,4}$ = 14.95; p = <.001). Although, we restricted our analysis to the high-density treatment due to the missing values present at the low-density treatment, for *Stachys annua* we found neither treatment effects nor species combinations effects or significant interactions.

Discussion

Our experiment provided evidence that spatial pattern affected growth and reproduction of plants within an experimental community in a short run. Our results showed that compared to a pilot experiment (Stoll and Prati 2001), using a slightly ‘different’ experimental plant community and soil treatment, not only did the competitive hierarchy change, but so did the spatial pattern effects for the individual species. Our data on *Capsella bursa-pastoris* and, to some extent *Stellaria media,* were consistent with the pilot experiment and support the hypothesis that weak competitors may increase their fitness (e.g. survival and seeds production) within neighborhoods of conspecifics compared to neighborhoods of heterospecifcs, especially when the superior competitors were present in the community. Moreover, data on *Stellaria* (which was the strongest competitor in the pilot experiment, see below) suggested that for the weakest competitors the species identity is not important and all other species are best avoided through intraspecific aggregation. In addition, our findings for *Poa annua* revealed considerable differences among species mixture and unexpected pattern effects. This suggests that the importance of spatial pattern might not only depend on competitive hierarchies, and aggregation might be beneficial, because there may be positive interactions (e.g. complimentarity, mutualisms) associated with some of the other species.

Based on the total above ground biomass production, our results suggest two ‘main groups’: one composed of *Stachys annua* and *Poa annua* as strong competitors and one group composed of *Capsella bursa-pastoris* and *Stellaria media* as weak competitors.

Capsella was among the weaker competitors both in the pilot and the present experiment and showed increased biomass production and number of individuals in the aggregated compared to the random spatial pattern, especially in combination with the competitively superior species. By contrast, *Stellaria*, was the strongest competitor in the pilot and a weak competitor in the present experiment. Although, this species only partly confirmed our hypothesis, the data suggest a benefit of intraspecific aggregation, once again in combination with the competitively superior species. Note that in the pilot experiment *Stellaria* produced more above ground biomass in the random compared to the aggregated pattern, while in the present experiment behaved like the other weak competitor *Capsella*. Our results are quite remarkable, because they not only show the positive advantage of intraspecific aggregation for weak competitors, but also that these advantages do not seem to depend on species identity.

Our data about the two superior competitors *Stachys* and *Poa* do not agree, however, with the pilot experiment, where superior competitors were suppressed in the neighborhood of conspecifics. In fact, neither *Stachys* nor *Poa* increased their biomass in the random pattern. Furthermore, contrary to our expectations, the superior competitor *Poa* increased the vegetative biomass in the aggregated pattern as opposed to the random pattern. These results were unexpected and quite difficult to explain. For *Stachys* it is possible that the high data variability and the rather high number of missing values present in the low density treatment may have masked a possible treatment effect. On the other hand, our findings on *Poa* were similar to results found in a study with two perennial grasses where the superior competitive ability of *Agropyron* did not emerge based on the relative performance of this species in monoculture and mixture (Huber-Sannwald et al. 1996).

Besides, *Poa* showed different responses depending on community composition. *Poa* generally increased its fitness (i.e. vegetative biomass and number of individuals) if associated with the other superior competitor *Stachys*. This result could be explained with some complimentarity of species' traits and/or below ground mutualisms (see below). Findings on *Poa* suggest that the position of a species within a community hierarchy is not sufficient to predict effects of spatial pattern and that the importance of spatial pattern might depend on which species composed the communities.

In contrast to Stoll and Prati (2001), we observed another plant hierarchy in the community, which might be explained by i) different species composition; ii) different soil treatment, and iii) trade-offs. *Stellaria,* which was the strongest competitor in the pilot experiment, turned out to be the weakest in the present experiment. *Poa* changed its position from the second weakest to the second strongest competitor. Performances of *Capsella* did not vary between the two experiments and it remained as third weakest competitor. The newly introduced species, *Stachys*, was the strongest competitor. Intuitively, the substitution of *Cardamine hirsuta* (a rosette-forming plant of the Brassicaceae) used in the pilot experiment with *Stachys* used in our experiment could have changed the competitive interactions between the experimental plant species leading to a new plant hierarchy. However, the different soil treatments, which were a steam sterilized nutrient-rich garden soil in the pilot experiment and an unsterilized heavy soil with high clay content in the present experiment, might also explain the different hierarchies. Therefore, the presence or absence of mycorrhizal fungi in the soil could have played an important role determining the community structure (van der Heijden et al. 1998, 2003). There is growing evidence that the below ground biota (e.g. mycorrhizal fungi) play an important role in determining the community structure and coexistence of competitors (e.g. Hartnett and Wilson 1999; Klironomos et al. 2000; Klironomos 2002; Bever 2003). Recently, Hart et al. (2003) reviewed the importance of arbuscular mycorrhizal fungi

(AMF) in mediating plant coexistence. For example, West (1996) showed that if a highly competitive plant species is more infected by AMF, then AMF would simply reinforce competitive dominance of that species. Based on those considerations and the mutualism and antagonism in the mycorrhizal symbiosis and the impact on plant community (Francis and Read 1995), we speculate that the two superior competitors in our experiment might have experienced a kind of below ground mutualism between each other. However, some studies (DeMars and Boerner 1994; Ishii et al. 1998), have reported some vesicular-arbuscular mycorrhizal infection also in members of the Brassicaceae and Caryophyllaceae. Although these authors suggested that the mycorrhizas might be non-functional, we cannot exclude possible root interactions between our experimental plants species.

Nevertheless, also the competition/colonization trade-off (Tilman 1994; Rees 1995; Turnbull et al. 1999, 2004) could in part explain the different plant hierarchies. As expected the large-seeded *Stachys* was one of the superior competitors, while the small-seeded *Capsella* was one of the inferior competitors. By contrast, the second large-seeded (*Stellaria*) and the second small-seeded (*Poa*) were respectively the second weakest competitor and the second strongest competitor. This suggests that the performance (i.e. competitive ability) of a plant species and therefore its position in a given hierarchy, is not simply correlated with the seed size. Indeed, when appropriate biological details are included in theoretical models, the performance of individuals varies in response to other factors such environmental heterogeneity and competition with surrounding neighbors. Furthermore, there is evidence that high competitive asymmetries, in addition to competition/colonization trade-off are needed to explain coexistence (Adler and Mosquera 2000; Levine and Rees 2002). Recently, in a review about colonization, tolerance, competition and seed-size variation, Coomes and Grubb (2003), stressed the limits on the potential of competition/colonization trade-off to allow long-term coexistence without other forms of niche differentiation. So far, it remains an open question to which extend seed size, in particular the competition/colonization trade-off, together with spatial pattern (i.e. intraspecific aggregation) might benefit weak competitors and hence allow long-term coexistence by slowing down competitive exclusion (see e.g. Turnbull et al. 2004).

In contrast to the pilot experiment, we could not find any interactions between density and spatial pattern. Hence our hypothesis that the spatial pattern effect should be more evident at high density because of the higher intensity of the competition must be rejected. However, we suspect that the high variability of our data might have hidden such interactions, and thus complicated the interpretation of the outcomes.

This huge variability could be partially explained by the fixed automatic irrigation system, which systematically irrigated some subplots more than others. In consideration of the fact that we did not find a direct correlation between the amount of water and the total biomass of all four species produced for each subplot, we assume that the fixed irrigation system was not the only reason for the observed variability. For instance, other factors such as the high soil water storage capacity, may have favored some species and killed others.

In conclusion, we showed that spatial pattern affected an experimental plant community at least in the short run. Moreover, our findings supported the hypothesis that weaker competitors might increase their fitness (e.g. biomass and seed production) within neighborhoods of consepecifics compared to neighborhoods of heterospecifics. Furthermore, our data suggested that the advantages of intraspecific aggregation for weaker competitors might be independent of species identity and that all other species are best avoided. In addition, our findings on *Poa annua* revealed considerable differences among species mixture and unexpected pattern effects. This suggests that the importance of spatial pattern might not only depend on competitive hierarchies, and aggregation might be beneficial, because there may be positive interactions (e.g. complimentarity, mutualisms) associated with some of the other species. Although we did show that spatial pattern had an impact on the plant population dynamics, it remains unclear as how important these processes are relative to other non-spatial factors. In addition, more long-term experiments are needed in order to understand whether or not intraspecific aggregation promotes coexistence by retarding competitive exclusion. Accordingly, further studies are needed to better comprehend under which conditions the spatial pattern will affect the dynamics of a given plant community and under which conditions it may be ignored. On the other hand, a better knowledge of spatial pattern and plant population dynamics is needed in order to build predictive models and address more fundamental questions, such as the prediction of the importance, rather whether or not, a mechanism may promote coexistence in plant communities.

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Table 1 Seed mass and total above ground biomass for the four experimental species.

Species	Seed mass (mg/100 seeds)	Total above ground biomass (g m^{-2})
Stachys annua	113.0	637.8
Stellaria media	42.8	172.8
Poa annua	32.3	559.8
Capsella bursa-pastoris	9.8	202.4

Table 2 Results of ANCOVA for *Capsella bursa-pastoris* testing effects of spatial pattern, density and species combinations on above ground biomass production and number of individuals. a) excluding monoculture; b) restricted to the species combinations with *Stachys annua* and *Poa annua*. Covariate: total above ground biomass of the four experimental species at the subplot level.

a)

		Vegetative biomass		Reproductive biomass		Number of individuals	
Source of variation	d.f.	F-values	p-values	F-values	p-values	F-values	p-values
Block	1	0.07	0.835	0.11	0.796	0.05	0.861
Pattern (P)	1	3.91	0.076	4.49	0.060	9.30	**0.012**
Density (D)	1	0.59	0.460	0.89	0.367	23.37	**<.001**
P x D	1	0.00	0.983	0.26	0.621	0.98	0.977
Covariate	1	10.42	**0.009**	11.3	**0.007**	2.45	0.149
Plot level	10	1.83		1.76		2.27	
Combinations (C)	3	0.96	0.423	0.7	0.561	0.35	0.793
P x C	3	0.47	0.703	0.53	0.664	0.68	0.569
D x C	3	0.63	0.602	0.52	0.672	2.24	0.101
P x D x C	3	0.38	0.769	0.33	0.801	0.19	0.901
Covariate	1	15.60	**<.001**	22	**<.001**	0.05	0.824
Residual	35						

b)

		Vegetative biomass		Reproductive biomass		Number of individuals	
Source of variation	d.f.	F-values	p-values	F-values	p-values	F-values	p-values
Block	1	0.00	0.980	0.01	0.936	0.25	0.705
Pattern (P)	1	4.36	0.063	5.15	**0.047**	2.57	0.140
Density (D)	1	0.04	0.850	1.87	0.202	7.82	**0.019**
P x D	1	0.09	0.771	0.16	0.696	0.07	0.794
Covariate	1	18.31	0.002	20.2	0.001	0.00	0.950
Plot level	10	1.84		1.84		3.37	0.488
Combinations (C)	1	0.47	0.505	0.7	0.419	0.51	0.888
P x C	1	0.44	0.521	0.43	0.524	0.02	0.069
D x C	1	0.42	0.532	1.2	0.297	4.05	0.505
P x D x C	1	0.72	0.415	0.58	0.463	0.48	0.371
Covariate	1	12.68	**0.004**	22.9	**<.001**	0.87	
Residual	31						

Table 3 Results of ANCOVA for *Stellaria media* testing effects of spatial pattern and density on aboveground biomass production and number of individuals limited to the species combinations with *Stachys annua* and *Poa annua*. ANCOVA with missing values (n = 2) replaced with a '0'. Covariate: total aboveground biomass of the four experimental species at the subplot level.

		Vegetative biomass		Reproductive biomass		Number of individuals	
Source of variation	d.f	F-values	p-values	F-values	p-values	F-values	p-values
Block	1 (1)[1]	1.40 (0.06)	0.447 (0.847)	3.91 (0.86)	0.298(0.524)	3.06 (0.02)	0.331 (0.911)
Pattern (P)	1 (1)	4.37 (2.19)	0.063 (0.177)	6.15 (3.42)	**0.033** (0.102)	2.60 (2.30)	0.138 (0.168)
Density (D)	1 (1)	3.29 (1.33)	0.100 (0.282)	0.31 (0.03)	0.589 (0.878)	23.85 (37.94)	**<.001 (<.001)**
Combinations (C)	(1)	(0.08)		(0.09)	(0.776)	(0.14)	(0.714)
P x D	1 (1)	0.10 (0.36)	0.755 (0.788)	0.23 (0.48)	0.644 (0.507)	0.03 (0.10)	0.867 (0.758)
P x C	(1)	(3.07)	(0.567)	(3.79)	(0.087)	(0.37)	(0.561)
Covariate	1(1)	8.51 (6.50)	**0.015 (0.034)**	10.29 (6.84)	**0.009 (0.031)**	2.05 (1.19)	0.183 (0.307)
Plot level	10 (8)	0.89 (0.90)		0.75 (0.85)		1.03 (1.22)	
C	1 (1)	3.64 (2.18)	0.083 (0.174)	0.82 (0.68)	0.385 (0.432)	3.11 (1.31)	0.105 (0.281)
P x C	1 (1)	0.21 (0.04)	0.659 (0.851)	0.03 (0.05)	0.867 (0.829)	0.13 (0.56)	0.722 (0.473)
D x C	1 (1)	1.54 (0.15)	0.240 (0.704)	0.01 (0.15)	0.944 (0.705)	3.50 (0.87)	0.088 (0.375)
P x D x C	1 (1)	0.00 (0.39)	0.968 (0.545)	0.14 (1.26)	0.716 (0.290)	0.00 (0.09)	0.985 (0.770)
Covariate	1 (1)	2.01 (5.13)	0.184 (**0.050**)	4.63 (7.92)	0.055 (**0.020**)	0.22 (0.04)	0.647 (0.842)
Residual	11 (9)						

[1] Number in brackets () represented results of ANCOVA excluding the missing values.

Table 4 Results of ANCOVA for *Poa annua* testing effects of spatial pattern, density and species combinations on aboveground biomass production and number of individuals. Covariate: total aboveground biomass of the four experimental species at the subplot level.

		Vegetative biomass		Number of individuals	
Source of variation	d.f.	F-values	p-values	F-values	p-values
Block	1	1.61	0.332	0.63	0.511
Subblock	2	16.38	**0.003**	14.15	**0.004**
Pattern (P)	1	5.97	**0.040**	2.12	0.184
Density (D)	1	3.21	0.111	27.42	**<.001**
P x D	1	0.00	0.985	0.03	0.869
Covariate	1	4.82	0.059	2.41	0.159
Plot level	8	1.41		1.52	
Combinations (C)	4	6.32	**<.001**	6.64	**<.001**
P x C	4	0.22	0.925	0.53	0.712
D x C	4	0.74	0.568	2.37	0.066
P x D x C	4	0.69	0.601	0.77	0.551
Covariate	1	1.74	0.194	0.25	0.621
Residual	47				

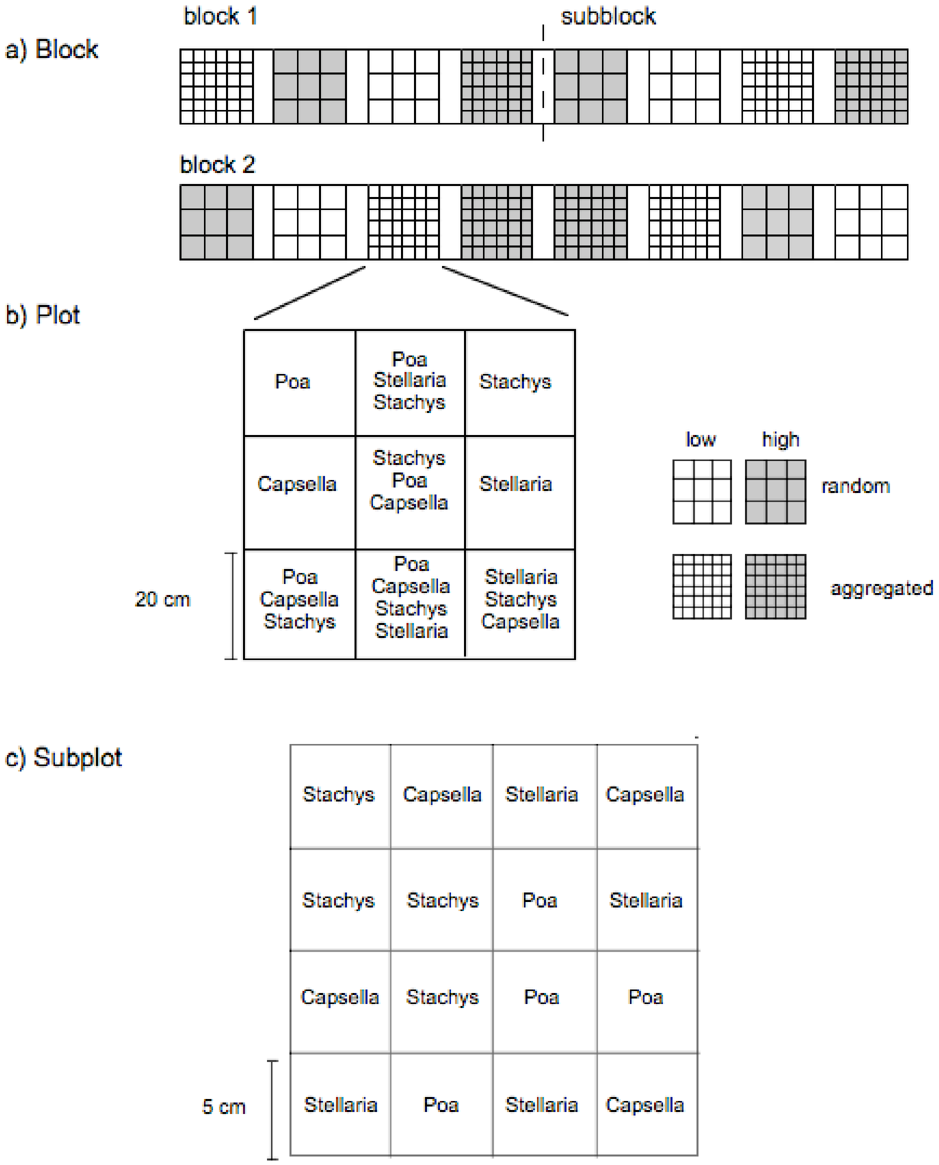

Figure 1 The experimental design. a) two blocks each containing four plots at either high or low density and random or aggregated pattern, twice replicated per treatment and species mixtures *n* = 4. b) Plots subdivided into nine sub-plots, each containing either a monoculture, one of the possible three-species mixtures, or the four-species mixture. c) an example of the intraspecifically aggregated pattern. In the four-species mixture each species occupied a single cell. In the random pattern, the corresponding number of seeds of all species was distributed throughout the 20x20 cm subplot.

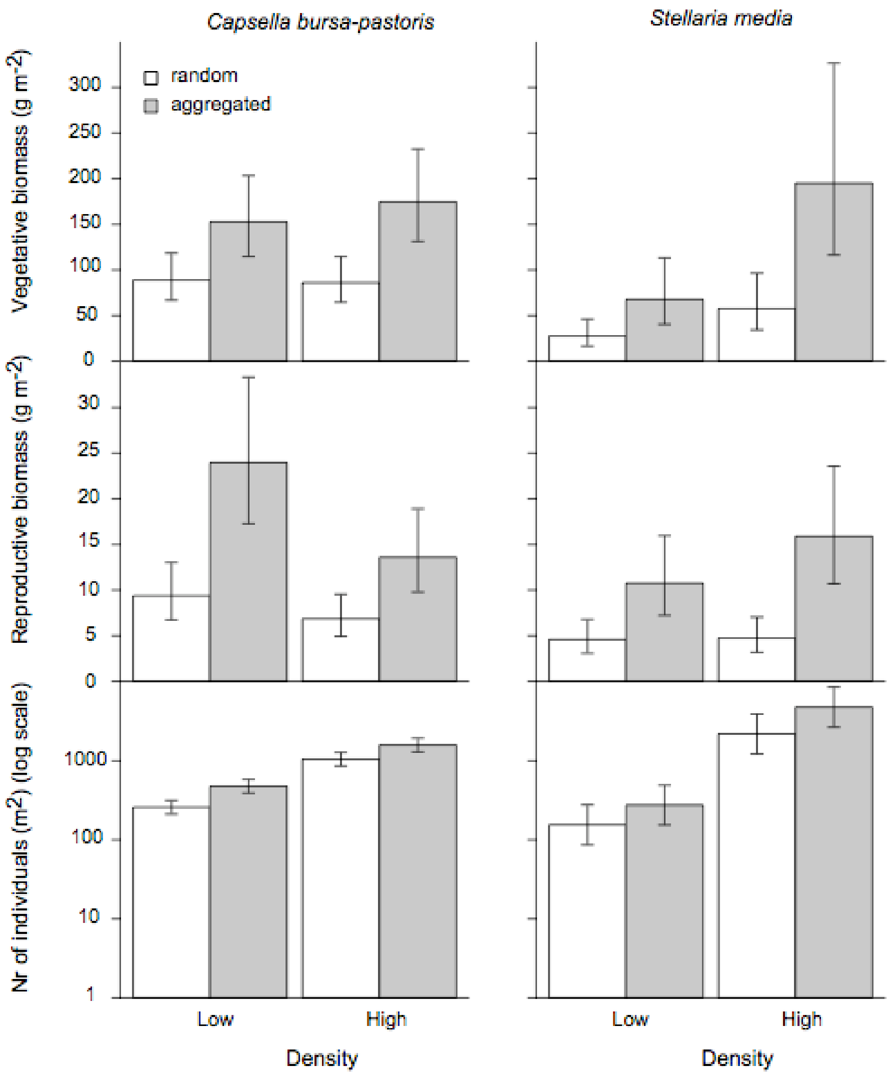

Figure 2 Aboveground biomass and number of individuals of *Capsella bursa-pastoris* and *Stellaria media* restricted to the species combinations with *Stachys annua* and *Poa annua*. White bars: random pattern, grey bars: aggregated pattern. The bars represented backtransformed means ±1 SE from ANCOVA of log-transformed data.

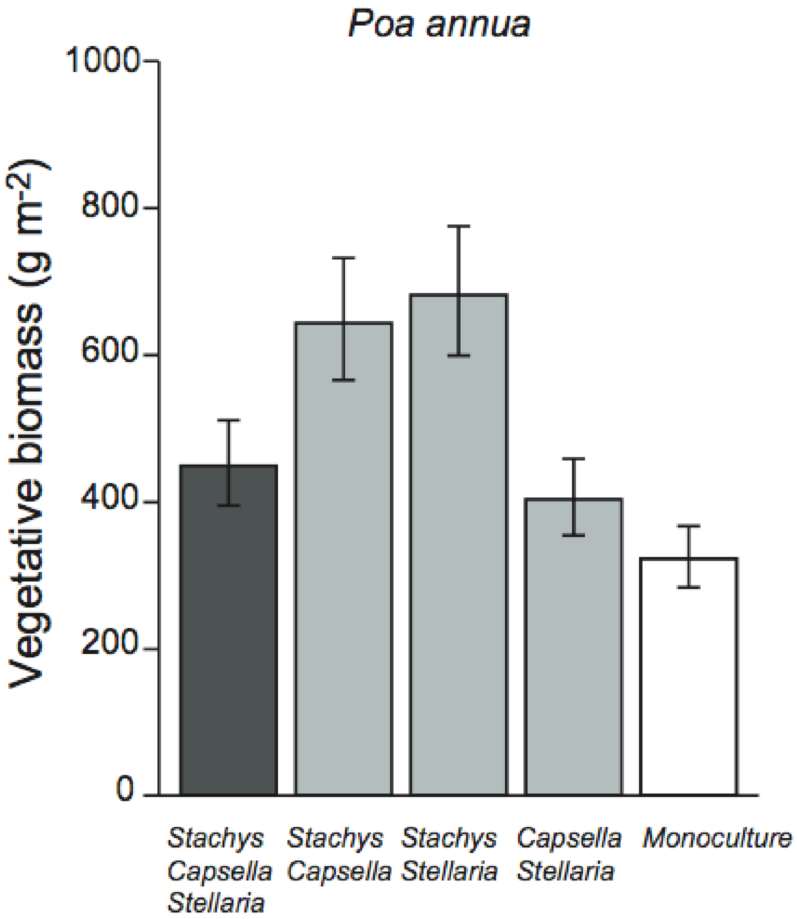

Figure 3 Total vegetative biomass of *Poa annua* on various combinations averaged over the treatments and densities. The bars represented backtransformed means ± 1SE from ANCOVA of log-transformed data.

