Intraspecific facilitation: generality, mechanisms and effects

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Declaration of my own working contribution to the present thesis

The present thesis is based on the work I carried out in the office, lab and greenhouse during my PhD project. I designed the experimental set-up in cooperation with my supervisor Katja Tielbörger. I conducted the reviews, collected data of experiments and performed statistical analyses myself. I wrote the draft of the entire thesis, but I have received many comments and suggestions from my supervisor Katja Tielbörger. Throughout the course of this research I was advised by my supervisor Katja Tielbörger.

Abstract

Since Darwin, ecologists have developed many theories to understand effects of competition in determining structure and dynamics of plant populations and communities. However, in the past two decades, an increasing body of literature has demonstrated the effect of positive plant-plant interactions (known as facilitation) is at least as important as other factors, e.g., competition, stress and physical disturbance.

However, facilitation studies have been largely restricted to a community-level. Compared to competition studies, we have very little theory predicting how facilitation affects populations and how such effects may propagate to a community level. Most research was conducted between species pairs (or between adults and seedlings) that differ dramatically in their morphology and/or physiology, while the idea of reciprocal interactions within conspecific cohorts has rarely been addressed. Furthermore, a major disadvantage of interspecific studies is that species identity may be confounded with the focal trait we want to study. An intraspecific approach is clearly superior to an interspecific setting because it could disentangle trait effects from species identity. Another issue is that facilitation is mainly studied qualitatively. Most studies evaluate facilitation by comparing performance of targets ‘with neighbors’ and ‘without neighbors’, and ignore the fact that neighbours have also a certain density. Recent studies have found the magnitude of facilitation could reach the maximum at intermediate densities of benefactors, thus challenging our view of the ubiquity of negative density-dependence in populations. However, the density-dependence of facilitation has never been systematically studied and we do not know how it may interact with environmental gradients.

The present thesis was designed to address the above research gaps and make a first attempt to take an intraspecific perspective on facilitation systematically. To do so, I took three steps. In a first step, I reviewed the existing literature about intraspecific facilitation in order to see what we can learn from this. In a second step, I used an intraspecific experimental study system to address major concepts in facilitation research with respect to their applicability on an intraspecific level. Finally, I studied whether density-dependence of facilitative might change our view on classical competition theory and competition effects on an individual level.

My overall results indicated that intraspecific facilitation is actually ubiquitous. It has been found in almost all biomes and climate zones. However, I did find evidence for reciprocal interactions being more common under stress such as salinity, heat, waterlogging rather than wind, burial, radiation, *etc*. Based on the intraspecific study system, my experimental results provided solid evidence for competitive ability-stress tolerance trade-off and demonstrated how this trade-off may influence facilitative effects and responses. I also proposed a conceptual model to predict how density-dependence of plant interactions may shift along stress gradients and how the shift may alter the balance between facilitation and competition. The model predictions were strongly supported by the experiment. I further found that when plants demonstrated a positive density-dependence in the intraspecific facilitation, they may decrease allocation to competitive traits to avoid suppressing and excluding neighbours. In summary, this thesis indicates the potential of intraspecific facilitation may be greatly underestimated and future studies should expand concepts in the context of competition (especially at the population-level) to facilitation.

Chapter 1

General introduction

The view of negative plant-plant interactions has dominated ecology since Darwin. Based on this view, ecologists have developed many theories to explain how competition can affect the structure and temporal dynamics of plant populations and communities. However, in the past two decades, an increasing body of literature has demonstrated that plants may also have positive effects on each other while they compete for resource and space, especially in stressful environments (Callaway 1995; Brooker *et al.* 2008). Positive plant-plant interactions have been known as facilitation and plants may facilitate each other through various mechanisms. For example, established plants may provide shade to smaller seedlings in environments where light and high temperatures are detrimental, e.g., in deserts (Tielbörger & Kadmon 1995; Madrigal-Gonzalez *et al.* 2013). This so-called nurse plant effect (Valientebanuet & Ezcurra 1991; Cavieres *et al.* 2002; Cavieres *et al.* 2005) is one of the most studied in the facilitation literature. Other mechanisms include enhancement of soil water content in dry environments via hydraulic lift (Dawson 1993; Sekiya *et al.* 2011), fertility islands in nutrient-poor habitats (Pugnaire *et al.* 1996a), alleviation of salt stress (Bertness 1991; He *et al.* 2011), protection from herbivory (Hjalten *et al.* 1993; Hierro & Cock 2013), attraction of pollinators by showy plants (Laverty 1992; Ghazoul 2006) , protection from cold temperatures or wind (Choler *et al.* 2001; Eränen & Kozlov 2008), and many more (see e.g. review by Callaway 1995).