Chapter 3

Effects of spatial pattern and relatedness in an experimental plant community

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Abstract

Many plant species show limited dispersal resulting in spatial and genetic substructures within populations. Consequently, neighbours are often related between each other, resulting in sibling competition. Using seed families of the annuals *Capsella bursa-pastoris* and *Stachys annua* we investigated effects of spatial pattern (i.e. random vs. aggregated) on total and individual performance at the level of species and seed families under field conditions.

At the level of species, we expected that inferior competitors increase, while superior competitors decrease their performance within neighbourhoods of conspecifics. Thus, we expected a species by spatial pattern interaction. Sibling competition, however, might reduce the performance of competitors, when genetically related, rather than non-related individuals are competing. Therefore, aggregations at the level of seed families could decrease the performance of competitors. Alternatively, if the opposite outcome would be observed, kin selection might be hypothesized to have occurred in the past. Because heavy seeds are expected to disperse less than light seeds, we further hypothesized that kin selection might be more likely to occur in superior competitors with heavy, locally dispersed seeds (e.g. *Stachys)* compared to inferior competitors with light, more distantly dispersed seeds (e.g. *Capsella*).

We found a significant species by spatial pattern interaction. Indeed, the inferior competitor, *Capsella,* showed increased reproductive biomass production in aggregated compared to random patterns. Whereas, the performance of the superior competitor, *Stachys,* was to some extent decreased by intraspecific aggregation.

Although statistically not significant, effects of intrafamily aggregations tended to be rather negative in *Capsella* but positive in *Stachys*. Our results confirmed that spatial patterns affect growth and reproduction of plant species promoting coexistence in plant communities. Although, we could not provide strong evidence for sibling competition or kin selection, our results suggested that competition among relatives was more severe for *Capsella* (lighter seeds) compared to *Stachys* (heavier seeds).

Keywords: annual species, coexistence, competition, kin selection, resource partitioning

Introduction

Elucidating the many ways in which competing plant species manage to coexist is a major unresolved question in community ecology (Hutchinson 1961; Silvertown and Charlesworth 2001) and many hypotheses have attempted to explain the coexistence of species with similar life histories (see e.g. Shmida and Ellner 1984; Chesson 2000a, b; Wright 2002; Barot 2004, Silvertown 2004). However, explaining how large numbers of competing plant species manage to coexistence in the absences of obvious niche differentiation, conspicuous life history trade-offs (e.g. competition/colonization trade-off; Rees 1995; Turnbull et al. 1999, 2004) or evident disturbance (Connell 1978) remains challenging and controversial (see e.g. Amarasekare 2003; Barot 2004; Silvertown 2004).

As a consequence of limited seed dispersal and/or clonal growth, most plant species aggregate intraspecifically, thereby increasing the importance of intra- versus interspecific competition (spatial segregation hypothesis, Pacala 1997). This is particularly relevant for sessile organisms where survivorship and fecundity are most affected by local population density rather than by the average global population density (Pacala and Silander 1985; Pacala 1997; Murrell et al. 2001). There is a large body of theory that underlines the importance of spatial pattern for ecological phenomena, such as coexistence and maintenance of biodiversity (Kareiva 1990; Bergelson 1990; Coomes et al. 2002; Bolker et al. 2003; Levine and Murrell 2003). However, compared to the large body of theory, there is still surprisingly little empirical evidence for the importance of spatial structure in shaping plant communities. Nevertheless, some experiments have shown that intraspecific aggregation might foster coexistence by allowing inferior competitors to increase their fitness (e.g. seed production). This might increase their persistence in the plant community and slow down competitive exclusion (Schmidt 1981; Bergelson 1990; Stoll and Prati 2001; Monzeglio and Stoll 2005). For example, if disturbances create gaps, inferior competitors might be able to colonize these gaps as long as they can produce enough seeds somewhere in the community. The few experimental studies that are available manipulated the spatial arrangement in an agricultural context (e.g. Harper et al. 1961; Brophy and Mundt 1991; Stauber et al. 1991; Norris et al. 2001). However, to our knowledge only one focused on natural communities (Turnbull et al. 2007). Therefore, the question to what extent and under which conditions intraspecific aggregation of species promotes coexistence by slowing down competitive exclusion remains controversial (Chesson 1991; Chesson and Neuhauser 2002; Murrell et. al 2002; Bolker et al. 2003).

Spatially limited seed dispersal can lead to pronounced aggregation of conspecifics (see e.g. Seidler and Plotkin 2006), with the additional consequence that neighbours are often genetically related (half- or full-siblings) to each other. In other words, when the prevailing pattern of dispersal results in relatives being aggregated in space and interacting primarily with one another, then local competition may become sibling competition (Cheplick 1992; 1993a, b; Kelly 1996; Lambin et al. 2001). Therefore, in plant species where dispersal is limited, the effects of spatial patterns (i.e. intraspecific aggregation) should not only operate at the level of species but also at the level of genotypes within species (Schmid 1990; Vuorisalo et al. 1997; Wilson and Nisbet 1997).

In general, the intensity of competition is thought to increase with genetic similarity of the competitors (Maynard Smith 1978). This hypothesis, known as the resource-partitioning hypothesis (Young 1981; Argyres and Schmitt 1992), states that genetically variable offspring will experience less severe competition than genetically similar or identical offspring, because more diverse offspring are predicted to show greater ability to partition limiting resources. In addition, parents will leave fewer offspring if there is severe competition between their descendants (Maynard Smith 1978). Therefore, sibling competition can be broadly considered as negative interactions between genetically related individuals and should in principle be avoided (Cheplick 1992, 1993a, b).

Conversely, relatedness of individuals in a population may lead to kin selection (Hamilton 1964). The kin selection hypothesis predicts that individuals will behave altruistic, when $rb\text{-}c > 0$, where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary and r is their genetic relatedness. In other words, an individual may behave altruistic (e.g. less competitive toward their relatives), even if the altruistic behaviour reduces its own fitness, if the costs are compensated with increased fitness of its relatives. In plant populations, kin selection may be a significant evolutionary force that counteracts sibling competition, because many species have limited seed dispersal (Goodnight 1985; Goodnight and Stevens 1997). Especially in plant species with heavy, locally dispersed seeds, local aggregation will increase sibling competition, but at the same time increase the potential for kin selection. On the other hand, in plant species with light far-dispersed seeds, seedlings are expected to be less aggregated and therefore sibling competition might occur less frequently. Thus, in plant species with frequent sibling interactions the possibility that kin selection might counteract potentially negative effects should not be excluded (Nakamura 1980; Cheplick 1993b; Kelly 1996; Griffin and West 2002). However, despite the straightforward predictions of the sibling competition hypotheses, few empirical tests have been made and the results are inconsistent. Amongst the studies, which investigated sibling competition in plants (Cheplick 1992), some showed that plants competing with genetically related individuals perform worse than plants competing with unrelated individuals (Willson et al. 1987; Kelley 1989; Argyres and Schmitt 1992; Karron and Marshall 1993). Others provide evidence that plants competing with genetic relatives outperform those competing with unrelated individuals (Willson et al. 1987; Tonsor 1989; Andalo et al. 2001; Donohue 2003). Hence, so far it remains difficult to unequivocally argue which of the both hypotheses is more likely to describe the dynamics of local competition in plant populations and communities.

The experiment reported here extends a previous spatial pattern experiment (Monzeglio and Stoll 2005) that assessed effects of intraspecific aggregation on species performance in experimental plant communities. The present experiment went further and aimed to evaluate effects of intraspecific aggregation at the level of seed families within species. Specifically, we collected seed families, which allowed us to assess not only effects of intraspecific aggregation but also effects of intrafamily aggregation on the growth and fitness of individuals. Based on our previous experiments, we expected that weak or competitively inferior species (e.g. *Capsella bursa-pastoris*) would produce more biomass when locally aggregated compared to randomly distributed and that intraspecific aggregation decreased biomass production of strong or competitively superior species (e.g. *Stachys annua*). In statistical terms, we expected a species by spatial pattern interaction.

Based on the sibling competition and the associated resource-partitioning hypothesis, we further expected that groups of relatives (i.e. intrafamily aggregation) would generally produce less vegetative and reproductive biomass compared to groups of non-relatives (i.e. intraspecific aggregation). In other words, biomass production in the intrafamily aggregation would be lower compared to the intraspecific aggregation. By contrast, if the opposite pattern would occur, than the operation of kin selection might be indicated. In this case, the performance of genetically related individuals would increase from intraspecific to intrafamily aggregations. Because *Capsella* has small and lighter seeds compared to *Stachys*, the former is expected to disperse its seeds less locally than the latter. Therefore, we hypothesized that kin selection might be more likely in *Stachys* where sibling competition should be more frequent compared to *Capsella*. Consequently we expected that intrafamily aggregation might be more likely to have positive effects in *Stachys* than *Capsella*.

Material and Methods

The purpose of this experiment was to investigate effects of spatial patterns (random vs. aggregated) at the level of species (intraspecific aggregation) and seed families (intrafamily aggregation) within a species mixture under experimental field conditions [at the Research Institute of Organic Agriculture (FiBL), Frick, Switzerland]. We used four annual plant species (*Capsella bursa-pastoris, Stachys annua, Stellaria media* and *Poa annua*) representing common species composition in natural communities. *Capsella* and *Stachys* were the target species, while *Poa* and *Stellaria* were the matrix species. Seeds of the target species were collected from single mother plants grown in a previous experiment (Monzeglio and Stoll, 2005) with a similar design as the present one. The mother plants were grown under four maternal treatments with different combinations of two spatial pattern (random vs. aggregated) and two densities (low vs. high). Seeds of the matrix species were obtained from a commercial seed supplier (Herbiseed, Wokingham, Berkshire, UK).

Plant species

Capsella bursa-pastoris L. (Brassicaceae) is a widely distributed, cosmopolitan annual pioneer species of disturbed ground and trampled sites. It forms rosettes with a multi-flowered erect stem up to 40 cm high. Flowers are usually self-pollinated; however small insects (e.g. flies, small bees) visit the flowers. In disturbed European sites, greater levels of genetic heterogeneity have been recorded for populations sampled from recently cultivated than from non-cultivated sites (Bosbach and Hurka 1981), suggesting a positive relationship between the degree of environmental variability and genetic variation. *Capsella* reproduces entirely by seeds, which are small and light, dispersed by wind or rain drops. The majority of the seeds usually fall between 15 and 30 (-50) cm of the parent plant (Aksoy et al. 1998). *Stachys annua* L. (Lamiaceae) is an annual species with a multi-flowered erect stem up to 40 cm high. This species grows for example in corn and tubercrop fields and gravel-pits. It prefers warm, dry and calcareous soils. *Stachys* is quite rare in most parts of Europe. It is predominately outcrossed and flowers from June – October. The hermaphroditic flowers are usually pollinated by hymenoptera, lepidoptera, or diptera. Although birds may disperse some seeds, *Stachys* seeds have no special structures aiding dispersal (e.g. elaisomes) and most of the relatively heavy seeds probably fall down in very close proximity of their mother plants. *Stellaria media* L. (Caryophyllaceae) is prostrate to ascending, with high adventitious rooting and a height of up to 40 cm. *Poa annua* L. (Poaceae) has adventitious roots at the first nodes and tillers up to 30 cm high and reproduces primarily by seeds. *Stellaria* and *Poa* are widely distributed, cosmopolitan annuals of disturbed habitats. Generally, *Capsella bursa-pastoris, Poa annua* and *Stellaria media* occur together.

Collection of seed families

Seed families of the target species *Capsella* and *Stachys* used in the present experiment were collected from mother plants grown in a previous spatial pattern experiment (see Monzeglio and Stoll 2005 for a detailed description of the experimental design) in which all four species (*Capsella, Stachys, Poa* and *Stellaria*) were grown in combinations of two different spatial patterns (random vs. aggregated) and two different densities (low vs. high). Since *Poa annua* and *Stellaria media* did not produce enough seeds, for the present experiment seeds were obtained from a commercial supplier (Herbiseed, Wokingham, Berkshire, UK). Seeds of *Capsella* and *Stachys* were collected in summer 2002 and the maternal environments (spatial pattern and density) recorded. All seeds from a single mother plant are referred to as seed family and are at least half-sibs. We started the seed collection of *Capsella* on August 8, and mature seeds were collected daily until August 15. The last collection was done on September 11 when collection of the *Stachys* seeds started. In this case, in order to avoid too much seed loss, we collected the whole plant and separated the seeds later in the laboratory. These collections were done on September 20, October 1 and 8 and November 12. Seeds of each mother plant were counted mechanically (seed counting machine, Elomor) and the seed families with the largest number of seeds were chosen for the present experiment. In total, 36 seed families of *Capsella* (nine from random and aggregated low densities, and eighteen from random high density) were used. For *Capsella* in aggregated high density no seed families produced enough seeds for the present experiment. As a result for the high density we had only mother plants grown in random spatial patterns. For *Stachys,* 36 seed families (nine for each species from each of the four maternal treatment combinations) yielded enough seeds for the present experiment. Because the experiment had to be started, only the remaining seeds could be counted and weighed. The mean seed mass of *Capsella* was much lower than that of *Stachys* (Table 1). *Capsella* grown in aggregated patterns produced heavier seeds than *Capsella* grown in random spatial patterns ($t = 2.21$, *d.f.* = 25, $P = 0.037$). *Stachys* did not show any significant differences in seed weight between mothers grown in random vs. aggregated spatial patterns or at high vs. low density. There was not significant interaction between maternal density and maternal spatial pattern ($F_{1,35} = 1.4$; $P = 0.253$).

Experimental design

The experiment was designed as randomized split-plot and contained 2 blocks (0.6 x 6.0 m, separated by 0.5 m) each with six main plots (0.6 x 0.6 m, separated by 0.3 m). The three spatial pattern treatments (see below) were used as plot-level treatments yielding 4 replicates per treatment (two per block). The plots were subdivided into nine subplots (0.2 x 0.2 m) that were divided in an upper and lower half, in such a way that each half contained 4 1/2 subplots (the central subplot was halved) (Fig. 1a).

In order to avoid any misunderstanding about the spatial patterns of the present experiment (i.e. random, intraspecific and intrafamily aggregation) and spatial patterns in which the mother plants grew (i.e. random and intraspecific aggregation, see *Experimental design for maternal environment*) we describe the main experimental design and the design corresponding to the maternal environment separately. We start with the spatial pattern of the present experiment.

In the present experiment, we used the four-species mixture and one density level (i.e. 100 seeds per cell, for a total of 40000 seeds / m^2). The three spatial pattern treatments were attained as follows. In the random pattern, 44 seeds of each of the nine seed families of *Capsella* and *Stachys* (i.e. for a total of app. 400 seeds for each species) together with 400 seeds of *Poa* and 400 seeds of *Stellaria* were mixed and randomly scattered over the subplots, such that the individuals experienced inter- and intraspecific as well as intrafamily encounters at similar frequencies. In the aggregated patterns (i.e. intraspecific and intrafamily aggregated patterns), the subplots were further subdivided into 16 cells (5 x 5 cm), and each cell contained only one species in such a way that individuals experienced more intra- than interspecific encounters. For the two species with seed families (*Capsella* and *Stachys*) seeds were aggregated at two levels. The first level consisted of groups of conspecifics, and will be referred to as intraspecific aggregation. In the intraspecifically aggregated pattern each cell contained app. 100 seeds made up of 11 seeds from each of the nine seed families. The second level was made up of individuals of the same seed families and will be referred to as intrafamily aggregation. In the intrafamily aggregated pattern each cell contained 100 seeds from the same seed family in such a way that individuals in the centre of the cells competed only with genetically related individuals (Fig. 1a). Two seed families were used per species and subplot. The species and seed families were randomly allocated to the cells. For the species without seed families (*Poa* and *Stellaria*) each cell always contained 100 seeds sown as the intraspecific aggregations.

Experimental design for maternal environment

The density in which the mother plants grew was used as plot-level treatments. Each block contained 6 plots, i.e. three plots with seeds from mother plants grown at low and three plots with seeds from mother plants grown at high density. The spatial pattern in which the mothers grew was used as within-plot treatment (i.e. half-plot). Randomly allocated lower or upper halves were either sown with seeds from mothers grown in random or spatially aggregated patterns (for *Capsella* this was only possible for seeds from low maternal densities and all seeds from mothers grown in high densities were from mothers grown in random spatial patterns) (Fig.1b).

Additional experimental settings

In order to assess the germination activity of the seed families, simple germination trials with and without Gibberellic acid (0.01%) both in the laboratory and in the field were carried out in May 2003. These experiments showed low germination rates of field collected seeds without Gibberellic acid. Therefore, to increase germination, seeds of *Capsella* and *Stachys* were soaked in a solution of Gibberellic acid at 4-5° C for three to five days before sowing.

The blocks were established on May 16 and harvested in fall 2003. During the first month the two blocks were covered with a plastic tunnel (200 holes/m^2, GVZ-Bolltec, AG) to protect the seedlings against sunlight and adverse weather. The tunnel was never completely closed, 20-30 cm from the ground were left open to permit the air to circulate and in July the tunnel was removed completely. Because of the heavy soil (high clay content), each plot was covered with a layer (2 cm) of commercial garden soil before sowing to increase seed germination. The plots were sown between June 16 and 19 and watered with an automatic irrigation system (Gardena AG, Bachenbülach, Switzerland). The system was programmed to give rain-cycles of 1 minute (app. 1 l water) starting at 5:15, 6:15, 7:15 a.m., and 7:15, 8:15, and 9:15 p.m. The duration of the 9:15 p.m. rain-cycle was changed from 1 min to 2 min on June 26. Because of the extremely hot summer 2003 on July 2, one additional nozzle was positioned in the middle of each plot. These additional nozzles were programmed to give rain-cycles lasting 2 minutes starting at 8:30, 9:30, 12:30 a.m., and 4:30, 8:30, 9:30 p.m. and removed on July 29. After sowing, the seeds were covered by sieving a thin layer of commercial garden soil, which was slightly pressed down to prevent the seeds from being washed away. A snail fence enclosed the entire experimental field.

Harvest

The aboveground biomass of the four species was harvested at the subplot level (0.2 x 0.2 m) between September 22 and October 15. Additionally, for the two species with seed families (*Capsella* and *Stachys*) the harvested biomass was separated into vegetative and reproductive parts and the total number of individuals was counted. Because *Capsella* started to produce mature seeds earlier, mature seeds were collected regularly from July 25 to August 15, 2003, and then added to the final reproductive biomass. The harvested biomass was dried for 12 h at 60° C and then stored. Before weighing, the biomass was dried again for 4-5 h at 60° C.

Statistical analysis

The data from *Capsella* and *Stachys* were analyzed with a multifactorial analysis of variance (ANOVA) for a split-plot design. Since maternal density, which varied at the plot level, never showed significant effects it was excluded from the analysis and ANOVA tables. Similarly, because maternal spatial pattern, which varied at the half-plot level, never showed significant effects, we pooled the data from the subplots at the plot level. That is, we summed the biomass and number of individuals of the nine subplots, and used the plots (N = 12 with 4 replicates per spatial pattern) as experimental units. This pooling allowed us to simplify the ANOVA tables and the communication of the results but it did not change any of the reported results. Since we had no seed families for *Poa* and *Stellaria*, these species were considered as matrix species and not further analyzed.

The spatial pattern treatments were tested against the plot-level residual mean square. In addition we used linear contrasts to separate them into (i) random versus aggregated (i.e. intraspecific & intrafamily aggregation), (ii) intraspecific versus intrafamily aggregated pattern. There was one plot with a random spatial pattern treatment, in which the plants germinated particularly poorly or died soon after they germinated because of the extremely hot and dry weather. This was the only plot in which *Capsella* produced less than 10 g/m^2 and the only plot in which biomass production of *Stachys* was less than the mean ± 3 standard errors. As it turned out that *Capsella* produced less biomass in plots with random spatial patterns than aggregated plots, including this plot in the *Capsella* analysis rendered all effects more significant than reported. On the other hand, *Stachys* produced most biomass in the plots with random spatial patterns, except this particular one. Including this plot in the *Stachys* analysis increased the residual variation so much that all effects for *Stachys* became non significant. Because the results of the analysis, especially for *Stachys,* changed significantly depending on whether we considered this plot or set the plot values as missing, we decided to present both analyses. The analysis in which the values for this unusual random plot were omitted is presented in the results (Table 3) and used to plot the charts. The analysis using all plots is presented as appendix.

We counted the number of seedlings one month after the beginning of the experiment and tested it as covariate. The covariate, however, had no significant effect and was consequently omitted. Even though the maternal environments had no significant effect on the main spatial pattern effect, we also tested initial seed mass for *Stachys* and *Capsella* as covariate. Again, the covariate had no significant effect and was omitted.

All data were expressed as number of individuals or grams per square meter for total biomass production or grams per individual for average biomass production. All biomass data were logarithmically transformed [log (y)] to obtain normal distribution of the residuals and homogeneity of variances. Means and standard errors from the analyses (back-transformed in the case of biomass) are presented throughout. All analyses were conducted using GENSTAT 5 (Payne et al. 1987).

Results

First of all, both species differed significantly in their overall performance (Table 2). Generally, total biomass production of *Capsella* was much lower (18.9 ± 4.0 g/m^2, average ± standard error over 11 plots) than that of *Stachys* (1166.7 ± 30.1 g/m^2). The matrix species *Stellaria* produced 54.2 ± 10.7 g/m^2 while *Poa* did not germinate.

The analysis including both species revealed a significant spatial pattern effect for total reproductive biomass and average vegetative and reproductive biomass (Table 2). For example, averaged over both species there was significantly more total reproductive biomass in the aggregated (intraspecific 46.9 g/m^2; intrafamily 39.9 g/m^2) than in the random patterns (15.2 g/m^2). There was a marginally significant species by spatial pattern interaction for total and average vegetative biomass and a significant interaction for total and average reproductive biomass (Table 2). The linear contrast showed that the main differences were between the random compared to the aggregated patterns.

Because the spatial pattern influenced the performance of the two species differently, we present species-specific results separately and begin with *Capsella*. *Capsella* generally had fewer individuals and produced less total and average biomass in the random compared to the aggregated patterns. The main spatial pattern effect was significant for total reproductive and average vegetative and reproductive biomass. The linear contrasts between random versus intraspecific and intrafamily aggregated pattern were highly significant. However, the differences between intraspecific vs. intrafamily aggregated pattern were not significant (Table 3, Fig. 2). Although *Capsella* produced app. 70% less total vegetative biomass in the random compared to both (pooled) aggregated pattern, this effects was only marginally significant. The number of individuals was not significantly affected by the spatial pattern (Table 3, Fig. 2).

Stachys was less affected by the spatial pattern than *Capsella*. Nevertheless, *Stachys* had more but on average smaller individuals in random compared to both aggregated patterns. The main spatial pattern effect was not significant for the number of individuals, but the linear contrasts showed that *Stachys* had slightly more individuals in the random compared to the intraspecific and intrafamily aggregated pattern (Table 3, Fig. 3). Total vegetative biomass production of *Stachys* was significantly affected by the spatial pattern, with more total vegetative biomass in the random compared to both intraspecific and intrafamily aggregated pattern (Table 3, Fig. 3). The average vegetative biomass was not significantly affected by the spatial pattern. Total and average reproductive biomass of *Stachys* was not affected by the spatial pattern.

Discussion

Based on aboveground biomass production we defined *Stachys annua* as a strong and *Capsella bursa-pastoris* as a weak competitor. The weak competitor produced much more reproductive biomass per individual in aggregated compared to random spatial patterns. Because they also tended to be more numerous in aggregated compared to random spatial patterns, total reproductive biomass production was much higher in aggregated compared to random spatial patterns. Individuals of the strong competitor in contrast, were more numerous in random compared to the aggregated spatial patterns. However, individuals in random patterns tended to produce less vegetative and reproductive biomass per individual compared to individuals in aggregated patterns. Thus, *Stachys* almost exactly compensated for the different number of individuals such that there were only small and insignificant differences in the production of total reproductive biomass between the different spatial patterns (516 g/m^2 in random, 463 and 488 g/m^2 in intraspecific and intrafamily aggregated patterns, respectively). Interestingly, our findings showed, averaged over both species, an overall increase in total reproductive biomass in the aggregated compared to random pattern. This suggested that *Capsella* produced overproportionally more total reproductive biomass in the aggregated pattern than *Stachys* in the random pattern. This result further supports the notion that spatial structure seems to be relatively more important for small seeded (e.g. *Capsella*) compared to large seeded species (e.g. *Stachys*) (Monzeglio and Stoll 2005; Turnbull et al. 2007).

Our results for the weak competitor were generally consistent with previous findings (Stoll and Prati 2001; Monzeglio and Stoll 2005). They support our expectation that weak competitors increased their fitness (e.g. survival and seed production) within neighbourhoods of conspecifics compared to neighbourhoods of heterospecifics, at least in the short run. In addition, data on *Stachys* showed that intraspecific aggregation decreased the number of individuals and to some extent the performance of strong competitors. Thus, our results at the species level generally agreed with our earlier work on the effects of spatial patterns on species performance.

However, experimental studies like ours have the limitation that the absolute and relative densities of the species, the structure and scale of the plant community and the strength of competition are determined by the experiment rather than natural processes. In real communities, the degree of spatial aggregation is often less extreme and the spatial structure is more complex. Turnbull et al. (2007) quantified the effects of spatial structure on individuals, population and community biomass within a natural community of annuals. They found that the effects of spatial structure on total community biomass were relatively small. This was because common species have generally weak spatial structure and they draw down the effect on the community as a whole. Therefore, intraspecific aggregation as process that may delay competitive exclusion would be far more important for rare and weak (e.g. small seeded species) than for common and strong (e.g. large seeded species) competitors. Our results lend further support to this general conclusion, because spatial pattern effects for the small seeded species *Capsella* were much stronger than for the large seeded species *Stachys*.

Our results at the level of seed families, however, were less clear and not statistically significant. Nevertheless, our results suggested, that effects of intrafamily aggregation differed depending on the species. Groups of relatives in the small seeded species (*Capsella*) tended to be less productive compared to groups of non-relatives in producing biomass. In particular, total reproductive biomass production in intrafamily aggregated patterns was only about half of that in intraspecifically aggregated patterns. This agrees with predictions from the sibling competition hypothesis and suggests that groups of relatives in *Capsella* indeed have a lower potential for resource partitioning than groups of non-relatives. For the large seeded species (*Stachys*), groups of relatives were slightly more productive compared to groups of non-relatives. Although the differences were not statistically significant, the general pattern agreed with our hypothesis that kin selection might be more likely to occur in plant species with heavy, locally dispersed seeds. Cheplick and Kane (2004) did a similar greenhouse experiment using *Triplasis purpurea* growing either alone or in inter- or intrafamily competition (note that what they call interfamily competition corresponds to our intraspecifc aggregated pattern). Their findings generally support the resource partitioning hypothesis. Similar to other studies (e.g. Taylor and Aarssen 1990; Donohue 2003), they showed, however, that the effects of neighbour relatedness on the growth and fitness differed among families . This suggests genetic variation of competitive ability among seed families. Contrary to Cheplick and Kane (2004), we could not obtain detailed information on the different competing seed families and our experiment was conducted under field conditions. To obtain information on the different competing seed families in the intrafamily aggregated pattern, we would have had to harvest the biomass at the cell level (5 x 5 cm) rather than the subplot level (20 x 20 cm). In addition, in the intraspecific and random pattern we would have had to label each individual seed in order to recover its family at harvest. This was impossible. However, we cannot exclude the possibility that one or more seed families performed better in the intrafamily compared to the intraspecific aggregation even though *Capsella*, on average, decreased its fitness in the intrafamily compared to the intraspecific aggregated pattern.

The very high density used in our experiment (40000 seeds/m^2) might be one reason for the prevailing effect of resource partitioning. Koelewijn (2004) investigated the effects of different densities on competing seed families and showed that density had stronger negative effects in absolute terms on the performance of the seed families and that the consequences of sibling competition depend on the frequency and relatedness of neighbours. Escarré et al. (1994) examined density effects and neighbour relatedness in a sib / non-sib competition experiment on the clonal *Rumex acetosella*. They found density-dependent effects of the degree of relatedness between plant individuals. At low densities, there were no growth differences, but when the density was doubled, the absolute sexual biomass was higher in non-sibs than in sib treatments, suggesting that competition was stronger between related plants. Therefore, we speculate that in our experiment, a lower density might have favoured the positive intrafamily effects observed in *Stachys*. By contrast, a higher density might have increased the negative effect of sibling competition observed in *Capsella*. Moreover, there is evidence that the effect of high relatedness may be modulated by the scale of competition (e.g. Queller 2004, Griffin et al. 2004, Frank 1998). Even if highly localized dispersal is likely to promote the evolution of altruism behavior (Hamilton 1964; Wilson 1987), the scale of competition may still play a major role. Limited dispersal may favour altruism because it increases relatedness between altruistic individuals. But it also increases relatedness between competitors, which opposes the selection for altruism (see e.g. Taylor 1992; Wilson et al. 1992).

Both species in our experiment had fewer individuals in groups of relatives compared to groups of non-relatives suggesting that groups of related individuals suffered increased mortality compared to groups of non-related individuals. These results further suggested negative sibling competition effects, supporting the resource-partitioning hypothesis and are in line with previous studies on sibling competition in plants (Willson et al. 1987; Kelley 1989; Argyres and Schmitt 1992; Karron and Marshall 1993). Within groups of related individuals, the strong competitor produced on average the highest individual biomass (vegetative and reproductive). However, because mortality was highest in intrafamily aggregations, and because there was no difference in the overall biomass production between groups of relatives and groups of non-relatives, we interpret this result as a simple density dependent effect rather than with kin selection.

Finally, alternative explanations for the relatively weak effects of spatial patterns at the level of seed families and different responses of the species to intrafamily aggregation must be considered. For example, there may be little or no genetic variation in our populations. Because we do not have any knowledge about the genetic variation in the different species we cannot really assess this possible explanation. Moreover, differences in seed weight of the two species do certainly not provide the only explanation for different responses to intrafamily aggregation. The different mating systems among the target species (i.e. highly selfing for *Capsella* and predominately outcrossing for *Stachys*) might provide an alternative explanation for some of the different responses of the species to intrafamily aggregation. That is, selfed seeds of *Capsella* are genetically more similar than outcrossed seeds of *Stachys*. Therefore, related individuals of *Capsella* might have suffered more intense sibling competition compared to *Stachys,* resulting in less resource partitioning and consequently reduced biomass production in intrafamily aggregations.

In summary, we provided further evidence that weak competitors increased their fitness within neighbourhoods of conspecifics compared to neighbourhoods of heterospecifics. By contrast, intraspecific aggregation decreased the performance of strong competitors. An additional aggregation at the level of seed families produced less clear results. Nevertheless, groups of relatives tended to perform worse than groups of non-relatives in *Capsella* whereas in *Stachys*, groups of relatives tended to perform slightly better than groups of non-relatives. Therefore our findings tended to support the resource partitioning hypothesis, rather than the kin selection hypothesis. However, there are many other factors (e.g. habitat selection) that may affect the way individuals interact and aggregate, and the circumstances under which neighbourhood competition between related individuals may lead to kin selection in plants remain largely unexplored. Thus, the consequences of genetic sub structuring for species coexistence and its ecological and evolutionary implication in plant population dynamics merits further investigation.

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Table 1 Mean seed mass (mg) of *Capsella bursa-pastoris* and *Stachys annua* across seed families (N = 9) collected from individual mother plants grown in two different spatial patterns (random vs. aggregated) and at two densities (low vs. high). For each spatial pattern / density combination nine different seed families were used (except for *Capsella* which had no seed families that produced enough seeds in high densities and aggregated pattern). For *Capsella* in high density and random pattern only nine, instead of eighteen, seed families had enough remaining seeds to be counted and weighed. Abbreviations: N = Number of mother plants or seed families, SE = standard error.

		Capsella bursa-pastoris			*Stachys annua*		
Maternal density	Maternal spatial pattern	*N*	Seed mass	*SE*	*N*	Seed mass	*SE*
low	random	9	0.109	0.002	9	2.84	0.26
	aggregated	9	0.117	0.004	9	2.75	0.15
	mean		0.113	0.002		2.79	0.15
high	random	9	0.107	0.004	9	3.05	0.31
	aggregated	0			9	2.37	0.28
	mean		0.107	0.004		2.71	0.22
mean	random	18	0.108	0.002	18	2.94	0.20
	aggregated	9	0.117	0.004	18	2.56	0.16

Table 2 Results of ANOVA combining both species *Capsella bursa-pastoris* and *Stachys annua* omitting one unusual random plot. Effects of spatial patterns (random vs. two levels of aggregation) on total (sum over plots) number of individuals, total and average (per individual) aboveground vegetative and reproductive biomass production were tested against plot-level residuals.

Abbreviations: *d.f.* = degrees of freedom; (m.v.) = missing values, *F* = F-value (variance ratio), *P* = error probability.

Source of variation			**Total**						**Average**			
			Number of individuals		Vegetative biomass		Reproductive biomass		Vegetative biomass		Reproductive biomass	
	d.f.	(m.v.)	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	1		6.4	0.039	0.0	0.964	1.0	0.353	8.2	0.024	16.3	0.005
Spatial pattern (SP)	2		3.3	0.100	1.8	0.236	7.3	0.019	4.8	0.049	16.3	0.002
random vs. aggregated [†]	1		4.8	0.064	3.0	0.129	14.4	0.007	9.2	0.019	31.6	< 0.001
intraspecific- vs. intrafamily aggregated [†]	1		1.7	0.235	0.6	0.459	0.3	0.63	0.4	0.565	1.0	0.361
Plot level	7	(1)	0.6		1.3		1.1		2.4		2.5	
Species (S)	1		69.1	< 0.001	322.9	< 0.001	480.2	< 0.001	168.9	< 0.001	566.6	< 0.001
S x SP	2		2.9	0.112	3.9	0.067	9.5	0.008	4.2	0.058	21.6	< 0.001
S x random vs. aggregated [†]	1		5.3	0.051	6.5	0.034	18.6	0.003	5.4	0.049	42.6	< 0.001
S x intraspecific vs. intrafamily aggregated [†]	1		0.6	0.478	1.2	0.301	0.5	0.512	2.9	0.126	0.6	0.469
Residual	8	(1)										
Total	21	(2)										

Notes: [†] Linear contrasts to separate the effects of spatial pattern into differences between random vs. aggregated (i.e. intraspecific and intrafamily aggregation) and intraspecific vs. intrafamily aggregation effects.

Table 3 Results of ANOVA for *Capsella bursa-pastoris* (top) and *Stachys annua* (bottom) omitting one unusual random plot. Effects of spatial patterns (random vs. two levels of aggregation) on total (sum over plots) number of individuals, total and average (per individual) aboveground vegetative and reproductive biomass production were tested against plot-level residuals.

Abbreviations: *d.f.* = degrees of freedom; (m.v.) = missing values, *F* = F-value (variance ratio), *P* = error probability.

Capsella bursa-pastoris			**Total**						**Average**			
Source of variation			Number of individuals		Vegetative biomass		Reproductive biomass		Vegetative biomass		Reproductive biomass	
	d.f.	(m.v.)	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	1		1.1	0.327	0.0	0.982	0.8	0.415	6.7	0.036	17.9	0.004
Spatial pattern	2		1.4	0.303	2.5	0.150	7.9	0.016	11.1	0.007	33.9	< 0.001
random vs. aggregated†	1		1.3	0.288	4.2	0.079	15.5	0.006	21.9	0.002	67.6	< 0.001
intraspecific vs. intrafamily aggregated†	1		1.5	0.257	0.8	0.394	0.3	0.576	0.3	0.631	0.2	0.683
Residual	7	(1)										
Total	10	(1)										

Stachys annua			**Total**						**Average**			
Source of variation			Number of individuals		Vegetative biomass		Reproductive biomass		Vegetative biomass		Reproductive biomass	
	d.f.	(m.v.)	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	1		5.3	0.056	0.0	0.847	2.2	0.185	5.3	0.056	7.3	0.031
Spatial pattern	2		3.2	0.103	6.1	0.030	1.9	0.218	1.3	0.329	1.8	0.234
random vs. aggregated†	1		5.2	0.056	10.8	0.013	2.9	0.133	1.1	0.321	2.0	0.199
intraspecific vs. intrafamily aggregated†	1		1.2	0.316	1.3	0.293	0.9	0.368	1.5	0.264	1.6	0.247
Residual	7	(1)										
Total	10	(1)										

Notes: † Linear contrasts to separate the effects of spatial pattern into differences between random vs. aggregated (i.e. intraspecific and intrafamily aggregation) and intraspecific vs. intrafamily aggregation effects.

Appendix Results of ANOVA for *Capsella bursa-pastoris* (top) and *Stachys annua* (bottom) using all plots. Effects of spatial patterns (random vs. two levels of aggregation) on total (sum over plots) number of individuals, total and average (per individual) aboveground vegetative and reproductive biomass production were tested against plot-level residuals.

Abbreviations: *d.f.* = degrees of freedom, *F* = F-value (variance ratio), *P* = error probability.

Capsella bursa-pastoris		**Total**						**Average**			
Source of variation		Number of individuals		Vegetative biomass		Reproductive biomass		Vegetative biomass		Reproductive biomass	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	1	1.4	0.271	0.1	0.760	0.2	0.667	6.0	0.039	13.0	0.007
Spatial pattern	2	1.7	0.236	3.6	0.078	10.0	0.007	13.6	0.003	36.2	< 0.001
random vs. aggregated[†]	1	1.7	0.223	6.3	0.037	19.6	0.002	27.0	< 0.001	72.3	< 0.001
intraspecific vs. intrafamily aggregated[†]	1	1.7	0.225	0.9	0.380	0.3	0.580	0.3	0.616	0.2	0.694
Residual	8										
Total	11										

Stachys annua		**Total**						**Average**			
Source of variation		Number of individuals		Vegetative biomass		Reproductive biomass		Vegetative biomass		Reproductive biomass	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Block	1	6.2	0.038	0.7	0.427	0.0	0.998	6.2	0.038	6.1	0.039
Spatial pattern	2	0.7	0.510	0.1	0.878	0.2	0.842	0.3	0.721	0.3	0.721
random vs. aggregated[†]	1	0.7	0.415	0.0	0.899	0.1	0.833	0.1	0.778	0.1	0.778
intraspecific vs. intrafamily aggregated[†]	1	0.7	0.418	0.3	0.632	0.3	0.596	0.6	0.462	0.6	0.462
Residual	8										
Total	11										

Notes: [†] Linear contrasts to separate the effects of spatial pattern into differences between random vs. aggregated (i.e. intraspecific and intrafamily aggregation) and intraspecific vs. intrafamily aggregation effects.

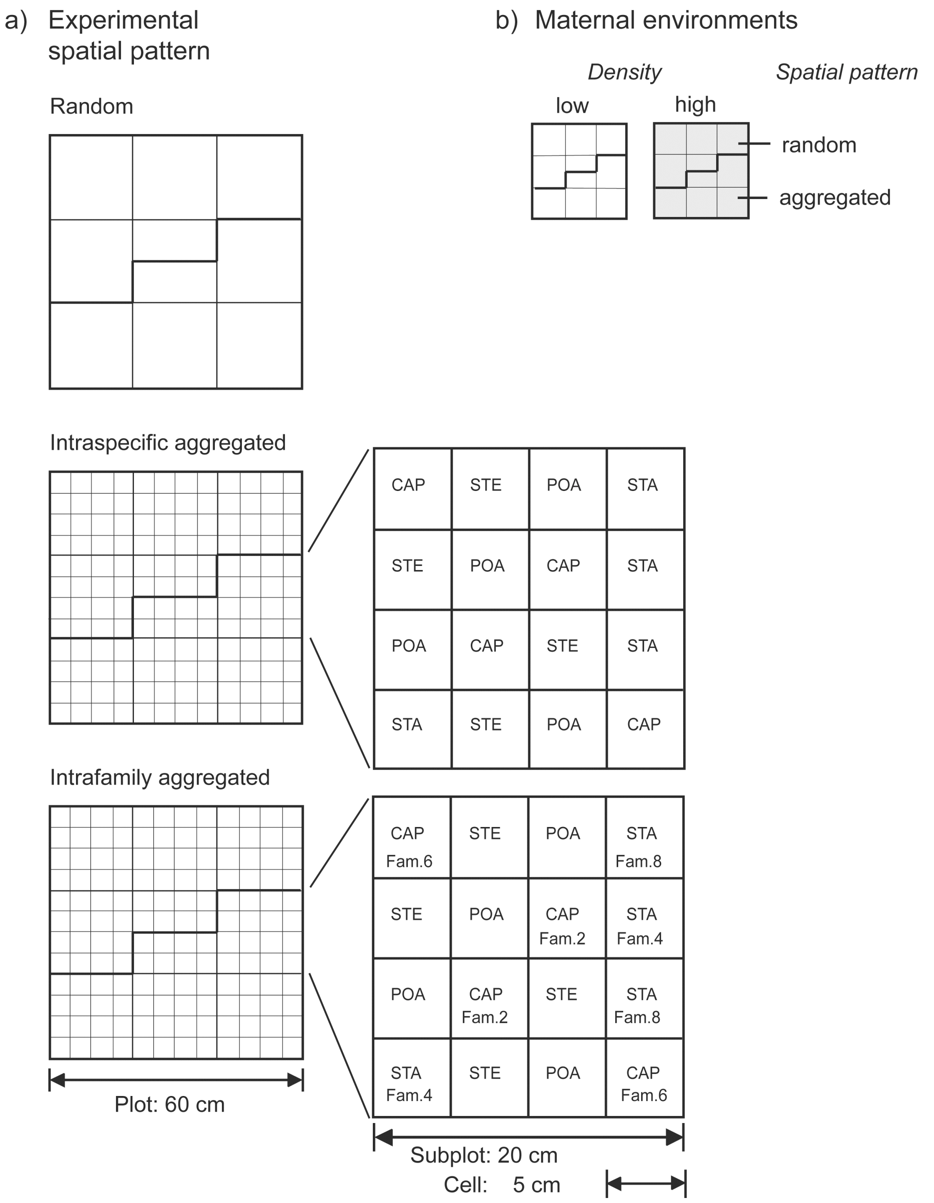

Figure 1 Experimental design. **a)** Experimental spatial pattern. Three different experimental spatial patterns, which varied at the plot (60 x 60 cm) level, were realized as follows. In the random spatial pattern, 44 seeds from each of 9 families of *Capsella* (CAP) and *Stachys* (STA) and 400 seeds of *Poa* (POA) and *Stellaria* (STE) were mixed and scattered over the subplots (20 x 20 cm). In the intraspecific aggregation, subplots were further divided into 16 cells (5 x 5 cm). Four randomly selected cells per species were sown with 11 seeds from each of 9 families of *Capsella* or *Stachys* or 100 seeds of *Poa* or *Stellaria*. In the intrafamily aggregated pattern, two randomly selected cells were sown with 100 seeds from one seed family and two with 100 seeds from another seed family of *Capsella* or *Stachys*. The other two species (*Poa* and *Stellaria*) were sown as in the intraspecific aggregations. Spatial pattern were replicated four times (two randomly assigned within each of two blocks). **b)** Maternal environments. The mother plants, from which seed families of *Capsella* and *Stachys* were collected, grew either in low or high density and random or aggregated patterns of a previous experiment. The maternal density (i.e. low vs. high) was varied at the plot level, while the maternal spatial pattern (random vs. aggregated) at the ‘half-plot’ level. One half (4 1/2 subplots) of each plot was sown with seeds from mothers grown in a random spatial pattern and the other half was sown with seeds from mothers grown in an aggregated spatial pattern. The maternal spatial pattern was randomly assigned.

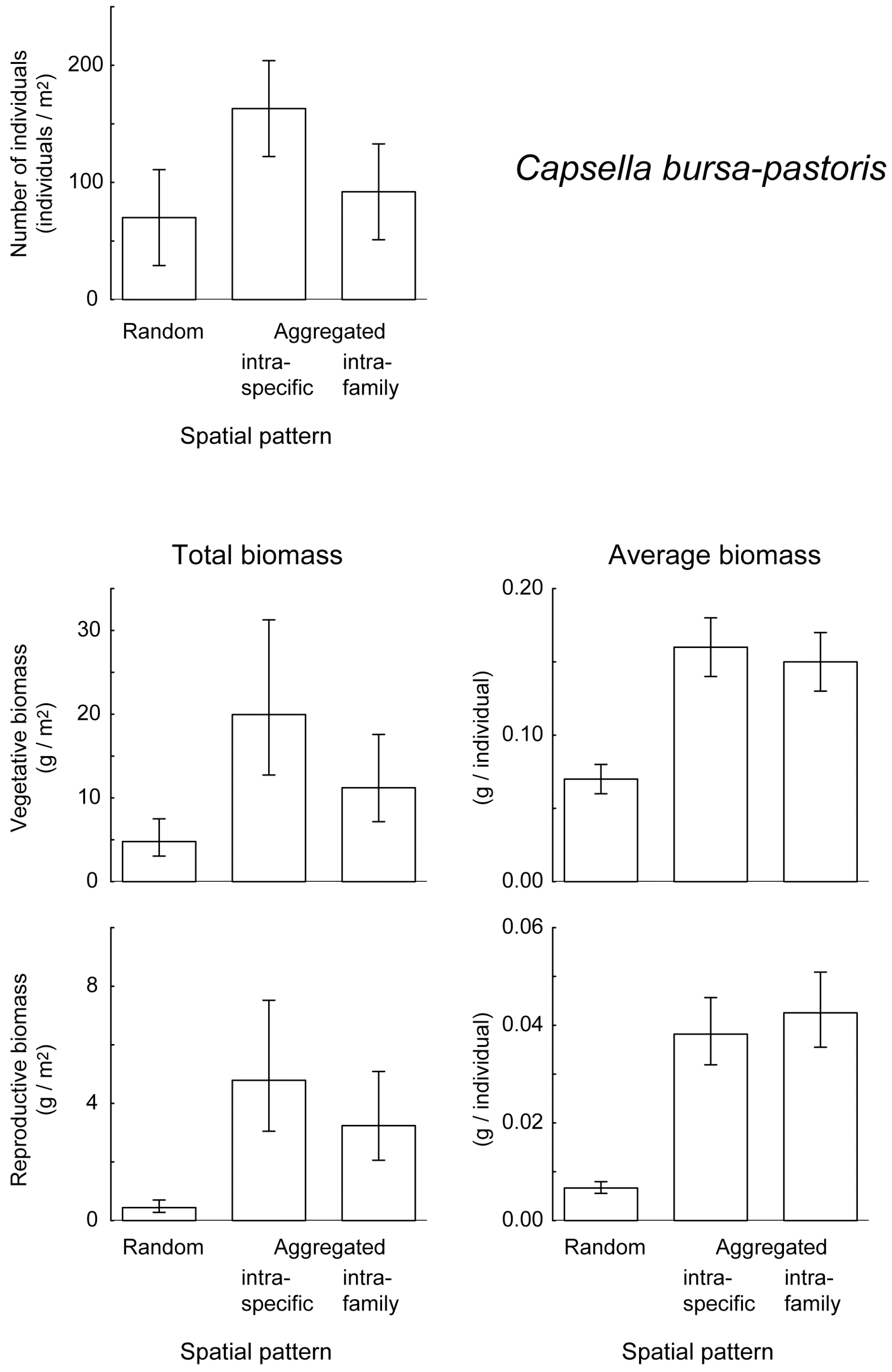

Figure 2 Number of *Capsella bursa-pastoris* individuals (top), total (left, g/m^2) and average (right, g per individual) aboveground vegetative (middle) and reproductive (bottom) biomass grown in random, intraspecific or intrafamily aggregated spatial patterns. The bars represent means ±1 *SE* from ANOVA for number of individuals and backtransformed means from $\log_{10}(Y)$-transformed data from ANOVA's for vegetative and reproductive biomass.