These studies indicate that most examples for positive plant-plant interactions stem from stressful environments. This also seems logical, because the main mechanisms in facilitative interactions operate via stress amelioration (Callaway 2007). Based on this intuitive concept and on the wealth of evidence, a core model in facilitation has been developed, the so-called stress gradient hypothesis (SGH, Bertness & Callaway 1994, Brooker & Callaghan 1998). The SGH assumes that facilitation always occurs simultaneously with competition, but their balance depends on the level of stress. Namely, the relative frequency and magnitude of plant interactions will shift from competition to facilitation along a gradient from benign to harsh environments. Due to its intuitive logic, myriads of empirical studies have been conducted to test the SGH and address where facilitation occurs in plant communities, i.e. under which conditions positive interactions could overwhelm competition and dominate. The bottom line of these studies, which have by now been reviewed several times (Maestre *et al.* 2009; Malkinson & Tielbörger 2010; He *et al.* 2013) is that studies confirming the SGH are somewhat more abundant but a very large number of studies do not confirm it. In fact there are also examples that show exactly the opposite patterns of plant-plant interactions along gradients (Tielbörger & Kadmon 2000; Maestre & Cortina 2004), i.e., increasingly negative interactions with increasing stress. Models to explain such discrepancies often included case-specific explanations, reflecting the fact that there is not yet any solid and quantitative theoretical framework around the SGH, and that most facilitation work is empirical.

One prominent difference between competition and facilitation studies is that the latter has been largely restricted to a community-level, and intraspecific studies are visually very rare. Therefore, theoretical progress related to facilitative interactions has been largely limited to community-level consequences (Soliveres *et al.* 2015). In addition, theory around facilitative interactions is rare in general and is rarely quantitative (but see Butterfield 2009).

The lack of intraspecific studies is regrettable, because we can learn a lot from an intraspecific perspective. In fact, a main conceptual advancement in studies of competition stems from an intraspecific perspective. For instance, our basic understanding of population dynamics and density-dependence is based on intraspecific approaches and negative plant-plant interactions (Begon *et al.* 2006). Derived from that, the law of constant final yield and self-thinning, some of the few widely-accepted principles in plant population biology, address plant populations and not communities. Furthermore, we have learned about the symmetry of competition from intraspecific models (Weiner 1990). On a community level, the idea that stronger intraspecific competition than competition between species promotes coexistence, has become the fundament of equilibrium theories of biodiversity (Chesson 2000). Compared to these, we have very little theory predicting how facilitation affects populations and how such population-level effects may propagate to a community level. The missing of population-level consequences of facilitation may be caused by the dominance of the notion ‘a large plant helping a small one’. Namely, most research was conducted between species pairs or diverse species that differ dramatically in their morphology and/or physiology, such as shrubs and trees *vs*. seedlings and herbs (Callaway 2007). Even if intraspecific facilitation has been studied, it is often concerned with interactions among unequal individuals, e.g. large adults shading small seedlings (Wied & Galen 1998; Armas & Pugnaire 2009), but the idea of reciprocal interactions within equal-aged cohorts of the same species has rarely been addressed.