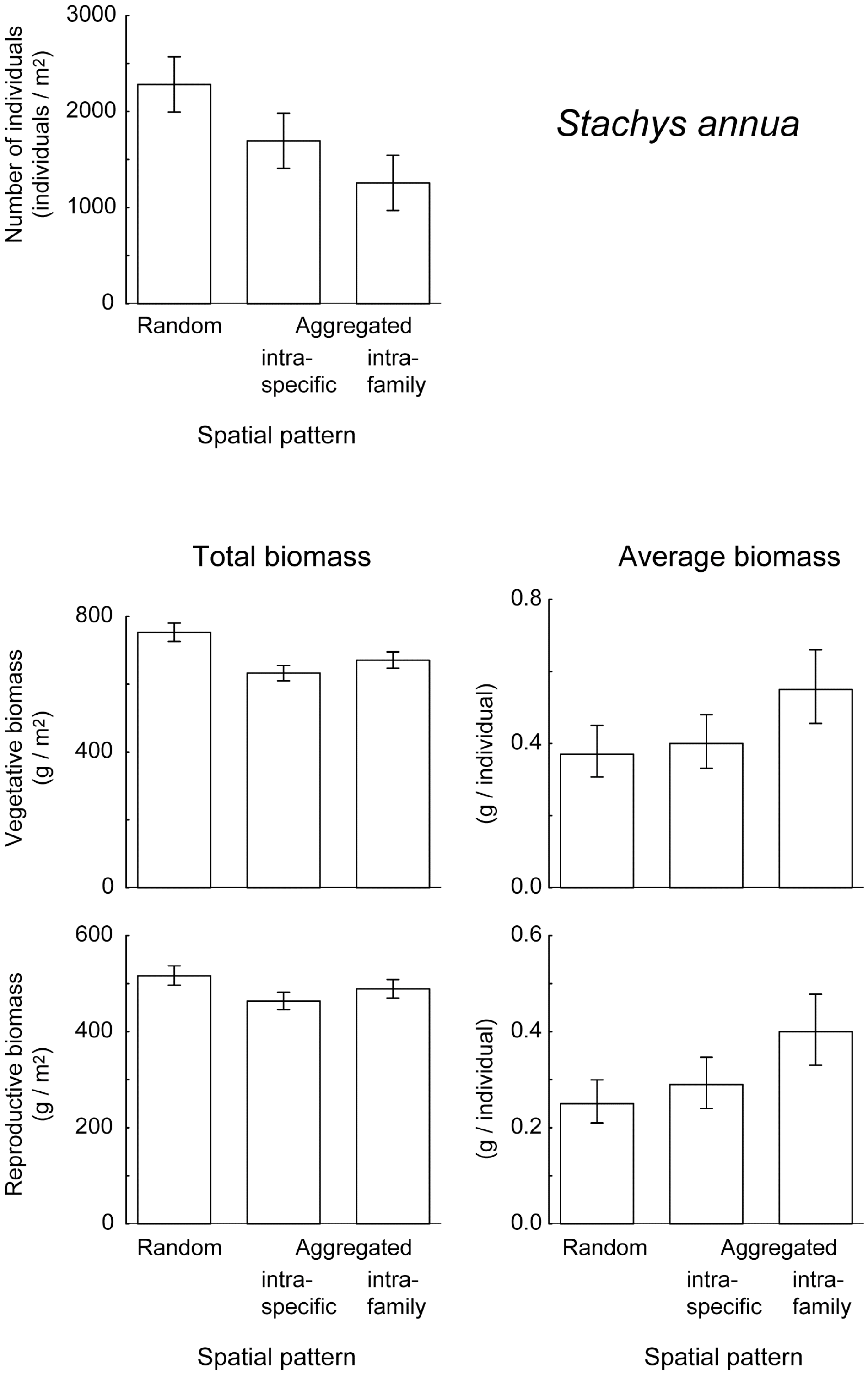

Figure 3 Number of *Stachys annua* individuals (top), total (left, g/m^2) and average (right, g per individual) aboveground vegetative (middle) and reproductive (bottom) biomass grown in random, intraspecific or intrafamily aggregated spatial patterns. The bars represent means ±1 *SE* from ANOVA for number of individuals and backtransformed means from $\log_{10}$(Y)-transformed data for vegetative and reproductive biomass.

Chapter 4

Sibling competition or kin selection in plant species (*Senecio jacobaea*) with dimorphic seeds

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Abstract

Dispersal in plants is spatially limited and neighbors are often conspecifics and genetically related. If genetically similar individuals grow together, they may have less potential to partition limiting resources than genetically variable individuals. Consequently, sibling competition might reduce individual fitness. Increased genetic relatedness, however, might also lead to symmetric competition and reduced size variation among relatives. Hence, genetically related individuals growing together, may show increased growth and reproduction as compared to unrelated individuals. Thus, kin selection might be hypothesized to have been operating in the past. Kin selection could be more frequent in plants with highly limited dispersal compared to species with good dispersal abilities. However, our empirical knowledge of sibling competition and kin selection in plants is scarce and inconsistent.

We compared biomass production and competition mode (asymmetric vs. symmetric) of individuals competing with genetically related (half-sibs) versus non-related individuals of *Senecio jacobaea* in a greenhouse pot experiment. Seeds of *Senecio* are dimorphic: small seeds with pappus and heavier seeds without pappus are produced within the same flower head. Hence, we investigated effects of sibling competition among individuals grown from seeds of the same mother plant but with different dispersal abilities.

After 17 weeks, pairs of related individuals produced 4% more total biomass than pairs of unrelated individuals. This difference was marginally significant ($P < 0.10$). Pairs of related individuals were significantly taller and had lower coefficients of variation in biomass than pairs of non-related individuals. Thus, relatives competed more symmetrically compared to non-relatives. Positive effects of growing among relatives were more pronounced in individuals grown from seeds without pappus compared to individuals grown from seeds with pappus. In conclusion, sibling competition had no negative effects. On the contrary, our data suggested that *Senecio* might have experienced some sort of kin selection in the past.

Key-words: asymmetric competition, dispersal, size variability, symmetric competition

Introduction

In plants, spatially limited seed dispersal can lead to a pronounced aggregation of conspecifics (see e.g. Seidler and Plotkin 2006) with the additional consequence that neighbors are often genetically related (half- or full-siblings) to each other. In other words, if dispersal results in relatives being aggregated in space and interacting primarily with one another, then local competition may become sibling competition (Cheplick 1992; 1993a, b; Kelly 1996; Lambin et al. 2001). Since the intensity of competition is thought to increase with genetic similarity of competitors (Maynard Smith 1978), individuals that produce a large number of badly dispersed offspring suffer fitness losses due to sibling competition. Consequently, intense sibling competition should in principle be avoided (Cheplick 1992, 1993a, b). According to the resource-partitioning hypothesis (Young 1981; Argyres and Schmitt 1992) genetically variable offspring might have greater potential to partition limiting resources than genetically similar or identical offspring. Thus, the negative effects on growth and reproduction that result from intraspecific competition can be greater among related than non-related individuals.

On the other side, relatedness among individuals can drive the evolution of altruism and kin selection theory shows how individuals may increase inclusive fitness (Hamilton 1964; Maynard Smith 1964). In its simplest form, Hamilton's rule states that altruistic behavior is favored when $rb-c > 0$; where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary and r is their genetic relatedness. In other words, an individual may reduce its own fitness, if the costs are compensated with increased fitness of its relatives. Highly localized dispersal (population viscosity) was proposed to increase the probability that positive interactions among group members will benefit relatives as opposed to unrelated individuals and thereby promotes the evolution of altruistic behavior (Hamilton 1964; Wilson 1987). However, Taylor (1992) showed theoretically, that competition in viscous populations can exactly counteract the advantage of being in a group with altruistic relatives such that limited dispersal ultimately does not influence the probability of the evolution of altruism (Queller 1992; 1994; Taylor 1992; Wilson et al. 1992). Nevertheless, because many plant species show limited seed dispersal (Goodnight 1985; Goodnight and Stevens 1997), kin selection may be a significant evolutionary force counteracting the negative consequences of sibling competition (Nakamura 1980; Cheplick 1993b; Kelly 1996; Griffin and West 2002).

Despite the straightforward predictions from sibling competition and kin selection hypotheses, few empirical tests with plants have been made and the results are inconsistent. Some studies showed that plants competing with genetically related individuals perform worse compared to plants competing with unrelated individuals (Willson et al. 1987; Kelley 1989; Argyres and Schmitt 1992; Karron and Marshall 1993). Other studies provided evidence for the contrary, namely that plants competing with genetic relatives outperformed those competing with unrelated individuals (Willson et al. 1987; Tonsor 1989; Andalo et al. 2001; Donohue 2003). Hence, our understanding of sibling competition and kin selection in plants is idiosyncratic and it remains difficult to predict whether or not and under which conditions, individual plants reduce or increase their fitness within neighborhoods of relatives.

Two modes of competition can be distinguished depending on how resources are partitioned among individuals. When larger individuals have a disproportionate advantage (relative to their size) in competition with smaller individuals and suppress their growth, competition is called ‘size-asymmetric’ (Begon 1984; Weiner 1985, 1990; Schwinning and Weiner 1998). By contrast, when resources are divided equally or proportionally to the size of competing individuals, competition is called ‘size-symmetric’ (Weiner 1990). The mode of competition is important since it has major consequences for population and community dynamics (e.g. Lomnicki 1980; Pacala and Weiner 1991; Schwinning and Fox 1995; Freckleton and Watkinson 2001). Because size inequality (measured as coefficient of variation) within a population changes depending on competition mode, the pattern of size inequality is often taken to indicate the degree of size asymmetry of competition (Weiner and Solbrig 1984; Schwinning and Weiner 1998). Amongst the several studies investigating the effects of competition mode on population dynamics (e.g. Hara and Wyszomirski 1994; Schwinning and Fox 1995; Freckleton and Watkinson 2001, Ogawa and Hagihara 2003), one empirical study went further and tested the effects of competition mode on density-dependent mortality (self-thinning). Stoll *et al.* (2002) compared self-thinning in wild type and mutant *A. thaliana* with decreased plasticity. Compared to more asymmetric competition among mutants, more symmetric competition among wild types led to increased biomass production because of less density-dependent mortality. Similar results might be expected if competition would be more symmetric in populations composed of genetically related and more asymmetric in populations of non-related individuals. Furthermore, a theoretical study showed that increased genetic relatedness might lead to reduced variation in size and more symmetrical competition (Aikio and Pakkasmaa 2003), which has also been observed empirically (Jasienski 1988; Tonsor 1989). Thus, genetic relatedness can be expected to differently affect the intensity of competition and / or sharing of resources in a population of relatives as compared to populations of non-related individuals (Pakkasmaa and Aikio 2003).

Seed heteromorphisms (Harper 1977) are known from several species in several plant families (e.g. Asteraceae, Brassicaceae, Poaceae). Individuals of these species produce two or more fruit types that differ morphologically and ecologically. The different suites of morphological and ecological characteristics typically result in distinct patterns of spatial and temporal seed dispersal between fruit types (Venable and Lawlor 1980; Venable 1985). Seeds without dispersal structures are expected to disperse more locally compared to seeds with dispersal structures (e.g. pappus). More generally, it might be argued that interactions among relatives are more frequent in species with more locally dispersed seeds compared to species with more distantly dispersed seeds. Consequently, kin selection might be expected to be more likely in species with more locally compared to more distantly dispersed seeds (Nakamura 1980; Cheplick 1993b; Kelly 1996; Griffin and West 2002). On the other hand, seeds that are dispersed over greater distances (e.g. by wind) produce individuals that interact less frequently with relatives. Therefore, kin selection might be less likely and negative effects of sibling competition might prevail in such species. Species, however, differ in many traits simultaneously and effects of different dispersal abilities on the intensity and direction of sibling interactions may be confounded with other species-specific traits. Therefore, in order to compare the response of individuals to sibling competition using seeds with different dispersal abilities, any potentially confounding species-specific traits should be avoided. For this purpose, dimorphic species provide an excellent opportunity to study the interactions between related and unrelated individuals with different dispersal abilities.

The aim of the present study was to increase our poor and inconsistent empirical knowledge of sibling competition and kin selection in plants. We compared biomass production, competition mode (symmetric vs. asymmetric) and effects of seed heteromorphism (i.e. seeds with vs. without pappus) of *Senecio jacobaea* (Asteraceae) individuals competing with genetically related (at least half-sibs) versus non-related individuals using a pot experiment under greenhouse conditions. Based on the sibling competition hypothesis, we expect first that individuals grown with relatives would decrease their biomass production compared to individuals grown with non-relatives. If so, the resource-partitioning hypothesis may be used to interpret the results. By contrast, if the opposite outcome would occur, i.e. individuals grown with relatives would increase their biomass production compared to individuals grown with non-relatives, kin selection might be hypothesized to have been operating in the past. Second, we expect more similar growth and equal resource share among related compared to non-related individuals, mostly because of more genetic uniformity. This would result in lower size variation (measured as coefficients of variation) and hence more symmetric competition among competing relatives compared to competing non-relatives. Third, we hypothesize that kin selection might be more likely (or sibling competition less severe) among individuals grown form locally dispersed seeds without pappus compared to individuals grown from more distantly dispersed seeds with pappus.

Material and Methods

Study species

Ragwort, *Senecio jacobaea* L. (Asteraceae) is a self-incompatible erect biennial or short-lived perennial of disturbed and open habitats. Rosettes are usually biennial, spending the first year vegetatively and producing flowering stalks in the second year. However, flowering is triggered by a cold period provided the plants have reached a certain critical threshold size (Wesselingh and Klimkhamer 1996). Disturbance, like defoliation by caterpillars, may result in a perennial life style and clonal growth (Van der Meijden and Van der Waals-Kooi 1979). Moreover, regeneration may occur from root fragments quite unconnected with shoot, especially when planted in damp soil or in a warm greenhouse (Harper and Wood 1957). Seeds of *S. jacobaea* have a distinct dimorphism. Seeds produced in the centre of the flower head (i.e. disk fruits) are lighter, more numerous and bear a pappus that aid wind dispersal. Seeds produced on the edge of the flower head (i.e. ray fruits) are heavier, less numerous and do not have a pappus (Harper and Wood 1957). Both seed morphs differ behaviorally (e.g. dormancy) and morphologically. Seeds without pappus have generally thicker pericarps and require more time to germinate than seeds with pappus (McEvoy 1984; McEvoy and Cox 1987).

Seed collection

Seeds of single mother plants were collected in the year 2000, in the region of Bern (Wankdorfplatz, Switzerland) and stored at room temperature. All seeds from a single mother plant are referred to as seed family and are at least half-sibs. Mean seed mass was measured by weighing 5 samples of 100 seeds (either with or without pappus) from each seed family. Four of nine seed families spanning the range of available seed mass (averaged over both seed morphs) were selected. We choose the seed family with the lightest seeds (F3), the seed family with the heaviest seeds (F9), and two seed families with intermediate seed mass (F2 and F5) (Table 1). Mean seed mass (with and without pappus) was compared using an analysis of variance with main factors seed families, seed morph and their interaction. In general, seeds with pappus were significantly lighter than seeds without pappus (Table 1).

Experimental design

The experiment was performed using pots with two individuals (pairs) per pot and all possible combinations between the four seed families and the two seed morphs, yielding 36 combinations in total (Fig.1). Each combination was replicated six times for a total of 216 pots. Pots were randomly allocated to two greenhouse chambers (called chamber 1 and chamber 2) such that 3 replicates per combination were allocated to each chamber. In addition to the experimental pots, extra pots for six sequential harvests were sown. For each harvest, 10 pots per seed family were sown: five pots with pairs of seeds with pappus (i.e. 10 individuals) and five pots with pairs of seeds without pappus, for a total of 40 pots (10 pots x 4 seed families) per harvest. Three harvests (i.e. 120 pots) were allocated randomly to each chamber. At every harvest, 40 pots from the same chamber were harvested. Within chambers, all pots were placed randomly and re-randomized every four weeks.

Additional experimental settings

The experiment was established between May 6 and 9, 2002 in a greenhouse at the Botanical Institute of the University of Basel. The seeds were sown in plastic pots (ø12 cm, volume 750 ml, type ESH, GVZ-Bolltec AG, Switzerland) filled with commercial garden soil. Three seeds per seed family and seed morph were initially sown about 1.5 cm from the pot centre using a template. The seeds were covered with a thin layer of sieved garden soil, which was slightly pressed to prevent them from being washed away. One week after sowing, the first seeds germinated**.** Excess seedlings were removed and used to complete combinations in which no seed germinated. Although the sieved soil was slightly pressed down to prevent relocation of seeds, in both chambers, some of the seeds were washed away. For the replicates in chamber 2, most combinations could be rescued using the excess plants, while chamber 1 was too mixed up to continue the experiment. For this reason, chamber 1 was completely re-seeded between June 14 and 15, 2002 (i.e. 6 weeks after the onset).

Although already in their second year, most plants did not flower. Therefore, in an attempt to induce flowering, on January 7 2004 we moved the pots from both chambers (which where warm and humid) into an open greenhouse section with cooler temperatures. Additionally, by the end of 2004, we transplanted all plants into bigger pots (ø 16 cm, volume 1560 ml, type ESN, GVZ-Bolltec AG, Switzerland). The soil around the roots was not washed away. Plants were watered by hand from the base as needed.

Morphological measurements and harvest

At each harvest date, we measured plant height and size (length and width) of the three biggest leaves of all individuals. Dry weight of the experimental plants was estimated non-destructively after harvesting the designated plants 5, 8, 17, 54, 102 and 122 weeks from the beginning of the experiment. The aboveground biomass of the harvested individuals was weighed after drying at 60° C for 24 h. Only vegetative biomass could be determined because most plants did not flower. Regressions between morphological measurements and dry weight were established to estimate dry weight of the plants still growing. In general, all morphological measurements were well correlated with dry weight (Fig. 2). The mean leaf width and mean leaf length (averaged over the three biggest leaves), however, showed the best (highest R^2) correlations with dry weight, followed by height while the number of leaves showed the weakest correlations. Consequently, mean leaf width was used to estimate dry weight non-destructively for the first three harvests (5, 8, 17 weeks) and after 102 weeks, while mean leaf length was used for harvests after 54 and 122 weeks.

Pest control and fertilization

Although yellow insect sticky ‘fly strips’ were placed in both chambers and regularly changed when full with trapped adult insects, the plants had to be treated several times against various pests (e.g. Sciaridae larvae, powdery mildew). The plants were fertilized four times during the experiment (on 5.5, 20.8, and 27.8. 2005, and 30.3.2006) with a solution of N(tot) 80g/l, NS 15 g/l, NU 65 g/l / P2O5 (PS) 40g/l / K2O 100g/l [Vegesan Gemüse and Blumen (Rapid), Hauert®].

Statistical analysis

Regression analysis was used to test for treatment effects (i.e. relatedness, seed family and seed morph) on aboveground biomass, height and size variability measured as coefficient of variation (CV). The factor ‘chamber‘ was used as block factor. We performed the analyses at two levels. The first was at the pot level and considered pairs of individuals as experimental units. The second was at the individual level, where single individuals within pots were considered as experimental units.

At the pot level we tested the effects of relatedness and seed morph on total and average biomass, average height and coefficient of variation within and between combinations. If the main effect of seed morph was significant, we calculated least significant differences (LSD, $P < 0.05$) for each harvest time (Sokal and Rohlf, p. 243) to evaluate which of the combinations (both individuals with or without pappus or one with and one without) differed significantly. We used $k = 1$, and $n = 70$ after 5 and 8 weeks, and $n = 69$ after 17 weeks. Since we restricted the analysis to pots with 2 surviving individuals, results on total and average biomass were comparable. For this reason only results on the total biomass are presented.

At the individual level, we could also test for the effects of seed family, which was not possible at the pot level. Because the design was not fully balanced, we controlled if the sequences of the terms influenced the relatedness effect (related vs. non-related). In a first analysis we tested the term ‘relatedness’ directly after the block factor ‘chamber’. In a second analysis, we tested the term ‘relatedness’ after the block factor ‘chamber’ and the terms ‘target family’ and ‘target family seed morph’. Since, generally both analyses showed comparable conclusions, we decided to present the first analysis. Since no three-way interactions were significant, they were excluded from the models. Furthermore, at the individual level, we tested for the effects of initial seed mass as covariate. However, because the residual variance remained similar in both models with or without the covariate, we present only the analysis without covariate.

In could be possible that relatedness effects differ depending on which family was used as neighbor. In order to test for such 'hierarchical family effects', effects of relatedness were tested separately for each seed family. That is, the analyses were restricted to one target and one neighbor family exclusively. In order to see whether or not the effects of growing with relatives were more often positive in pairs of a certain seed morph, the analyses were further restricted to include only pairs in which both individuals grew from seeds with or without pappus. Because results for total biomass and height were similar, we present only the results for total biomass.

We analyzed data from all six surveys and present their results in all tables. However, only results from the first three surveys are presented graphically because: (i) the first three surveys were all done in 2002; (ii) the biomass of the fourth und subsequent surveys was lower (< 1 g per pot) compared to the third survey (1.5 g per pot), probably due to damages from pests; (iii) after 54, 102, and 122 weeks the treatment effects were either not or only marginally significant.

CVs were logarithmically transformed [$\log_{10}(y)$] to obtain normal distributions of the residuals and homogeneity of variances and back transformed means from $\log_{10}$ (y)-transformed data are presented. Data on biomass and height were also $\log_{10}$-transformed for the analysis at the individual level after 54, 102 and 122 weeks. All analyses were conducted using GENSTAT 5 (Payne et al. 1987). The regressions between morphological measurements and dry weight were estimated using R Statistical Software (R Development Core Team 2003).

Results

Effects of relatedness and seed morph at the pot level

Total biomass production per pot at the first and second survey did not differ between pairs of related or non-related individuals. However, at the third survey (17 weeks), pairs of related competitors were marginally heavier compared to pairs of non-related competitors (Table 2, Fig. 3). In addition, at the second and third survey, pairs of related competitors were marginally or significantly taller than pairs of non-related competitors (Table 2, Fig. 3).

Total biomass and average height at the first three surveys always differed significantly between seed morph combinations (i.e. both seeds with pappus, both seeds without pappus, or mix) (Table 2, Fig. 4). In general, pairs of plants grown from seeds with pappus, produced heavier and taller individuals, followed by the mixed pairs (i.e. one competitor with pappus, one without) and by pairs grown from seeds without pappus (Fig. 4).

The CV of biomass was significantly lower among related compared to non-related competitors after 5, 8 and 17 weeks (Table 3, Fig. 5). Analogous, related individuals showed a significantly lower CV of height after 17 weeks compared to non-related competitors (Table 3, Fig. 5). In general the CVs did not differ between the seed morph combinations. However, after 54 weeks we observed a significant relatedness by seed morph combination interaction for both CV of biomass and height (Table 3), while at the end of the experiment (i.e. after 122 weeks) this interaction was significant only for the CV of height. After 54 weeks, non-related individuals grown from seeds with pappus had higher CVs compared to related individuals (CV biomass: non-related 45.78%; related 19.74%; CV height: non-related 26.17%; related 13.65%). However, the opposite pattern was observed for individuals grown from seeds without pappus (CV biomass: non-related 28.99%; related 33.91%; CV height: non-related 20.14%; related 25.22%).

Effects of relatedness, seed family and seed morph at the individual level

Contrary to the other surveys, at the third survey (17 weeks), total biomass was significantly different between individuals grown with related and non-related individuals. That is, related individuals were heavier compared to non-related individuals (Table 4, Fig. 6). In addition, linear contrasts showed that differences between related versus non-related individuals, were more evident amongst individuals grown from seeds without pappus than individuals grown form seeds with pappus (Fig. 6). Moreover, after 17 weeks, related individuals grown from seeds without pappus were significantly heavier than individuals grown from non-related seeds (Fig. 6). Related individuals were also taller compared to non-related individuals. This effect was marginally significant at the fourth survey, while significant at the second and third surveys (Table 4, Fig.6). The linear contrasts reveled that differences between related versus non-related individuals, were either significant or marginally significant amongst individuals grown from seeds without pappus at the first two harvests. No significant differences were found between individuals grown form seeds with pappus. However, after 17 weeks, relatedness effects were also significant for individuals grown from seeds with pappus (Fig. 6). Overall, the target seed family as well as the seed morph (i.e. with vs. without a pappus) of the target family, had large and significant effects on biomass production and height (Table 4). In general target individuals grown from seeds with pappus were heavier and taller compared to individuals grown from seeds without pappus (Fig. 6).

The analyses, which compared each seed family with either members of its own family or members of one of the other seed families (i.e. target vs. neighbor seed family), showed that not all seed families reacted in the same way and with the same magnitude regarding relatedness effects. At the second survey (i.e. after 8 weeks from the beginning of the experiment), related members of the target seed family number 2 (F2) produced slightly more biomass than non-related individuals (Fig. 7). Individuals form target F3 competing with members of F9 showed opposite effects regarding biomass depending on seed morph. When both competitors were grown from seeds with pappus, non-related individuals performed better compared to related individuals. By contrast, when competitors were grown form seeds without pappus, related individuals produced more biomass than non-related competitors (Fig. 7). In general, if positive relatedness effects were present, they were more often observed in individuals grown from seeds without pappus (9 cases) compared to individuals grown from seeds with pappus (3 cases) (Fig. 7).