Furthermore, a major disadvantage of interspecific studies is that species identity may be confounded with the factors that determine the very mechanisms we want to study. For example, another conceptual but not quantitative idea is that both facilitative response of beneficiaries and positive effects of benefactors depend on specific traits. Namely, the structure of the canopy may determine facilitative effects on understory (Pugnaire *et al.* 1996b; Linstädter *et al.* 2016), species-specific symbioses with soil organisms may change facilitative effects (Nara & Hogetsu 2004) and stress-tolerant species are likely to benefit more from facilitation than species that are less tolerant (Liancourt *et al.* 2005). However, the trait-specificity cannot be unequivocally determined in an interspecific setting because species rarely differ in only a single trait. Therefore, facilitation is also species-specific and species identity will always be confounded with effects of the focal trait. An intraspecific approach is clearly superior to an interspecific setting because it could disentangle trait effects from species identity. However, it is then a challenge to identify an ideal study system to address intraspecific trait differences because within species, trait differences might be small.

Indeed, studies of facilitation have greatly improved our knowledge about the role of positive interactions for ecological and evolutionary processes. For example, facilitation can increase individual fitness (Goldenheim *et al.* 2008), maintain species richness (Cavieres *et al.* 2014), restore phylogenetic diversity (Navarro-Cano *et al.* 2016), improve ecosystem services (Mulder *et al.* 2001) or drive community dynamics (Butterfield 2009). However, as outlined above, the literature about facilitation is largely dominated by case studies and empirical research while the theoretical progress is quite limited. One reason could be that facilitation is only studied qualitatively, while very few quantitative models have been put forward to predict the relative importance of positive interactions for structuring populations and communities. In fact, most studies evaluate facilitation by comparing performance of target plants ‘with neighbors’ and ‘without neighbors’, and ignore the fact that neighbours have also a certain density, and that this density may vary across environments, too. Negative density-dependence has been explored intensively and it is paramount for many well-known ecological rules, while density-dependence of facilitation has been studied only very rarely. These notable exceptions have found the magnitude of facilitation could reach the maximum at intermediate densities of benefactors (Chu *et al.* 2008; Linstädter *et al.* 2016), thus challenging our view of the ubiquity of negative density-dependence in populations. However, there is still no general theory about how density-dependence of plant interactions may interact with stress gradients and this interaction may influence the balance between competition and facilitation, i.e. density-dependence of facilitation has not been systematically addressed.

The present thesis was designed to address the above research gaps and make a first attempt to take an intraspecific perspective on facilitation and study the theoretical implications of the results. Ideally, these will initiate a series of quantitative modeling studies designed to increase the theoretical advancement in facilitation research and to integrate facilitation and competition into a coherent framework.

To do so, I took three steps. In a first step, I reviewed the existing literature about intraspecific facilitation in order to see what we can learn from this. In a second step, I used an intraspecific experimental study system to address major concepts in facilitation research with respect to their applicability on an intraspecific level. Finally, I studied whether by addressing density-dependence of facilitative and competitive interactions simultaneously might change our view on classical competition theory and competition effects on an individual level.

Chapter 2 mainly consists of two literature reviews. I firstly reviewed 1189 articles to find out how common is intraspecific facilitation and where does it occur. Among this wealth of studies, 79 intraspecific facilitation cases in 52 studies were found, i.e. less than 5% of the studies were included. The results indicate that intraspecific facilitation is ubiquitous and not restricted to any specific climate or ecosystem (tropical, arid, warm temperate, Mediterranean, snow and polar). Since unidirectional interactions are not likely to happen among individuals with similar size, i.e., the even-aged population, the 79 cases were classified into even-aged and adult-seedling populations. Then if intraspecific facilitation in a certain stressful condition has been found in an even-aged population, it could be reciprocal or even symmetric. *Vice-versa*, if only occurs between adults and seedlings, the facilitation should be unidirectional. Here, we did find evidence for reciprocal interactions being more common under salinity, heat and waterlogging stress rather than wind, burial and radiation stress.