Discussion

The present experiment showed that neighbor relatedness influenced individual performance of *Senecio jacobaea* in such a way that related individuals growing together increased their fitness (e.g. biomass production) compared to non-related individuals. Therefore, the sibling competition hypothesis must be rejected because pairs of related never showed less biomass production than pairs of non-related individuals. As expected, the coefficients of variation (CV) clearly showed that relatives had lower CVs than non-relatives. This indicated less asymmetric competition among related individuals and supported our second hypothesis that related individuals had more similar growth and even resource partitioning compared to non-related competitors. Finally, the relatedness effects were more evident among individuals grown from seeds without pappus (locally dispersed) than among individuals grown from seeds with pappus. Thus, sibling competition must not only be rejected but there is at least some support for the kin selection hypothesis.

Our results were in line with the few empirical studies that found that individuals growing with genetically similar plants outperformed those growing with unrelated individuals (Willson et al. 1987; Tonsor 1989; Andalo et al. 2001; Donohue 2003). In an experiment comparing genotypes at two CO_2 concentrations (ambient vs. elevated), Andalo et al. (2001) found that at ambient CO_2 concentration, the fitness of a genotype was greater when surrounded by the same genotype than when surrounded by individuals of different genotypes. Tonsor (1989) showed that the number of *Plantago lanceolata* flowering per pot increased with an increase in genetic relatedness from non-sibs to half-sibs to full-sibs and Willson et al. (1987) observed that *Phytolacca americana* plants growing with their siblings showed some enhancement of size compared to plants growing with non-siblings. Field experiments with the annual dune species *Cakile edentula* provided solid evidence for kin selection. Individuals growing with siblings had higher reproductive success compared to individuals growing with non-siblings (Donohue 2003). However, such positive sibling competition effects are rather unusual. Most studies designed to detect effects of neighbor relatedness on fitness did either detect only slight effects or none at all (e.g. Schmitt and Ehrhardt 1987; Argyres and Schmitt 1992; Cheplick 1992; Cheplick and Kane 2004).

Density is an important factor in competitive interaction and results may be affected by the arbitrary choice of density and frequencies of competing relatives (Connolly 1987). Although relatedness is important in competitive interactions, it may be modulated by the scale of competition (i.e. when competition is local the effect of high relatedness cancel out). This is supported by studies with microorganism (Queller 2004; Griffin et al. 2004) and by the extended version of Hamilton's rule proposed by Frank (1998). Frank (1998) demonstrated that the success of cooperators depends on the scale of competition and its interactions with relatedness and that selection for altruism depends upon the scale of competition. The density in our experiment was relatively low (app. 177 plants per m^2) and perhaps lower than in natural populations of *S. jacobaea*. This may have favored the positive (or less negative) interactions among siblings. Nevertheless, other studies used few individuals per pot but could not observe effects of neighbor relatedness on individual fitness (e.g. Schmitt and Ehrhardt 1987; Argyres and Schmitt 1992; Cheplick 1992; Cheplick and Kane 2004). However, because (i) seed dispersal of *S. jacobaea* is rather local (< 1m, see e.g. McEvoy and Cox 1987) and therefore sibling competition might be likely, and (ii) because we observed positive effects of neighbor relatedness especially among individuals grown form seeds which are expected to aggregated more locally (i.e. seeds without pappus), we speculate that this species may have acquired adaptations in order to alleviate the negative effects of sibling competition.

Size asymmetry appears to be caused by competition for light, in that larger individuals overtop and shade smaller individuals, whereas smaller individuals have almost no effect on the light available to their larger neighbors. Hence, under asymmetric competition populations show greatest size inequality and stronger hierarchies, while under symmetric competition size variation within the population increases only slightly during stand development, resulting in weak hierarchies. Our data supported our prediction and showed less size variation (i.e. low coefficient of variation) and asymmetric competition between related compared to non-related individuals. This might probably be explained by more equal resource share and similar growth compared to non-related individuals. Previous theoretical (Aikio and Pakkasmaa 2003) and empirical studies on amphibians (Jasienski 1988) and plants (Tonsor 1989) also showed that increased genetic relatedness might lead to reduced variation in size and more symmetrical competition. The decreased size variability among related individuals may be a consequence of higher genotypic uniformity and / or kin selection among related as compared to non-related individuals. Furthermore, this result taken together with increased biomass production observed among related individuals, agreed with a theoretical (Weiner et al. 2001) and an empirical (Stoll et al. 2002) study showing that biomass production increased under symmetric competition due to decreased density-dependent mortality.

As expected, we found pronounced differences in performance between seed families (i.e. genotypes). Not all seed families performed better when surrounded by individuals with similar genotypes. Although we used only four seed families, our results indicated that selection for competitive ability will depend on the genetic relatedness of competitors and suggested that competitive ability in *S. jacobaea* varies between genotypes. Similar effects of neighbor relatedness on the growth and fitness of particular genotypes have been reported by others (e.g. Taylor and Aarssen 1990; Donohue 2003; Cheplick and Kane 2004).

Seed size is well correlated with individual fitness and larger seeds produce larger seedlings (Harper 1977). In contrast to this expectation, we observed that individuals grown from seeds with pappus (i.e. lighter seeds) were heavier and taller compared to individuals grown from seeds without pappus (i.e. heavier seeds). This could be explained by the morphological and ecological differences between the two morphs (McEvoy 1984; McEvoy and Cox 1987). McEvoy (1984) showed that seeds with pappus require less time to germinate compared to seeds without pappus at the same temperature. We suppose that seeds with pappus germinated faster than seeds without pappus and gained a temporal advantage.

Unfortunately, the majority of the plants did not flower at the end of the second year. This made the assessment of the reproductive biomass impossible. Since flowering by *S. jacobaea* is triggered by a cold period provided the plants have reached a threshold size (Wesselingh and Klimkhamer 1996), we suspected that temperatures and humidity in the greenhouse were too high to stimulate flowering. In addition, the damages caused by the Sciaridae larvae (sometimes there was almost nothing left of the attacked rosette) had two consequences. First, plants did not reach the threshold size to flower. Second, plants switched to a perennial life style and clonal growth rather than reproducing by seeds (Van der Meijden and Van der Waals-Kooi 1979). Indeed, also in the following years (2005 and 2006), only few additional individuals flowered. Furthermore, we found considerable chamber effects. Thus, the reseeding of chamber 1 might have created a problem, although we considered that plants in chamber 1 were 6 weeks younger than plants in chamber 2. The pest attacks as well as treatments against the various pests, however, were done for both chambers simultaneously. Hence, younger plants might have recovered from the damages less well than older plants.

The spatially limited dispersal of many plant species may lead siblings to be aggregated in space and competing for limited resources. The genetic similarity of competitors may lead to increased intensity of competition, but create at the same time the opportunity for kin selection to operate. Our results provided evidence for increased fitness and less asymmetric competition among genetically similar compared to genetically dissimilar individuals. This indicated that competition among related individuals was less severe than among non-related individuals. Taken together, our results lend support for the kin selection rather than for the sibling competition hypothesis. Additionally, we showed that relatedness effects were more evident for individuals grown from seeds expected to aggregate more locally (i.e. without pappus) compared to individuals grown from seeds with a wider dispersal range (i.e. with pappus). Although our experiment was conducted under greenhouse rather than natural conditions, our results showed that positive effects among competing siblings might occur. Nevertheless, implications of kin selection in plants remain challenging and further experiments under more natural conditions and for other plant species are needed.

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Table 1 Mean seed mass measured by weighing 5 samples of 100 seeds of *Senecio jacobaea* seed families (four out of nine) with or without pappus (mg of 100 seeds ± standard error of mean) and results of analysis of variance testing the effects of seed family, seed morph (i.e. seeds with or without pappus) and their interaction. *Notes*: * $P < 0.05$; *** $P < 0.001$. Abbreviations: d.f. = degree of freedom, F = F-value (variance ratio).

	Pappus		
Seed family	with	without	*Mean*
F2	29.6 ± 1.3	41.0 ± 1.1	35.3 ± 5.7
F3	19.6 ± 0.4	26.2 ± 0.5	22.9 ± 3.3
F5	30.7 ± 0.5	37.2 ± 1.8	33.9 ± 3.3
F9	43.3 ± 0.7	56.8 ± 2.4	50.1 ± 6.8
Mean	30.8± 9.7	40.3 ± 12.7	

Source of variation	d.f.	F	
seed family (SF)	3	130.2	***
seed morph (SM)	1	94.4	***
SF x SM	3	3.2	*
residuals	32		
total	40		

Table 2 Results of regression analysis of total biomass and average height of *Senecio jacobaea* per pot. Individuals were grown in pairs with all possible combinations of relatedness (i.e. related vs. non-related) and seed morph (i.e. both with, both without pappus or mixed). Abbreviations: d.f. = degree of freedom, F = F-value (variance ratio). *Notes*: (*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The total number of observations differs between survey dates because both individuals of a different number of pots may have died or recovered.

Total biomass

Source of variation	after 5 weeks		after 8 weeks		after 17 weeks		after 54 weeks		after 102 weeks		after 122 weeks	
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F
chamber	1	0.3	1	28.1***	1	3.3 (*)	1	81.2 ***	1	102.2 ***	1	48.2 ***
relatedness (R)	1	0.8	1	1.1	1	3.2 (*)	1	0.1	1	0.0	1	1.2
seed morph (SM)	2	7.2 ***	2	5.9 **	2	3.8 *	2	1.7	2	0.2	2	0.4
R * SM	2	0.0	2	0.4	2	0.3	2	0.1	2	0.1	2	0.3
residual	201		202		196		178		178		186	
total	207		208		202		184		184		192	

Average height

Source of variation	after 5 weeks		after 8 weeks		after 17 weeks		after 54 weeks		after 102 weeks		after 122 weeks	
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F
chamber	1	0.7	1	134.9***	1	107.2 ***	1	88.7 ***	1	37.1 ***	1	0.0
relatedness (R)	1	1.7	1	2.9 (*)	1	5.2 *	1	0.4	1	2.1	1	0.9
seed morph (SM)	2	8.8 ***	2	6.2 **	2	4.9 **	2	0.9	2	0.4	2	0.4
R * SM	2	0.0	2	0.1	2	0.40.651	2	0.0	2	0.2	2	1.3
residual	201		202		196		178		178		186	
total	207		208		202		184		184		192	

Table 3 Results of regression analysis of the coefficient of variations of biomass and height of *Senecio jacobaea* per pot. Individuals were grown in pairs with all possible combinations of relatedness (i.e. related vs. non-related) and seed morph (i.e. both with, both without pappus or mixed). Abbreviations: d.f. = degree of freedom, F = F-value (variance ratio), CV = coefficient of variation. *Notes*: (*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The total number of observations differs between survey dates because both individuals of a different number of pots may have died or recovered. The total number of observations may also differ between CV for biomass and height because if both individuals in a pot have identical values CV equals zero.

CV biomass

Source of variation	after 5 weeks		after 8 weeks		after 17 weeks		after 54 weeks		after 102 weeks		after 122 weeks	
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F
chamber	1	0.3	1	0.9	1	0.6	1	1.53	1	0.1	1	0.3
relatedness (R)	1	5.8 *	1	5.5 *	1	6.6 *	1	0.73	1	0.0	1	0.2
seed morph (SM)	2	0.4	2	1.0	2	0.5	2	0.12	2	0.6	2	0.4
R * SM	2	1.4	2	0.9	2	0.4	2	3.93 *	2	0.0	2	1.3
residual	195		200		194		174		174		186	
total	201		206		200		180		180		192	

CV height

Source of variation	after 5 weeks		after 8 weeks		after 17 weeks		after 54 weeks		after 102 weeks		after 122 weeks	
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F
chamber	1	0.7	1	3.8 (*)	1	2.3	1	0.0	1	0.1	1	2.3
relatedness (R)	1	1.6	1	1.7	1	7.3 **	1	0.6	1	10.4 **	1	4.4 *
seed morph (SM)	2	1.2	2	0.5	2	2.3	2	1.9	2	0.5	2	0.7
R * SM	2	0.1	2	0.5	2	0.0	2	3.2 *	2	0.4	2	4.0 *
residual	200		198		194		172		175		184	
total	206		204		200		178		181		190	

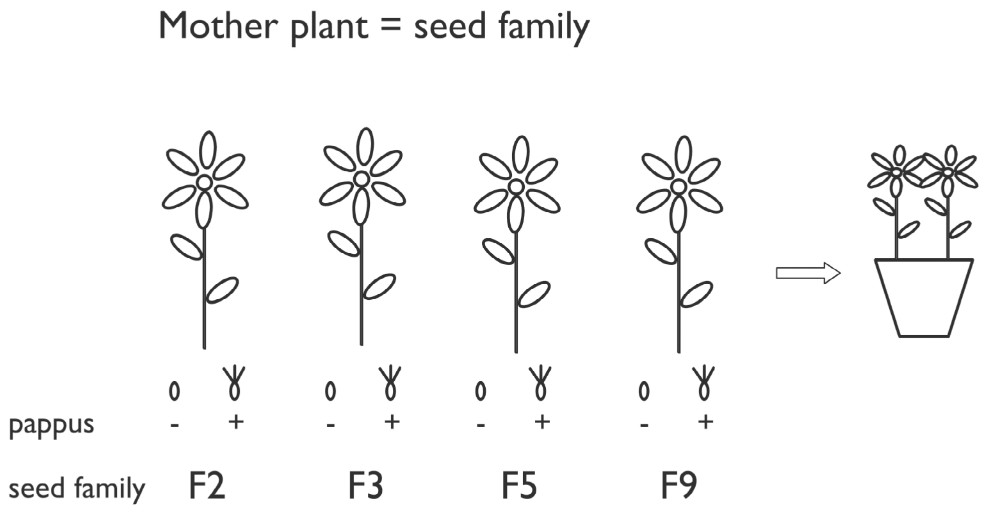
Table 4 Results of regression analysis of the biomass and height of *Senecio jacobaea* at the individual level testing the effects of relatedness (i.e. related vs. non-related), target family, and seed morph of both target and neighbor family on the total biomass and average height. Since no three-way interactions were significant, they were excluded from the model. Abbreviations: d.f. = degree of freedom, F = F-value (variance ratio). *Notes*: (*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The total number of observations differs between survey dates because individuals may have died or recovered. After 54, 102 and 122 weeks, data were $\log_{10}$-transformed to obtain normal distribution of the residuals and homogeneity of variances. For this reason, the total number of observations may differ between biomass and height because of possible negative biomass values obtained form the estimation of the biomass using regressions between morphological measurements and dry weight.

Total biomass

Source of variation	after 5 weeks			after 8 weeks			after 17 weeks			after 54 weeks			after 102 weeks			after 122 weeks		
	d.f.	F		d.f.	F		d.f.	F		d.f.	F		d.f.	F		d.f.	F	
chamber	1	0.4		1	32.1	***	1	3.4	(*)	1	109.5	***	1	125.5	***	1	21.4	***
relatedness (R)	1	1.2		1	1.5		1	3.9	*	1	1.5		1	0.2		1	0.4	
target family (TF)	3	13.1	***	3	8.9	***	3	5.7	***	3	7.2	***	3	3.3	*	3	16.8	***
target family seed morph (TSM)	1	14.0	***	1	11.2	***	1	9.3	**	1	0.3		1	0.1		1	0.0	
neighbor family seed morph (NSM)	1	6.2	*	1	2.8	(*)	1	1.0		1	0.7		1	0.0		1	0.1	
R x TF	3	0.5		3	2.6	(*)	3	1.9		3	2.1		3	1.2		3	0.4	
TF x TSM	3	4.1	**	3	5.0	**	3	3.3	*	3	0.5		3	0.5		3	4.3	**
R x TSM	1	2.2		1	0.9		1	0.7		1	0.7		1	0.7		1	0.0	
TF x NSM	3	1.4		3	0.9		3	0.9		3	0.4		3	0.7		3	0.6	
TP x NSM	1	0.0		1	0.4		1	0.1		1	0.9		1	0.1		1	0.1	
R x NSM	1	3.7	(*)	1	5.1	*	1	2.6		1	1.5		1	0.2		1	0.5	
residual	401			402			396			369			376			380		
total	420			421			415			388			395			399		

Average height

Source of variation	after 5 weeks		after 8 weeks		after 17 weeks		after 54 weeks		after 102 weeks		after 122 weeks	
	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F	d.f.	F
chamber	1	1.26	1	193.84 ***	1	158.13 ***	1	118.64 ***	1	66.47 ***	1	0.33
relatedness (R)	1	2.66	1	4.61 *	1	8.42 **	1	3.14 (*)	1	0.29	1	0.28
target family (TF)	3	3.67 *	3	8.07 ***	3	14.47 ***	3	4.24 **	3	12.76 ***	3	13.78 ***
target family seed morph (TSM)	1	23.60 ***	1	11.20 ***	1	8.33 **	1	0.26	1	0.51	1	1.03
neighbor family seed morph (NSM)	1	5.53 *	1	6.43 *	1	7.01 **	1	0.51	1	0.27	1	0.04
R x TF	3	0.28	3	2.26 (*)	3	1.01	3	1.41	3	3.51 *	3	1.74
TF x TSM	3	3.87 *	3	3.49 *	3	3.30 *	3	0.39	3	1.47	3	1.86
R x TSM	1	3.97 *	1	0.61	1	0.05	1	0.24	1	0.93	1	0.08
TF x NSM	3	1.12	3	0.42	3	0.20	3	0.43	3	0.82	3	1.39
TP x NSM	1	0.00	1	0.50	1	0.20	1	0.68	1	0.09	1	0.07
R x NSM	1	3.20 (*)	1	1.97	1	2.63	1	0.54	1	0.40	1	3.79 (*)
residual	401		402		396		375		378		387	
total	420		421		415		394		397		406	



Seed families

Seed families

	F2+	F3+	F5+	F9+	F2-	F3-	F5-	F9-
F2+	2+ / 2+							
F3+	2+ / 3+	3+ / 3+						
F5+	2+ / 5+	3+ / 5+	5+ / 5+					
F9+	2+ / 9+	3+ / 9+	5+ / 9+	9+ /9+				
F2-	2+ / 2-	3+ / 2-	5+ / 2-	9+ / 2-	2- / 2-			
F3-	2+ / 3-	3+ / 3-	5+ / 3-	9+ / 3-	2- / 3-	3- / 3-		
F5-	2+ / 5-	3+ / 5-	5+ / 5-	9+ / 5-	2- / 5-	3- / 5-	5- / 5-	
F9-	2+ / 9-	3+ / 9-	5+ / 9-	9+ / 9-	2- / 9-	3- / 9-	5- / 9-	9- / 9-

Total: 36 combinations

Figure 1 *Senecio jacobaea* seed families used in a pot experiment. Two individual plants were grown per pot in all possible combinations between four (out of nine) selected seed families (F2, F3, F5, F9) and seeds with (+) or without (-) pappus. Each of the 36 possible combinations was replicated six times yielding a total of 216 pots.

a)

Harvest	Mean leaf width vs. dry weight		Mean leaf length vs. dry weight	
	R^2		R^2	
after 5 weeks	0.98	$y = 0.0014x + 0.007x^2$	0.95	$y = 0.0004x + 0.005x^2$
after 8 weeks	0.94	$y = -0.0497x + 0.029x^2$	0.85	$y = 0.0276x + 0.004x^2$
after 17 weeks	0.94	$y = -0.0246x + 0.028x^2$	0.92	$y = 0.0317x + 0.004x^2$
after 54 weeks	0.83	$y = 0.0495x + 0.021x^2$	0.89	$y = 0.0313x + 0.010x^2$
after 102 weeks	0.80	$y = -0.0996x + 0.109x^2$	0.78	$y = 0.0419x + 0.011x^2$
after 122 weeks	0.81	$y = -0.0129x + 0.093x^2$	0.88	$y = 0.0146x + 0.010x^2$

b)

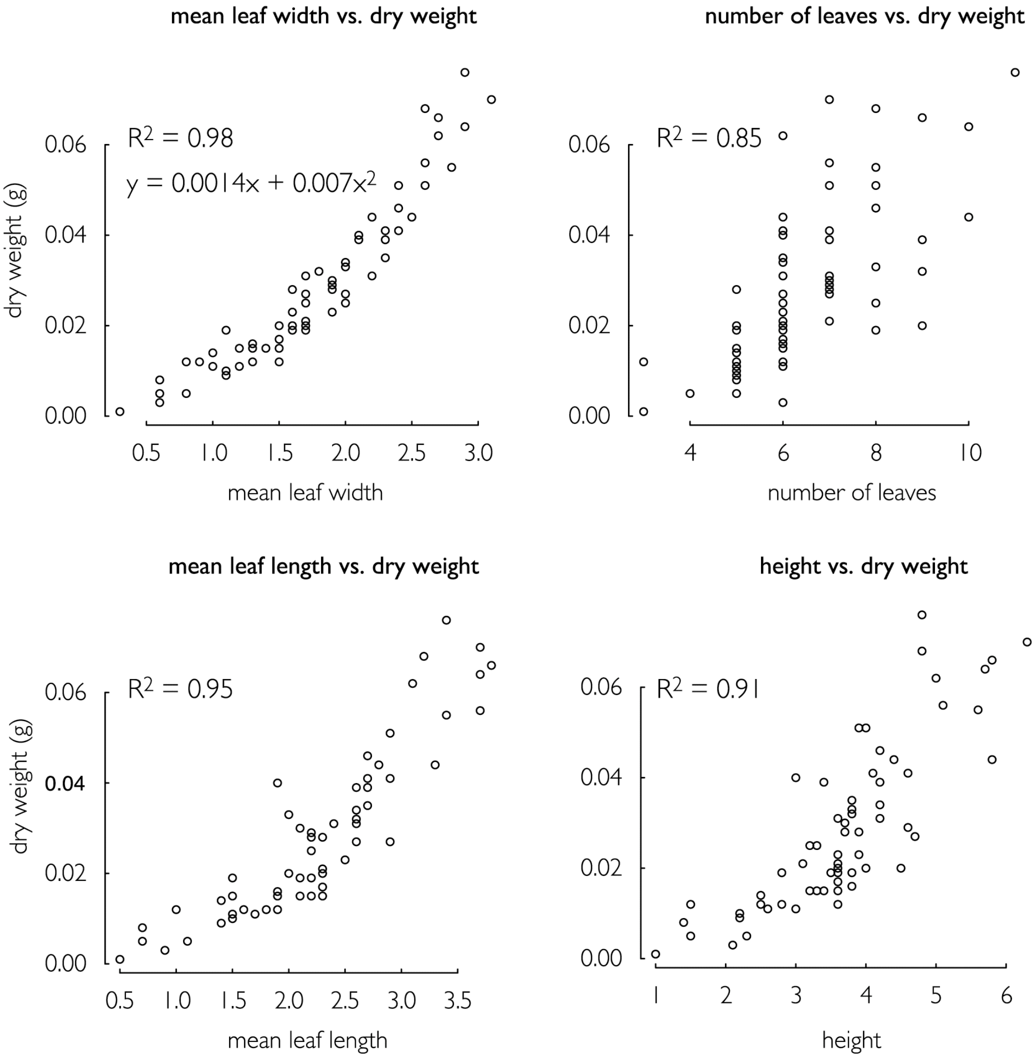


Figure 2 a) Allometric equations between morphological parameters (mean leaf width and mean leaf length, averaged over the three biggest leaves) and dry weight for the harvested individuals of *Senecio jacobaea*. **b)** Detailed example after 5 weeks from the beginning of the experiment (first harvest).

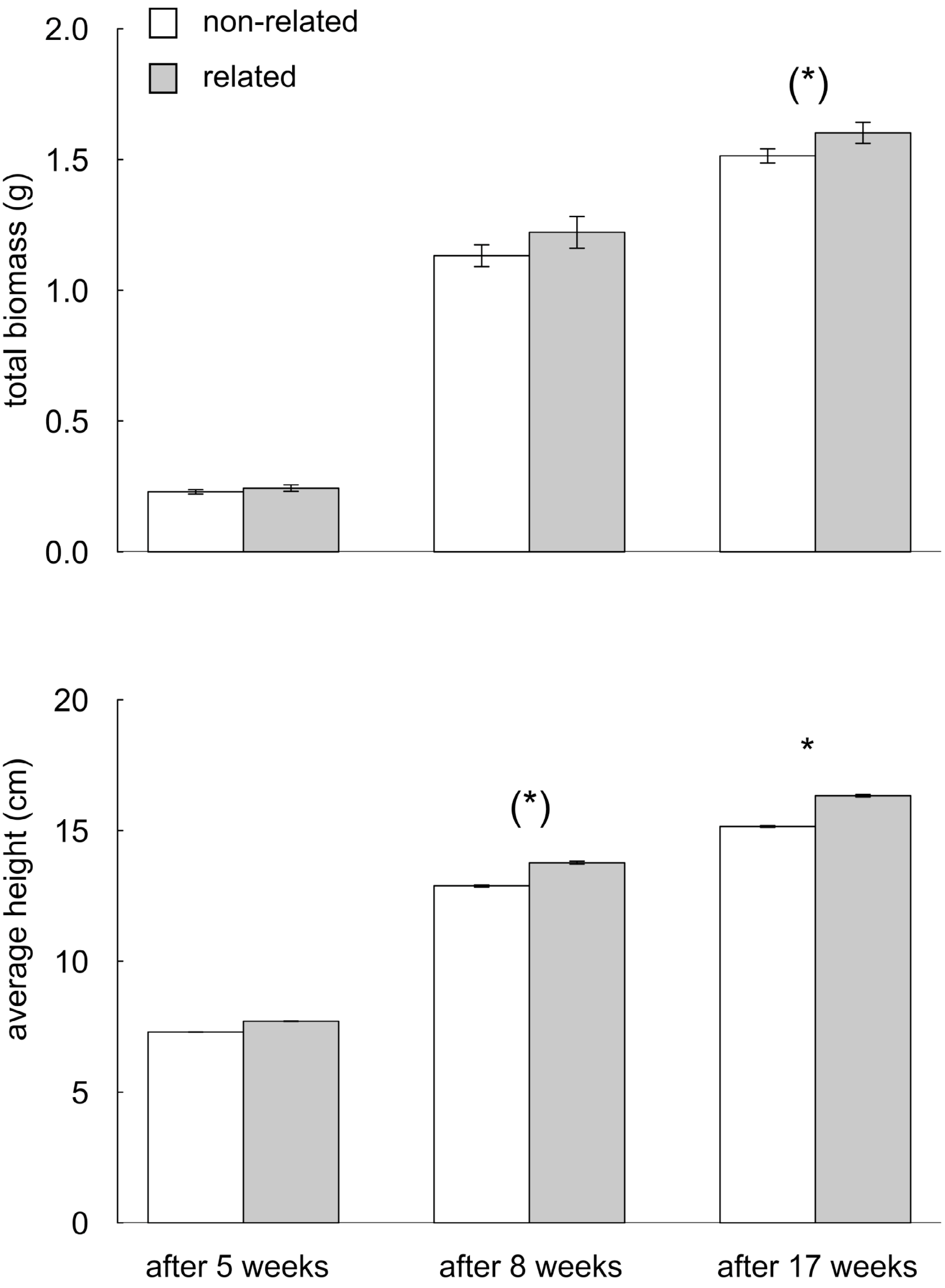


Figure 3 Total biomass per pot and average height of non-related (white bars) and related (grey bars) pairs of *Senecio jacobaea* individuals averaged over both seed morphs. The bars represent means ±1 SE from regression analysis. *Notes*: (*) $P < 0.1$; * $P < 0.05$.

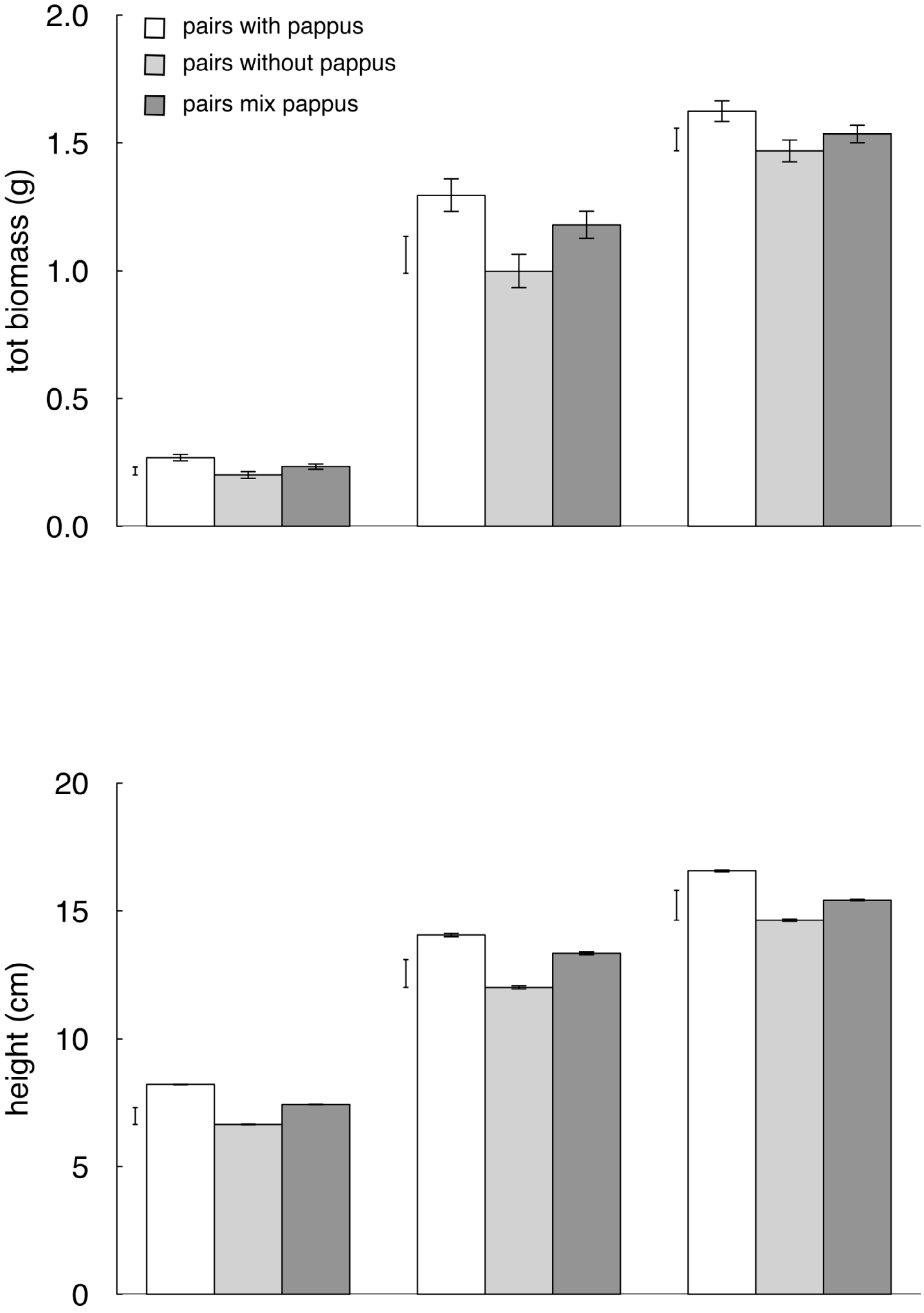


Figure 4 Total biomass per pot and average height of *Senecio jacobaea* individuals grown in pairs from seeds with pappus, pairs from seeds without pappus, and mixed pairs (i.e. one seed with and one without pappus). The bars represent means ±1 SE from a regression analysis. The error bar outside the data columns represents the least significant difference (LSD) at 5%.

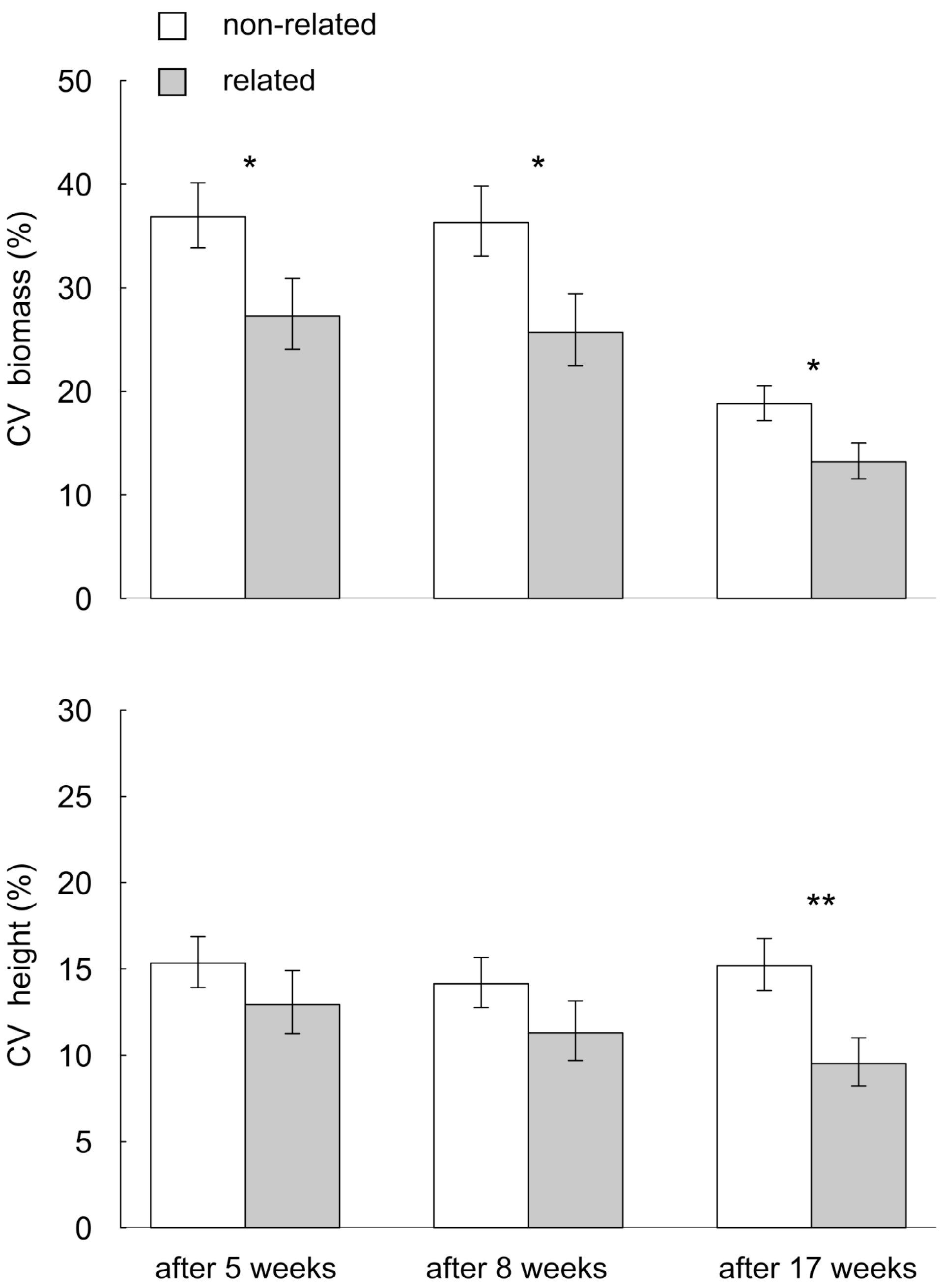


Figure 5 Coefficient of variation (CV) of total biomass and height between non-related (white bars) and related (grey bars) pairs of *Senecio jacobaea* individuals. The bars represent means ±1 SE from a regression analysis, back transformed from $\log_{10}(Y)$-transformed data. *Notes*: * $P < 0.05$; ** $P < 0.01$.

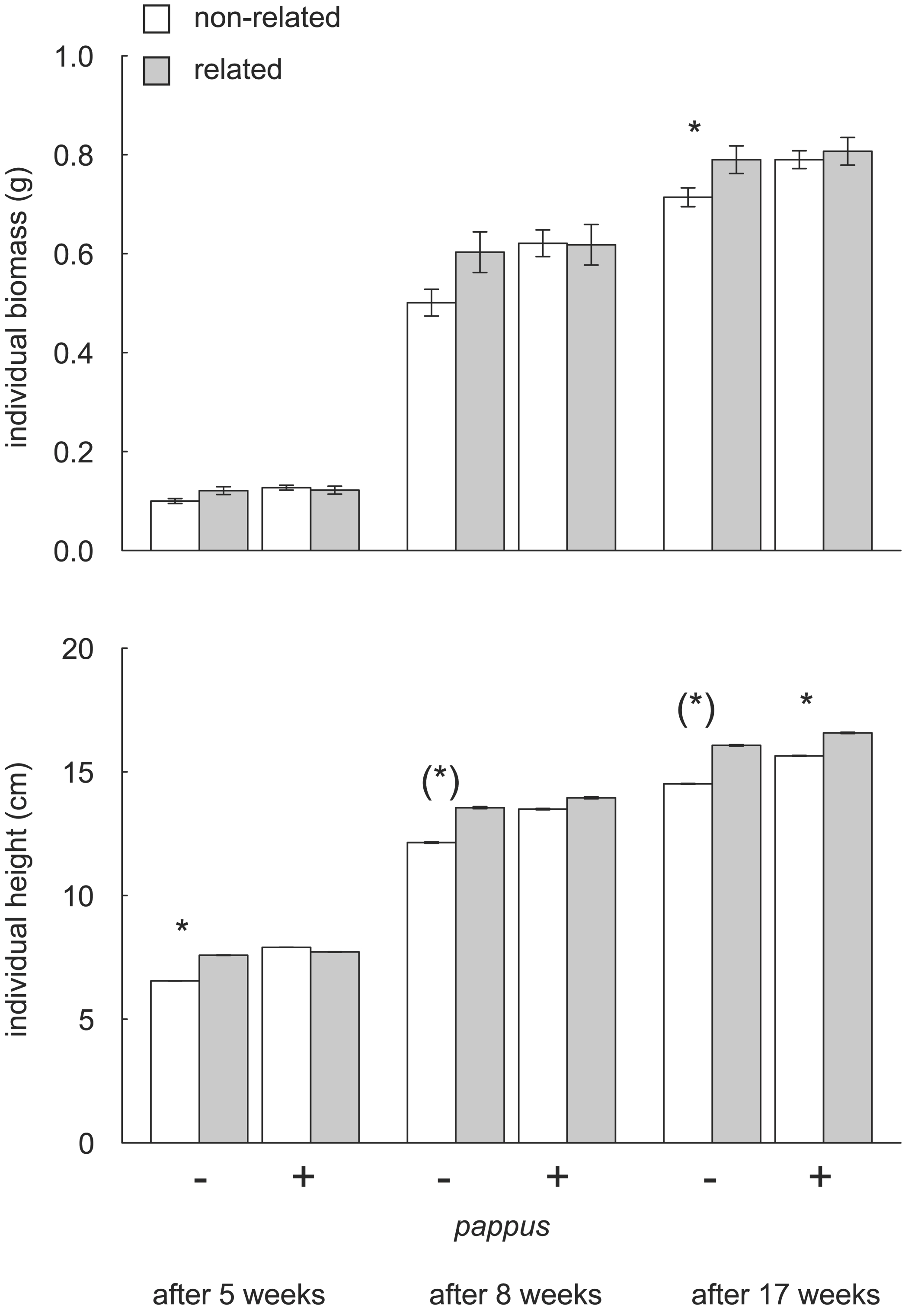


Figure 6 Average biomass and height of *Senecio jacobaea* individuals grown in pairs with related (white bars) and non-related (grey bars) individuals, from seeds without (-) or with (+) pappus. The bars represent means ±1 SE from a regression analysis. *Notes*: (*) $P < 0.1$; * $P < 0.05$.

Overall

	after 5 weeks				after 8 weeks				after 17 weeks			
	neighbor fam				neighbor fam				neighbor fam			
target fam	2	3	5	9	2	3	5	9	2	3	5	9
2		n.s.	n.s.	n.s.		(+)	(+)	(+)		n.s.	+	+
3	n.s.		n.s.	n.s.	n.s.		n.s	n.s.	n.s.		+	n.s.
5	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.
9	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	

Pairs with pappus

	after 5 weeks				after 8 weeks				after 17 weeks			
	neighbor fam				neighbor fam				neighbor fam			
target fam	2	3	5	9	2	3	5	9	2	3	5	9
2		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.
3	n.s.		n.s.	n.s.	n.s.		n.s.	(-)	n.s.		n.s.	(-)
5	n.s.	n.s.		n.s.	n.s.	(+)		n.s.	n.s.	n.s.		n.s.
9	n.s.	n.s.	n.s.		(+)	n.s.	n.s.		(+)	n.s.	n.s.	

Pairs without pappus

	after 5 weeks				after 8 weeks				after 17 weeks			
	neighbor fam				neighbor fam				neighbor fam			
target fam	2	3	5	9	2	3	5	9	2	3	5	9
2		n.s.	+	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	+
3	+		(+)	+	(+)		n.s.	+	n.s.		++	(+)
5	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.		(-)
9	n.s.	n.s.	n.s.		n.s.	n.s.	n.s.		n.s.	n.s.	n.s.	

Figure 7 Summary of regression analyses restricted to one particular target and neighbor seed family of *Senecio jacobaea*. The symbols reflect the significance of the term 'relatedness' in the analysis of variance table. A ‘+’ / ‘-‘ symbolizes that individuals from the target families grown with relatives on average produced more / less biomass than individuals of target families grown with non-relatives. In order to see whether or not the effects of growing with relatives were more often positive in pairs of a certain pappus type, the analyses were further restricted to include only pairs in which both individuals grew from seeds with or without pappus. Significance levels: (+/-) $P < 0.1$; +/- $P < 0.05$; ++/-- $P < 0.01$.

Chapter 5

Intraspecific competition among genetically related and non-related sunflower individuals

Ursula Monzeglio and Peter Stoll

Abstract

As a consequence of limited dispersal, individuals in natural plant populations are very often surrounded by plants arising form the same parent plant and thus having the same (or similar) genotype. Generally, it is well accepted that negative effects on growth and reproduction that result form intraspecific competition are smaller among genetically variable compared to genetically similar competitors. According to the sibling competition and the associated resource-partitioning hypothesis, the more the competitors are genetically different the greater is the potential to partition limiting resources. Alternatively, relatedness among individuals can drive the evolution of altruism (kin selection). In plant species with highly aggregated siblings, this could minimize the negative effects of sibling competition and increase growth and reproduction of genetically related individuals. However, so far our empirical knowledge of sibling competition and kin selection in plants is scarce and inconsistent, and based mostly on greenhouse experiments.

Using six maternal seed families of sunflower (*Helianthus annuus* L.), we compared reproduction, growth and size variation (measured as coefficient of variation) of groups of related (half-sibs) versus groups of non-related individuals under field conditions.

We found similar height between groups of genetically related and non-related individuals. By contrast, early in stand development (after 25 days from the onset), total vegetative biomass production was slightly higher in groups of related compared to groups of non-related individuals. However, later in stand development (84 and 112 days from the beginning) the pattern changed: groups of non-related outperformed groups of related individuals. At the end of the experiment, groups of non-related individuals produced 30% more reproductive biomass compared to groups of related individuals. At the end of the experiment groups of related showed less size variation (i.e. lower coefficient of variation) compared to groups of non-related individuals.

Therefore, our findings suggested that groups of genetically dissimilar individuals have greater potential to partition limited resources than groups of similar individuals, lending support for the sibling competition and the associated resource-partitioning hypothesis.

Key-words: annual plant, *Helianthus annuus*, kin selection, relatedness, sibling competition, size variation

Introduction

In many plants species, spatially limited seed dispersal can lead to a pronounced aggregation of conspecifics (see e.g. Seidler and Plotkin 2006). Additionally, individuals in natural plant populations are very often surrounded by plants arising form the same parent plant and thus having the same (or similar) genotype. In other words, when the prevailing pattern of dispersal results in relatives being aggregated in space and interacting primarily with one another, then local competition may become sibling competition (Cheplick 1992; 1993a, b; Kelly 1996; Lambin et al. 2001). This is particularly relevant for sessile organisms where growth, survivorship and fecundity are most affected by the local density rather than by the average global density (Pacala and Silander 1985; Pacala 1997; Murrell et al. 2001). Furthermore, the neighbor's identity is an important factor influencing plant-plant interactions. The negative effects on growth and reproduction that result from intraspecific competition can be less severe among genetically variable competitors than among genetically similar competitors. According to the sibling competition and the associated resource-partitioning hypothesis, the more the competitors are genetically different the greater is the potential to partition limited resources (Young 1981; Argyres and Schmitt 1992).

Alternatively, relatedness among individuals can drive the evolution of altruism. According to the kin selection hypothesis (Hamilton 1964; Maynard Smith 1978) related individuals will behave more altruistic, when $rb\text{-}c > 0$, where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary and r is their genetic relatedness. In other words, an individual may reduce its own fitness (e.g. less competitive toward their relatives) if the costs are compensated with increased fitness of its relative. For example, for plant species with frequent sibling interactions (e.g. heavy, locally dispersed seeds), kin selection might favor the inclusive fitness of maternal parent and its offspring by reducing the negative consequences of sibling competition. Therefore, even though there is theoretical evidence that highly localized dispersal (population viscosity) alone is not enough to promote altruism and may even counteract the advantage of being relatives (Queller 1992, 1994; Taylor 1992; Wilson et al. 1992), kin selection may be a significant force in plant evolution (Nakamura 1980; Cheplick 1993b; Kelly 1996; Griffin and West 2002). Despite the straightforward predictions from sibling competition and kin selection hypotheses, empirical work on plants still lags behind and the current understanding is scanty and equivocal. Some studies showed that genetically different competitors increased the fitness compared to genetically similar or identical individuals (Willson et al. 1987; Kelley 1989; Argyres & Schmitt 1992; Karron and Marshall 1993). Others provided evidence for the opposite pattern (Willson et al. 1987;

Tonsor 1989; Andalo et al. 2001; Donohue 2003). Furthermore, since most studies on sibling competition were conducted under greenhouse conditions, it remains to be established whether or not groups of relatives would increase their fitness within neighborhoods of genetically similar individuals under more realistic ecological conditions.

Within a population, plants vary in their size. Most plant populations consist of relatively few large individuals and many small ones, and the few large individuals produce most of the population biomass (e.g. Ogden 1970; Mohler et al. 1978). Such size inequalities have been called ‘size-hierarchies’. Depending on how resources are partitioned among individuals it is possible to distinguish between two modes of competition. When larger individuals have a disproportionate advantage (relative to their size) in competition with smaller individuals and suppress their growth, competition is called ‘size-asymmetric’ competition (Begon 1984; Weiner 1985, 1990; Schwinning and Weiner 1998). By contrast, when resources are divided equally or proportionally to the size of competing individuals, competition is called ‘size-symmetric’ (Weiner 1990). Because size inequality (measured as coefficient of variation) within a population changes depending on competition mode, the pattern of size inequality is often taken to be indicative of the degree of size asymmetry of competition (Weiner and Solbrig 1984; Schwinning and Weiner 1998). This means, that the more the competition mode is asymmetric the greatest would be the size inequality and stronger the size-hierarchies within a population. Furthermore, there is theoretical (Aikio and Pakkasmaa 2003) and empirical (Jasienski 1988; Tonsor 1989) evidence that increased genetic relatedness might lead to reduced variation in size and more symmetrical competition, due probably to more genetic uniformity and therefore similar growth of competitors.

In this experiment we compared aboveground biomass production (vegetative and reproductive), height and size variation among groups of related versus groups of non-related individuals under field conditions. We used six maternal seed families (seeds were at least half-sibs) of the annual species *Helianthus annuus* L. (sunflower). We tested the null hypothesis that there are no differences in biomass production and height among groups of genetically related and non-related individuals. However, if groups of non-related individuals outperformed groups of related individuals, than we might conclude that the potential to partition limiting resources was greater among groups of non-related compared to groups of related individuals. This would support the resource-partitioning hypothesis. By contrast, if the opposite pattern would occur, kin selection might be hypothesized to have been operating in the past. In this case we would expect that groups of related individuals would outperform groups of non-related individuals. Additionally, mainly because of similar growth, we would expect lower size variation (i.e. lower coefficients of variation) and hence more symmetric competition among groups of related compared to groups of non-related individuals.

Materials and Methods

Plant species

Sunflower, *Helianthus annuus* L. (Asteraceae), is a widely distributed annual plant species inhabiting disturbed areas (Heiser 1976). Modern cultivated varieties reach a plant height of between 150 cm and 250 cm. The flower heads are generally 8-15 cm up to 30 cm wide. Flowers produced on the edge of the flower head (ray flower) are yellow, while flowers produced in the centre of the flower head (disk flower) are reddish-brown. The flowers tend to be cross-pollinating. Wild sunflower and the early varieties were self-incompatible and required insect pollination. However, current hybrid varieties possess high levels of self-compatibility.

Seed collection

In fall 2002, ten sunflower heads were collected from an agricultural field (Frick, AG, Switzerland) and stored at room temperature until spring 2003. All seeds collected from a single head are referred to as a seed family and are at least half-sibs. For the experiment we choose the six seed families with the highest number of seeds. Mean seed mass was measured by weighing five samples of 10 seeds from each seed family (Table 1) and seed family effects were compared using an analysis of variance. Seed mass differed significantly between seed families ($F_{5,24} = 24.36$; $P < 0.001$).

Experimental design

The experiment was designed as randomized split-plot and contained 2 blocks (2.4 x 0.9 m, separated by 0.5 m). Each block included three plots (0.9 x 0.6 m; separated by 0.3 m) and each plot was subdivided into six subplots (0.3 x 0.3 m) (Fig. 1a). Two different combinations (i.e. monoculture or mixture, see below) were used as within-subplot treatment. Three subplots per plot were sown as monocultures and three subplots were sown as mixtures, arranged in alternating positions (Fig.1a). Each subplot was further subdivided into six cells (10 x 15 cm). In the monoculture subplots, each cell was sown with 30 seeds of one particular seed family, while in the mixtures, each cell was sown with 5 seeds from each of the six seed families, yielding a total of 30 seeds. Each treatment (i.e. monoculture vs. mixture) was replicated three times per plot (i.e. six times per harvest, see below). We used the same seed-position template with randomized positions for each subplot. Consequently, only treatments (but not number of seed families, number of seeds or seed position) varied at the subplot level. Each seed position was marked with a wood stick with a different color depending on the seed family. Each seed was positioned (by hand) in front of the corresponding stick (Fig. 1b). In this way it was possible to recognize the maternal identity of every individual during the harvests.

Additional experimental settings

Prior to sowing, the seeds were vernalized for 10 days at 4-5° C and placed in water the night before sowing (ca. 12 h). Only seeds that swelled up were used for the experiment. The experiment was set up at the Research Institute of Organic Agriculture (FiBL, Switzerland). The blocks were established on May 16 and harvested in fall 2003. Because of the heavy soil (high clay content), each plot was covered with a layer (3 cm) of commercial garden soil before sowing to increase seed germination. The plots were sown between May 24 and 31 and watered by hand as required. During the first month each plot was covered with a plastic tarp (200 holes/m^2, GVZ-Bolltec AG) to protect the seedlings from sunlight, adverse weather and birds. Despite the tarps, birds ate some seeds from two of the plots and those seeds were replaced the following day. To prevent plants from leaning into neighboring subplots, which could influence the growth of other plants, a grid was build (height from 20 to 150 cm depending on the harvest time) to separate the subplots.

Harvest

Each pair of plots represented a harvest (Fig.1). We performed three destructive harvests: after 25 (between June 19 and 25), 84 (between August 19 and 21), and 112 days (between September 16 and 18) from the beginning of the experiment. At each harvest, aboveground biomass (i.e. vegetative and reproductive), total number of individuals of each seed family and the individual height was recorded. At the second and third harvests, we further separated the biomass into stem and leaves (vegetative biomass) and head (reproductive biomass) tissue. The harvested aboveground biomass was dried for 12 h at 60° C and then stored at room temperature. Before weighing the biomass was dried again for 3 h at 60° C.

Statistical analysis

The data were analyzed with a multifactorial analysis of covariance (ANCOVA) for a split-plot design. The treatment effect (monoculture vs. mixture) was tested against residual mean square of the subplot. The seed family effect and its interaction with the treatment were tested against the residual mean square of the cell. Aboveground biomass (vegetative and head), height and size variability measured as coefficient of variation were tested. We controlled for the effects of density using the number of surviving individuals per seed family at the subplot level (max. 30 individuals) as covariate.

Shortly before the third harvest, birds ate almost all seeds. Therefore, we used the remaining heads full of seeds to estimate a relationship between seed mass and head biomass (Fig. 2). This relationship was linear and had an R^2 of 86%. Thus we considered head biomass as an accurate proxy of reproductive biomass and used it to estimate total reproductive biomass for those individuals with considerable seed loss due to bird predation.

For the second and third harvests, we divided the individuals into flowering (i.e. head biomass > 0) and non-flowering (i.e. head biomass = 0) individuals. For the analysis of the reproductive biomass only flowering individuals were considered.

All data were logarithmically transformed to obtain normal distributions of the residuals and homogeneity of variances. Back-transformed means and least significant differences (LSD, $P < 0.05$) are presented throughout. All analyses were conducted using the program GENSTAT 5 (Payne et al. 1987).

Results

The analysis of covariance showed that the total vegetative biomass was marginally significant affected by the treatment (i.e. monoculture vs. mixture) after 25 and 112 days from the beginning of the experiment. After 25 days, groups of related individuals (monoculture) produced slightly more total vegetative biomass compared to groups of non-related individuals (mixture) (Table 2, Fig. 3). In contrast, at the second and third harvests (84 and 112 days) groups of non-related produced higher total vegetative and head biomass compared to groups of related individuals (Table 2, Fig. 3). At the end of the experiment (112 days) these effects were marginally significant for the total vegetative biomass and significant for the total head biomass (Table 2).

Similar to the total head biomass, at the end of the experiment, the total reproductive biomass (i.e. head biomass added to the estimated seed mass) (monocultures: 4.5 g; mixtures: 5.8 g; $F_{1,8} = 6.3$; $P = 0.037$), as well as the total estimated seed mass (monocultures: 1.5 g; mixtures: 1.9 g; $F_{1,8} = 5.7$; $P = 0.044$) were significantly higher in the mixture as compared to the monoculture treatment.

Average height was never significantly affected by the treatments (Table 2).

Seed family effects were significant for total vegetative biomass and average height after 25 days (Table 2, Fig. 3). Later in stand development (84 and 112 days), there was no seed family effect for total biomass, while average height was marginally affected after 84 and significantly affected after 112 days (Table 2, Fig.3).

Generally, ratios between total head biomass and total vegetative biomass were higher in mixtures compared to monocultures (Fig.4). At the third harvest (112 days) this effect was significant (Table 3). Similar results were found for the ratios between total reproductive biomass (i.e. total head biomass added to the total estimated seed mass) and total vegetative biomass ($F_{1,8} = 8.0$; $P = 0.022$), as well as between total estimated seed mass and total vegetative biomass ($F_{1,8} = 4.7$; $P = 0.062$).

The number of surviving individuals per seed family at the subplot level (covariate) had always a significant effect (Table 2 and Table 3). However, there was no significant treatment effect on the covariate (first harvest: $F_{1,9} = 2.7$; $P = 0.132$; second harvest $F_{1,9} = 0.3$; $P = 0.626$; third harvest: $F_{1,9} = 0.1$; $P = 0.732$). Similarly, the number of flowering individuals per seed family at the subplot level (at second and third harvest) did not differ significantly between treatments ($F_{1,9} = 0.13$; $P = 0.730$; $F_{1,9} = 0.03$; $P = 0.870$, respectively).

Coefficients of variation (CV) of biomass (vegetative and head) and height were generally not significantly affected by the treatments. Nevertheless, at the third harvest, CV of total vegetative and head biomass and CV of height were higher in the mixtures (vegetative: 88%; head: 112%; height: 36%) compared to the monocultures (vegetative: 74%; head: 96%; height: 32%). These effects were marginally significant for the CV of total vegetative biomass ($F_{1,8}$ = 3.5; P = 0.098). However, the treatment effect became significant when the analysis was restricted only to flowering individuals. In this case, the CV of vegetative biomass was significantly higher in the mixtures compared to the monocultures ($F_{1,8}$ = 6.7; P = 0.030), as well as the CV of height ($F_{1,8}$ = 7.6; P = 0.025).

Discussion

This experiment was designed to investigate intraspecific competition effects on the biomass production (i.e. vegetative and reproductive), individual height and size variation among groups of genetically related (half-sibs) and groups of non-related individuals. Our null hypothesis was that there would be no differences between groups of genetically related and non-related individuals. This null hypothesis was fully supported by our data on individual height, but not by the data on the aboveground biomass production. Indeed, after 25 days form the start of the experiment, groups of related individuals produced slightly more total vegetative biomass than groups of non-related individuals. By contrast, at the end of the experiment (112 days after the onset), groups of non-related individuals showed increased biomass production (i.e. vegetative and reproductive) within neighborhoods of genetically dissimilar individuals compared to neighborhoods of genetically similar individuals. Hence, our data suggested that early in stand development kin selection might be indicated to interpret the results. At the end of the experiment, however, they suggested that there was a greater potential to partition limited resources between groups of non-related than groups of related individuals. Thus, our results on aboveground biomass are to some extent contrasting. However, because at the first harvest (25 days) there was probably not much competition for light, we explained the increased total vegetative biomass production of monocultures with more genetic uniformity and therefore similar growth between competitors rather than kin selection effects.

Our findings on size variation (measured as coefficients of variation) were mostly not significant. Nevertheless, they suggested that, especially at the end of the experiment, groups of non-related had higher size variation than groups of related individuals. This indicated more asymmetric competition among groups of non-related compared to groups of related-individuals. This result agreed with our initial expectation that genetically similar individuals would have more symmetric competition compared to genetically variable individuals.

The increased biomass production (vegetative and reproductive) in the mixtures observed at the third harvest could be explained (i) by more surviving individuals per family at the subplot level in mixtures compared to monocultures and / or by (ii) different size-hierarchies between the treatments. Because we did not find significant differences in the number of surviving individuals per seed family at the subplot level between groups of related (monocultures) and groups of non-related (mixtures) individuals, we excluded the first possibility. The second possibility seems to be more plausible. It could be argued that in mixtures there were stronger size-hierarchies (i.e. higher coefficients of variation, CV) than in the monocultures. This would suggest that in mixtures there were stronger size-hierarchies with more large individuals compared to monocultures, which would raise the total biomass production. Actually, we found at the third harvest, that groups of non-related individuals had generally higher CVs compared to groups of related individuals. This indicated more asymmetric competition and stronger size-hierarchies among groups of non-related compared to groups of related individuals. Despite the more symmetrical competition among groups of related individuals, there was less total biomass production compared to groups of non-related individuals. This result disagreed with theoretical predictions (Weiner et al. 2001) and empirical observations (Stoll et al. 2002) that showed that under more symmetric competition individuals increased the biomass production because of decreased density-dependent mortality.

However, we suggest that reduced size variation and more symmetric competition might have two opposing effects. Weak size-hierarchies and more equal resource share may decrease density-dependent mortality allowing more individuals to reach the reproductive size and hence increase the overall reproductive output. By contrast, evenness within a population (weak size hierarchies) might have also the consequence that individuals hold back each other's growth in such a way that size of all individuals decreased. Hence, the number of individuals who remain rather small would increase. Since, within a population of plants, size is highly correlated with reproductive output (Samson and Werk 1986), this would result in an overall reduction in the reproductive biomass.

Therefore, we suppose that larger individuals within groups of related individuals were comparatively smaller than larger individuals within groups of non-related individuals. This would have decreased the overall reproductive biomass production in monocultures and would also explain the higher ratios of total head biomass to total vegetative biomass in the mixtures. Thus, the genetic heterogeneity among groups of non-related individuals might allow a better partitioning of limiting resources (e.g. space, light) compared to groups of related individuals. Therefore, our findings taken together, agreed more with those studies that support, at least in part, the resource-partitioning hypothesis (Willson et al. 1987; Kelley 1989; Karron and Marshall 1993).

Nevertheless, a field experiment provided solid evidence for the opposite, lending support to the kin selection hypothesis (Donohue 2003). Donohue (2003) showed that higher reproductive success occurred when individuals grew with genetic relatives compared to non-related individuals. A possible explanation for the contrast between our and her results might be the different experimental species. Donohue (2003) used the annual plant species *Cakile* *edentula*. This species grows on the open beach or up on primary dune on the shores of the great lakes of North America and often occurs in extremely high-density clumps with hundreds of individuals within a 100-cm^2 area (Donohue 2003). For our experiment we used sunflower seeds collected from an agriculture field. Although, we did not have specific information on the density of natural sunflower populations, we speculate that sibling interactions in sunflowers might be less frequent or not strong enough in order to create the conditions for kin selection to operate.

These considerations draw attention to the fact that different experimental plant species (but also experimental design and experimental conditions) could lead to completely different conclusions. Furthermore, experimental studies like ours have the limitation that the absolute and relative densities of the species and the strength of competition are determined by the experiment rather than natural processes. Therefore, the arbitrary choice of our experimental density (2000 individulas/m^2) might have in part influenced the outcome. Koelewijn (2004) investigated the effects of different densities on competing seed families. He could show that density had strong negative effects in absolute terms on the performance of seed families and that the consequences of sibling competition depend on the frequency and relatedness of neighbors. Escarré et al. (1994) examined the density effects and neighbor relatedness in a sib / non-sib competition experiment on the clonal *Rumex acetosella*. He found density-dependent effects of the degree of relatedness between plant individuals. At low densities, there were no growth differences, but when the density was doubled, the absolute sexual biomass was higher in non-sibs than in sib treatments, suggesting that competition was stronger between related plants. These density-dependent relatedness effects were further support by the consistent significant covariate (i.e. number of survival individuals per seed family at the subplot level) effect in our experiment.

Furthermore, studies with microorganism (Queller 2004; Griffin et al. 2004) and the extended version of Hamilton's rule proposed by Frank (1998) showed that relatedness is crucial in competitive interactions, but may be modulated by the scale of competition (i.e. when competition is local the effect of high relatedness were cancel out). Moreover, theoretical models suggest that the mechanism proposed by Hamilton (i.e. that limited dispersal leads to increased local relatedness and population viscosity should be sufficient to allow altruism to evolve) does not necessarily work (Taylor 1992; Wilson et al. 1992). Nevertheless, positive relatedness effects among siblings in plants, even unusual, have been shown (Willson et al. 1987; Tonsor 1989; Andalo et al. 2001; Donohue 2003). Hence, kin selection in plants should not be excluded, but the precise balance between the intensity of competition and neighbor relatedness deserve further investigations.

As expected, we found pronounced differences between genotypes (e.g. seed families). Not all seed families decreased the biomass production within neighborhoods of genetically similar individuals (e.g. seed family *'yellow'*, Fig. 3) and the magnitude of the effects varied among the seed families. The differences among seed families can be attributed both to genetic differences and to maternal effects, since the seeds used were collected form a field. Those results agreed with previous studies (e.g. Taylor and Aarssen 1990; Donohue 2003; Cheplick and Kane 2004) that also found similar effects of neighbor relatedness on the growth and fitness of particular genotypes. The evidence that intraspecific genetic diversity has significant impacts on community diversity (e.g. Booth and Grime 2003; Cahill 2005) emphasized the importance of functional variation at levels below that of species. In line with this hypothesis, Vellend (2006) demonstrated the importance of genetic diversity in communities theoretically. He showed that genetic diversity allows species to respond to complex selection pressures in diverse communities in such a way that promotes coexistence.

The general decrease in the total head biomass form the second (84 days) to the third harvest (112 days) (grand means: 7.3 g and 3.5 g, respectively) could be explained by the seed production. In fact, if at the third harvest, we added the total estimated seed mass to the total head biomass (i.e. total reproductive biomass) we reached a comparable biomass (grand mean: 5.1 g) as at the second harvest. Moreover, the general conclusion that groups of non-related individuals produced more total biomass than groups of related individuals, was independent of which variable (total head biomass, total estimated seed mass or the sum of them) was used in the analyses.

In conclusion, our null hypothesis that there were no differences in the aboveground biomass production and height among genetically related and non-related individuals was supported by our data on height, but not by data on aboveground biomass. We provided evidence that groups of non-related individuals increased the total aboveground biomass production (i.e. vegetative and reproductive) within neighborhoods of genetically variable individuals compared to neighborhoods of genetically similar individuals. Furthermore, at the end of the experiment, the data suggested lower size variation (i.e. lower coefficient of variation) among groups of related compared to groups of non-related individuals. This suggested more symmetric competition and weaker size-hierarchies among groups of related compared to groups of non-related, probably due to genetic uniformity and therefore similar growth. Therefore, because groups of non-related individuals increased their growth and reproduction and showed more asymmetric competition compared to groups of related individuals, our findings support the sibling competition and the associated resource-partitioning hypothesis. However, studies like ours, investigating sibling competition under ecologically realistic conditions are quite rare and the current knowledge inconsistent. Further investigations with different plant species and under more natural conditions are needed in order to increase our knowledge on the ecological and evolutionary consequences of sibling competition in plant populations.

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Table 1 Mean seed mass of 5 samples of 10 seeds of *Helianthus annuus* seed families (g of 10 seeds ± standard error of mean). Color names are used to refer to specific seed families.

Seed family	Seed mass
red	0.381 ± 0.03
blue	0.439 ± 0.02
yellow	0.504 ± 0.02
green	0.567 ± 0.02
white	0.658 ± 0.02
black	0.674 ± 0.03

Table 2 Results of analysis of covariance for *Helianthus annuus* grown among groups of related (monoculture) and groups of non-related (mixture) individuals in a split-plot experiment using six seed families. Effects of treatment (monoculture vs. mixture) on total aboveground biomass (i.e. vegetative and head) and average height were tested against residual mean square of the subplot. After 25 days individuals had only vegetative biomass. For the analysis of head biomass only flowering individuals were considered. Covariate: number of individuals per subplot and seed family (max. 30 individuals).
Abbreviations: d.f. = degrees of freedom; F = F-value (variance ratio); P = error probability.

Total biomass

Source of variation		after 25 days		after 84 days				after 112 days			
		vegetative		vegetative		head		vegetative		head	
	d.f.	F	P	F	P	F	P	F	P	F	P
bloc	1	1.2	0.308	2.8	0.127	0.6	0.458	1.1	0.322	0.8	0.388
treatment (T)	1	3.8	0.086	1.2	0.302	1.5	0.255	3.6	0.095	6.5	0.034
covariate	1	8.4	0.020	7.3	0.027	6.8	0.031	52.7	< 0.001	40.5	< 0.001
subplot level residual	8	1.4		2.0		2.4		0.5		0.8	
seed family (SF)	5	8.6	< 0.001	1.1	0.381	0.7	0.626	1.8	0.137	0.9	0.506
T x SF	5	0.6	0.720	0.4	0.861	0.4	0.840	0.8	0.565	1.0	0.415
covariate	1	29.3	< 0.001	66.8	< 0.001	60.4	< 0.001	62.7	< 0.001	42.0	< 0.001
residual	49										
total	71										

Average height

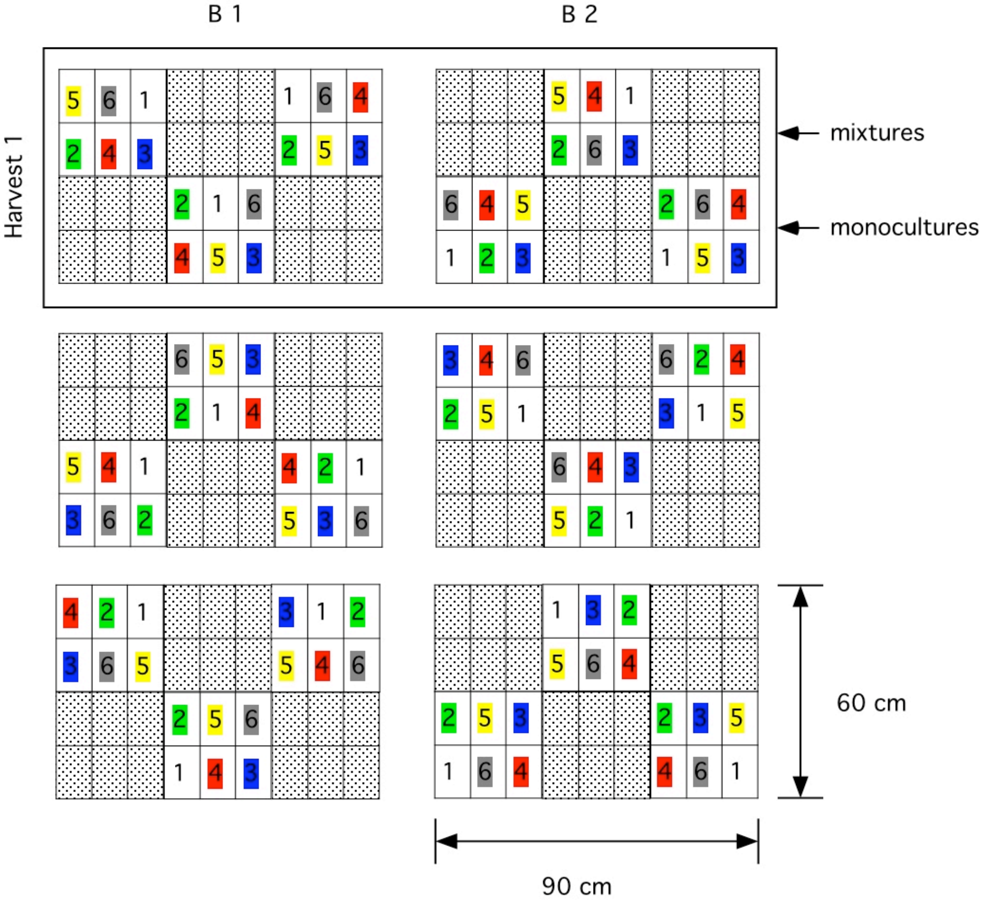
Source of variation		after 25 days		after 84 days		after 112 days	
	d.f.	F	P	F	P	F	P
bloc	1	0.0	0.866	3.8	0.083	2.5	0.148
treatment (T)	1	3.4	0.105	0.3	0.581	0.3	0.616
covariate	1	6.3	0.037	0.1	0.760	1.7	0.227
subplot level residual	8	7.5		5.5		3.4	
seed family (SF)	5	4.9	< 0.001	2.1	0.086	3.1	0.018
T x SF	5	0.8	0.573	0.4	0.844	0.3	0.892
covariate	1	2.1	0.157	1.5	0.221	0.0	0.867
residual	49						
total	71						

Table 3 Results of analysis of covariance for *Helianthus annuus* grown among groups of related (monoculture) and groups of non-related (mixture) individuals in a split-plot experiment using six seed families. Effects of treatment (monoculture vs. mixture) on the ratios between total head biomass and total vegetative biomass after 84 and 112 days from the beginning of the experiment were tested against residual mean square of the subplot. Only flowering individuals were considered. Covariate: number of individuals per subplot and seed family (max. 30 individuals).

Abbreviations: d.f. = degree of freedom; F = F-value (variance ratio); P = error probability.

Source of variation		after 84 days		after 112 days	
	d.f.	F	P	F	P
bloc	1	0.1	0.759	1.1	0.322
treatment (T)	1	3.4	0.101	5.6	0.046
covariate	1	33.3	< 0.001	59.9	< 0.001
subplot level residual	8	2.4		2.0	
seed family (SF)	5	0.3	0.896	0.7	0.642
T x SF	5	0.2	0.963	1.3	0.277
covariate	1	157.0	< 0.001	125.5	< 0.001
residual	49				
total	71				

a)



b)

Figure 1 a) The experimental design with two blocks (B1, B2), each containing three plots (90 x 60 cm). Each pair of plots corresponded to one of three harvests. The plots were subdivided into six subplots (30 x 30 cm) and the subplots were further subdivided into six cells (10 x 15 cm). Subplots were sown either as monocultures or as mixtures and arranged in alternating positions. In the monoculture treatment, each cell was sown with 30 seeds of one particular seed family. In the mixture treatment, each cell was sown with 5 seeds from each of the six seed families. Numbers and colors are used to refer to specific seed families.
b) Detailed pictures of a mixture combination at the cell level

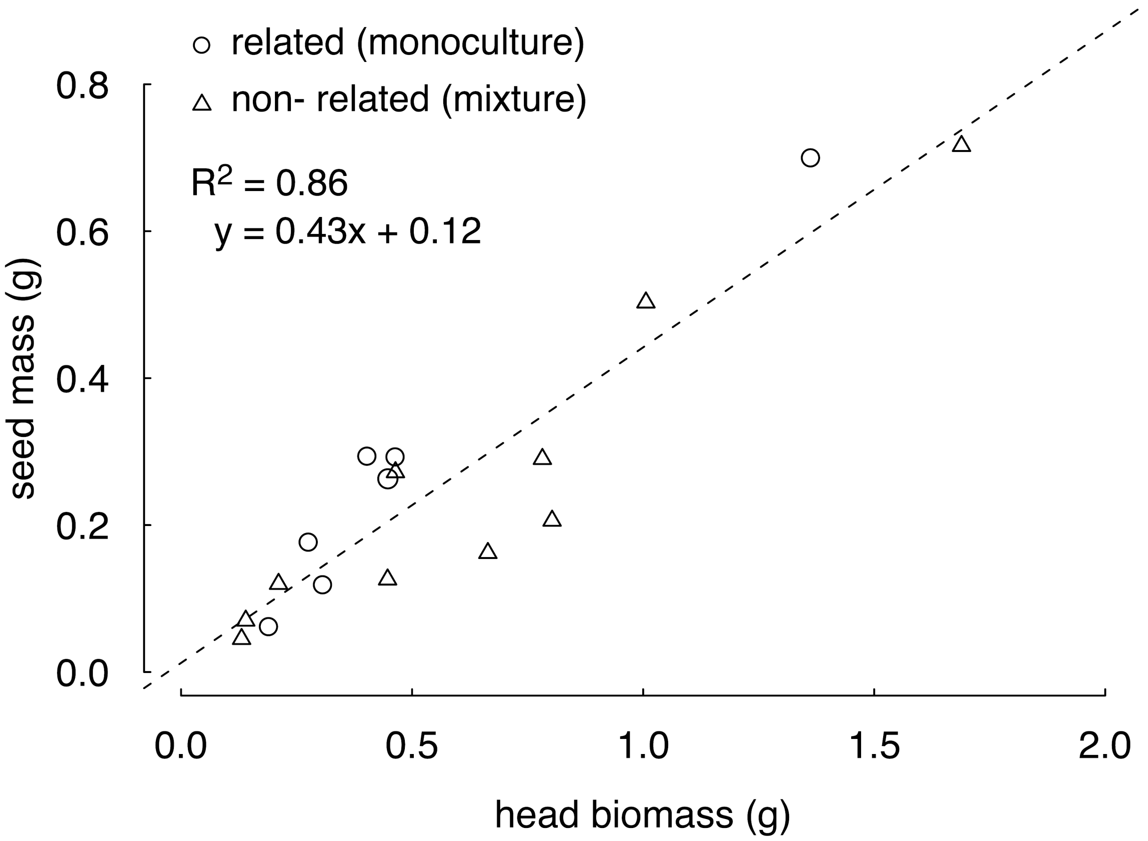


Figure 2 Relationship between head biomass and seed mass of *Helianthus annuus*. Plants were grown among groups of related individuals (monocultures) or groups of non-related individuals (mixtures) and harvested after 112 days from the beginning of the experiment.

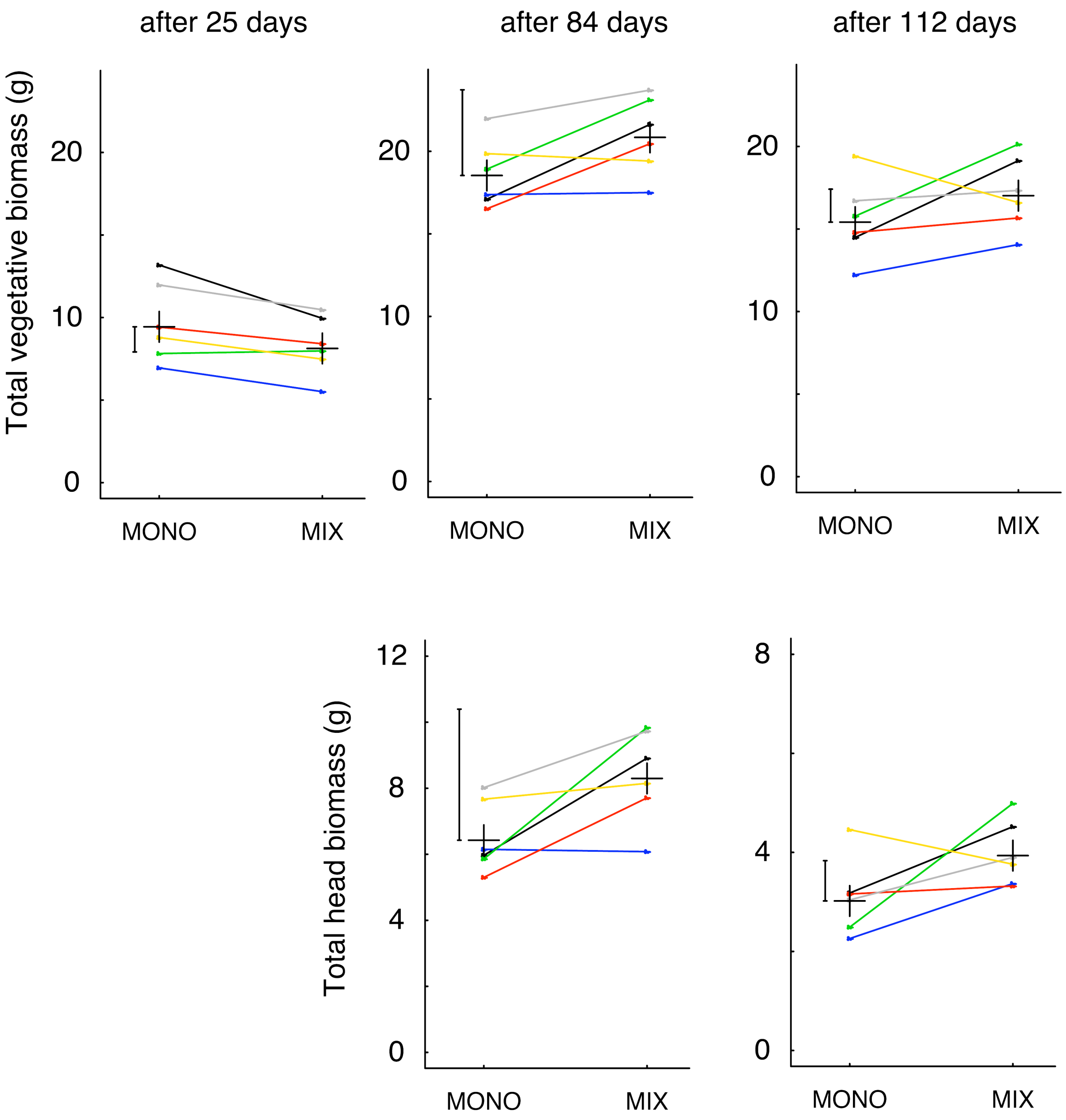


Figure 3 Total aboveground vegetative biomass (top) and total head biomass (bottom) of *Helianthus annuus* individuals grown among groups of related individuals (monocultures) or groups of non-related individuals (mixtures). For the total head biomass, only flowering individuals were considered. Datapoints represent back-transformed means for different seed families (different colors). The crosses represent the average over the six seed families and the bars the least significant difference (LSD 5%) for the monoculture vs. mixture means across seed families. Abbreviations: mono = monocultures; mix = mixtures.

Note: different y-axis scale for the total head biomass.

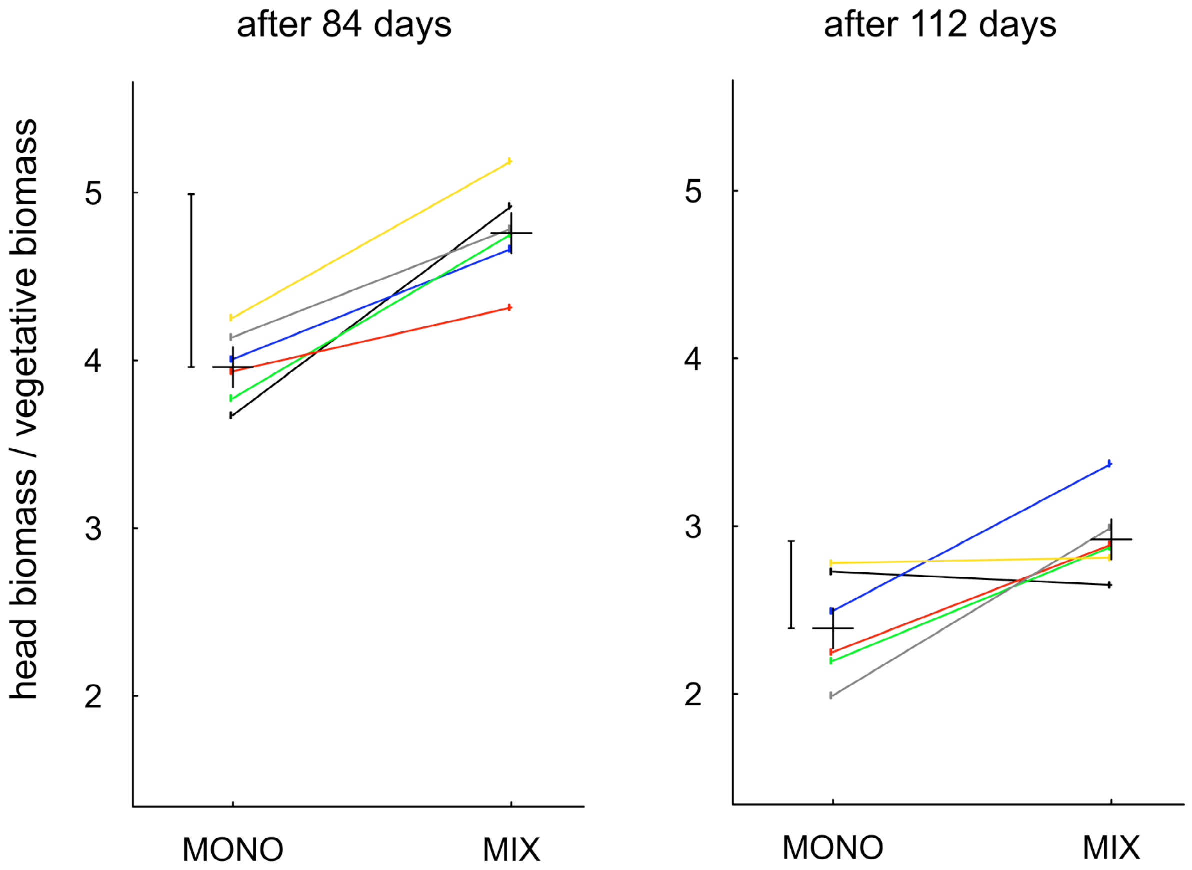


Figure 4 Ratios between total reproductive biomass and total vegetative biomass of *Helianthus annuus* individuals grown among groups of related individuals (monocultures) or groups of non-related individuals (mixtures). Only flowering individuals were considered. Datapoints represent back-transformed means for different seed families (different colors). The crosses represent the average over the six seed families and the bars the least significant difference (LSD 5%) for the monoculture vs. mixture means across seed families. Abbreviations: mono = monocultures; mix = mixtures.

Chapter 6

Epilogue: caveats and outlook

Coexistence is a complex balance between superior and inferior competitors. Every organism is subject to trade-offs that prevent it form excelling in every way in every environment. Trade-offs lead to speciation, and this is the key for diversity.

Invasive species are a good example for what may happen when the balance between all mechanisms that enable coexistence, is disrupted. Invading plants transported to new areas without their natural enemies might become so dominant to suppress all the other species. In the worst cases, this may result into veritable ecological disasters.

The experiments of this thesis were explicitly designed to test precise and focused hypotheses on the effects of spatial patterns (random vs. intraspecific aggregated) on experimental plant communities at the level of species, as well at the level of genotypes within species. They effectively accomplished their objectives allowing to find out interesting aspects. Nevertheless, experiments like these have also some limitations.

For example, the absolute and relative densities of the species, the structure and the scale of the plant community and the strength of competition are determined by the experiment rather than natural processes. In real communities, the degree of spatial aggregation is often less extreme and the spatial structure is more complex (Turnbull et al. 2007). Furthermore, Lortie et al. (2005) pointed out that examining plant communities at single more or less arbitrary scale could lead to incomplete estimates of the importance of particular factors such as aggregation and negative density dependence. Another problem faced by ecological studies is that the spatial and temporal scales, at which measurements are practical, are typically smaller than those at which the most important phenomena occur. Hence, it is unclear how to extrapolate the results to real communities. Additionally, Turnbull et al. (2007) showed that the nature of competition, and spatial pattern could vary between years even within a single community. Hence, studies over multiple years are required to understand long-term effects.

Actually, in this thesis, a long-term spatial pattern experiment was also planed. In summer 2002 together with the first spatial pattern experiment (see Chapter 2), two additional replicates of this experiment were established (i.e. I established three times the same experiment). Plants grown in the first replicate were used to produce seed families for the second spatial pattern experiment (see Chapter 3). Plants grown in the second replicate should have grown over three years without additional watering and weeding. After this time, I would have harvested the total aboveground biomass in order to determine the influence of initial spatial patterns on the natural dynamics over three years. However, the extremely high temperatures of the summer 2003 killed most of the experimental plants designed for this purpose, and therefore this experiment was abandoned. A general solution to face unexpected environmental effects is to have the experiment replicated at different sites. However, especially for long-term experiments this may be often barely feasible, mainly because of logistical constraints. This emphasized two important aspects of every ecological study. First, the importance of an accurate planning of the experiment (e.g. feasibility, physical and economical effort) with particular attention to the experimental design. A good planned experiment would ensure accurate data, which could be, despite the natural variation among replicates or unexpected environmental factors, further statistically analyzed in order to answer the questions of interest. Second, even thought field experiments have a high degree of realism, their generality remain rather low, mainly because of year-to-year variation (e.g. climate, herbivore density).

In my experiments, I considered the aboveground biomass production (vegetative and reproductive) as a good proxy of individual fitness. However, especially for the experiments which contrasted genetically related and non-related individuals this could lead to misleading conclusions. For instance, little or no genetic variation might lead to no significant differences in biomass production between relatives and non-relatives. Moreover, the field experiments lasted over one growing season. Therefore, even though, I had data on the reproductive output, I do not know how many seeds would have survived in the second generation. Moreover, I do not known if seeds and / or seedling mortality was caused by external factors such herbivores or by the treatments themselves. For example, counting the number of surviving seedlings just after the germination would have given useful information.

In studies of plant population dynamics, it would be interesting to have information that can be used to quantify population level characteristics (whether it is increasing, decreasing or stable). Indeed, such information can potentially be useful in conservation management of a population or in understanding the success of invasive species. However, construction of life-tables require data on seed production, seed viability and germination, seed dormancy, seed bank, and seedling emergence. Moreover, growth of individuals should be followed from seedling emergence until senescence. Nevertheless, because bigger plants usually produce more seeds and have higher survival probabilities than smaller plants, aboveground biomass can be taken as surrogate or proxy for fitness.

Furthermore, I do not have any information on belowground processes. There is, however, growing evidence that the belowground biota (e.g. mycorrhizal fungi) play an important role in determining the community structure and coexistence of competitors (e.g. Hartnett and Wilson 1999; Klironomos et al. 2000; Klironomos 2002; Bever 2003; van der Heijden at al. 2003). For instance, the first spatial pattern experiment (Chapter 1) suggested that the importance of spatial pattern for the other competitors might not only depend on the position within the hierarchy but also on belowground interactions. Consequently, future investigations on plant-plant interactions, should, if possible, considerate above- and belowground interactions at the same time.

Although, I found contrasting results regarding the effects of relatedness, I believe that relatedness among plants, especially for species with highly localized dispersal, should play a considerable role in the regulation of local population dynamics. Similar to the species level, there must be subtle trade-offs (e.g. between neighbor relatedness and density) that determine the complicated local dynamics of plant communities.

The conflicting results may be explained either by the fact that different plant species were used or by the different experimental design. Indeed, the different life histories of the experimental plants may have had considerable effects. This ‘problem’ might have been avoided using always the same experimental plant species. However, this would have automatically lead to another critic, namely that the conclusions from the experiments cannot be generalized from one species to others.

Furthermore, the different experimental conditions (i.e. greenhouse conditions for the experiment with *Senecio* and field conditions for the experiments with *Capsella* and *Helianthus*) as well as the chosen experimental densities may explain the different results. It is possible that the rather uniform, artificial nature of the greenhouse environment has influenced the outcome. For example, rooting volume is constrained by pot dimensions. This might lead to misleading conclusions. Nevertheless, greenhouse and pot experiments remain an important tool in ecological research, but generalization to nature should be made only with caution. Therefore, such experiments have to be combined with more nature-like experiments in order to achieve a full understanding of a particular issue. Remarkably, in spite of different experimental species as well as experimental design in both field experiments, *Capsella* and *Helianthus* showed similar results regarding the relatedness effects (Chapter 3 and Chapter 4).

The experimental design, especially the experimental density, might have considerably influenced the outcomes. Density is fundamental in competitive interactions and results may be affected by the arbitrary choice of density and frequencies of competing relatives (Connolly 1987). The experimental density for *Capsella* and *Helianthus* was relatively high (40000 seeds / m^2 and 2000 seeds / m^2, respectively). While in the case of *Senecio* there were only two seeds per pot (∅ 12 cm).

Only few experiments, investigated the effects of different densities on competing seed families (e.g. Escarré et al. 1994; Koelewijn 2004). Koelewijn (2004) could show that density had strong negative effects in absolute terms on the performance of seed families and that the consequences of sibling competition depend on the frequency and relatedness of neighbors. Escarré et al. (1994) found density-dependent effects of the degree of relatedness between plant individuals. At low densities, there were no growth differences, but when the density was doubled, the absolute sexual biomass was higher in non-sibs than in sib treatments, suggesting that competition was stronger between related plants. Therefore, similar to the spatial pattern experiments that compared the effects of spatial patterns at two different densities (low vs. high), also the effects of relatedness should have been compared at different densities. Nonetheless, both experiments with the highest densities (Chapter 3 and Chapter 4) provided comparable conclusions regarding relatedness.

The degree of neighbor relatedness should also be taken under consideration in planning experiments contrasting related versus non-related individuals. In my experiments, the different degrees of relatedness were realized by collecting seeds from individual mother plants. This method was very useful and efficient. The disadvantage, however, was that I had only one degree of relatedness. Very few studies investigated the effects of sibling competition on the performance of competitors using different degrees of relatedness (e.g. full- and half-sibs) (e.g. Tonsor 1989). However, it could be argued that because Hamilton' rule and kin selection (Hamilton 1964; Maynard Smith 1978) is based on genetic relatedness between individuals, different degrees of relatedness among conspecifics would lead to different outcomes. High degrees of relatedness between neighbors would be expected to favor altruism in a stronger way than less degrees of relatedness between neighbors. To test this hypothesis, similar experiments in which only the degree of relatedness would vary (but not the plant species and experimental design) should have been done. In spite of the fact that in plants with limited dispersal groups of sibling are the rule rather the exception, the current understanding on sibling competition and kin selection is poor and inconsistent. Moreover, most of our understanding on mechanism favoring the evolution of altruism (see e.g. Lehmann and Keller 2006; Novak 2006) come from models focused on animals. Hence, it remains to be establish how and to which extent such mechanisms may be considered plausible to operate in plants.

Outlook

Intraspecific aggregation is only one proposed mechanism that can enable coexistence. However, other alternative hypotheses (e.g. disturbances, temporal and resource partitioning, competition-colonization trade-off, mycorrhizal networks) have been proposed to foster plants coexistence, and these should not be forgotten.

Designing and achieving experiments to test all or many possible mechanisms of coexistence at the level of species as well as the level of genotypes, for even a single community is a huge amount of work. Although, recently multiple concurrent mechanisms of coexistence begun to receive (theoretical) attention (see e.g. Chesson 2000; Levin 2000; Amarasekare et al. 2004), future empirical studies should try to test thoroughly for two or more possible mechanisms that have been shown to foster coexistence. More fundamental questions, such as the prediction of the importance, rather whether or not, a mechanism may promote coexistence in plant communities have to be addressed. Additionally, further empirical work at the genotype level is required in order to estimate the ecological and evolutionary importance of sibling competition and kin selection in plants.

This would first increase the present understand on the forces structuring plant communities and second help to better predict potential changes in community structure due to global change, extinction of species, introduction of alien species, changes in management practices, pollution and other anthropogenic factors threatening biodiversity.

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Curriculum vitae

Personal details

Name	Ursula Monzeglio
Date of birth	15th January 1973
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Place of origin	Locarno (TI)

Education

2002-2007	University of Basel. PhD in Botany. Dissertation title: ‘Small-scale spatial pattern and dynamics of experimental plant communities.’ Advisor: Dr. Peter Stoll
1992-1999	University of Basel. Diploma Biology I. Main subject: Invertebrates with focus on herbivory. Diploma thesis: ‘Gypsy moth feeding on beech under global change condition’. Supervised by Prof. Ch. Körner, Prof. P. Duelli and Dr. Stephan Hättenschwiller Secondary subjects: Vertebrates, phytopathology and plant ecology
1988-1992	High school, Locarno (TI). Matura Type C

During my studies I attended lectures by:

Arbe W, Barnett P, Baroni Urbani C, Baur B, Boesch C, Boller Th, Bruderer B, Burckhardt D, Duelli P, Erhardt A, Flückiger W, Freyvogel T, Gehring WJ, Gisi U, Hartmann K, Jacomet S, Jenni L, Körner Ch, Küry D, Lüdin E, Peduzzi R, Reichert H, Rowell HF, Schatz G, Sanders I, Schmid B, Schmid V, Schneider H, Senn D, Sequin U, Siegel H, Stearns SC, Stöcklin J, Stoll P, Studer P, Sturm A, Tamm Ch, Weber C, Wiemken A, Wiemken V

Publications

Günthardt-Goerg MS, Landolt W, Vollenweider P, Wonisch A, McQuattie CJ, Monzeglio U, Prati D, Hauff K, Steinbrecher R, Grill D (2001) Qualitätsveränderungen in Organen und Geweben. *In:* Brunold C, Balsiger PW, Bucher JB, Körner C (Eds) 'Wald und CO_2. Ergebnisse eines ökologischen Modellversuchs. Eidgenössische Forschungsanstalt WSL, Birmensdorf'; Haupt, Bern, Stuttgart, Wien, pp. 131-144.

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Monzeglio U & Stoll P (2007) Effects of spatial pattern and relatedness in an experimental plant community. Evolutionary Ecology *in press*

Conference contributions / published abstracts

October 2005	Monzeglio U (2005) Effects of intraspecific competition on size variation among genetically related and non-related individuals. 12th ZOeK Conference, Entlebuch.
August 2005	Monzeglio U & Stoll P (2005) Effects of intraspecific competition on size variation among genetically related and non-related individuals. 90th Annual Meeting of the Ecological Society of America (ESA), Montréal (CA)
December 2004	Monzeglio U & Stoll P (2004) Competition and size variation among genetically related and non-related individuals. Annual Symposium of the Zurich-Basel Plant Science Center
February 2004	Monzeglio U & Stoll P (2004) Weak competitors may benefit from intraspecific aggregation in experimental plant communities. Biology04, Fribourg
September 2003	Monzeglio U & Stoll P (2003) Does intraspecific aggregation delay loss of biodiversity in experimental plant communities? Verhandlungen der Gesellschaft für Ökologie 33:192
February 2003	Monzeglio U & Stoll P (2003) Altruistic behavior in plants? Kin competition and seed dimorphism in *Senecio jacobaea* L. (Asteraceae). Biology03, Zurich

Awards and Invited talks

17.12.2004	Poster awards 2004 of the Symposium of the Zurich-Basel Plant Science Center. Title of the poster: 'Competition and size variation among genetically related and non-related individuals'.
20.09. 2006	Agroecology, Georg-August-Universität, Göttingen. Title: 'Spatial pattern and dynamics of experimental plant communities'

Fieldwork and courses

October 2002-2006	Courses at the Graduate Study in Plant Sciences; Zurich-Basel Plant Science Center.
01 July-27 Sept. 2000	Internship whales research project: behavior, ecology, and photo identification of minke whales. Canada (Grandes Bergeronnes, Qc), Center of Costal Field Studies (ORES). Supervisor: Dr. N. Lynas
07 -10 July 1999	Internship 'Ecology of alpine plants' on the Furka pass, University of Basel
01 -13 Sept. 1997	Experimental development biology by marine invertebrates. Roscoff (F), University of Basel
05 -12 July 1997	Botanical workshop – Binntal, University of Basel
21 -26 July 1996	Internship on the microbial and alpine ecology ('Stage pratique ecologie microbienne et alpine') – Piora (TI). Focus on the ecology of the lake Cadagno.

Working experience

2002-2006	Research assistant at the Department of Environmental Sciences, Section of Conservation Biology, University of Basel.
May – Dec. 2001	Professional practical training at the Swiss Federal Research Station for Agroecology and Agriculture (Zurich) in the ecotoxicology group (Supervisor: Dr. O. Daniel). Focus on earthworms and their parasites. Development of a quantification method using microscopy and images analysis.

Hobbies

Rowing, hiking, sailing
Nature and architecture photography