The problem of these studies was that for a particular harsh habitat, plants could have multiple mechanisms leading to different modes of facilitation (reciprocal or unidirectional). Unfortunately, many of the 52 studies were not designed specifically to explore mechanisms. Therefore, it was impossible draw sound conclusions by focusing only on these studies. In the next step, a second review was conducted to summarize and classify possible mechanism in facilitation studies in both intra- and interspecific studies. I reviewed 1759 articles and found 488 cases in 235 studies which experimentally explored or strictly considered possible mechanisms. Reciprocal facilitation between species pairs in these studies was identified to reinforce conclusions based on the first review. Finally, based on the synthesis of the two reviews, I was able to build a conceptual framework about which of the main mechanisms of facilitation are prone to be reciprocal than unidirectional and which of the reciprocal interactions may be more likely symmetric than asymmetric.

The main aim of Chapter 3 was to observe intraspecific facilitation and use this un-confounded intraspecific setting to investigate how life history related traits (competitive ability and stress-tolerance) may determine facilitative effects and responses. Based on Chapter 2, I selected salt as the stress factor, under which facilitation should be symmetrical. Using an approach with even-aged conspecifics (*Arabidopsis thaliana*) and genetically defined stress tolerance (salt-sensitive mutants *vs.* relatively tolerant wildtypes), trait-dependence of facilitation was tested. I found salt-sensitive genotypes to be more dependent on facilitation, consistent with the initial hypotheses. They also exhibited a large competitive ability indicating new evidence for the occurrence of a competition-stress tolerance trade-off. Also, the sensitive plants had a stronger facilitative response compared tolerant genotypes. However, sensitive genotypes also imposed consistently stronger facilitative effects despite being smaller under high salinity. This indicates a novel 'suicidal' facilitation mechanisms mediated via increased salt uptake from the soil.

In Chapter 4, a conceptual model was proposed to predict how density-dependence of plant interactions may shift along stress gradients and how the shift may alter the relative importance of facilitation and competition. To test the two model predictions, I used the un-confounded intraspecific approach and a similar study system (*Arabidopsis thaliana* and salt stress) established in Chapter 3. By growing plants under different densities and salinity levels, results indicated both model predictions were strongly supported: the strength of facilitation will peak at a higher density with increasing stress. Furthermore, the stress-gradient hypothesis (SGH) which predicts the highest intensity of positive interactions under highest stress was only confirmed at high densities. This challenges the view of the ubiquity of the SGH and provides a mechanistic explanation for the circumstances under which it should apply. It highlights that density-dependence must not be ignored in facilitation research but it should be explicitly considered, just as in competition studies.

In Chapter 5, I used the same experimental setup from Chapter 4 to address the individual-level consequences of facilitation, competition and density. Namely, I looked at the allometric relationship (rosette size-body mass) to test the hypothesis that the classical shade-avoidance syndrome exhibited by plants under high density and negative interactions, would be weakened when facilitation occurs. Indeed, I found in benign and low stress conditions where competition dominated, plants could build a relatively larger rosette to compete with neighbours, which is consistent with the classical shade-avoidance response. However, the shade-avoidance syndrome was not found and allometric relationships changed oppositely when facilitation dominated under high stress levels. Form an evolutionary point of view, this may be explained by the fact that it is advantageous for plants to avoid suppressing their neighbours when depending on facilitation by them. However, mechanisms, especially the physiological mechanism behind the observed pattern is not clear and should be subject to further studies.

My overall results indicated that the potential of intraspecific facilitation may be greatly underestimated. Namely, the explicit study of concepts that have been investigated in the context of competition should be expanded to facilitation and merged with current facilitation theory. Ideally, this would be a cornerstone for the development of a unified quantitative theory of plant-plant interactions. In summary, I advocate the utilization of controlled and unconfounded intraspecific approach in facilitation studies for parameterizing quantitative models about plant-plant interactions.

Chapter 2

A review on reciprocity and asymmetry/symmetry in facilitation: the foundation for exploring population-level consequences of facilitation

Abstract

In the past two decades, studies of facilitation have greatly improved our knowledge about the role of positive interactions for ecological and evolutionary processes. However, most facilitation research has been largely restricted to a community-level and intraspecific studies have drawn much less attention. This is prominently different from competition studies and very regrettable. In fact, a main conceptual advancement in studies of competition stems from an intraspecific perspective and many classical patterns regarding how competition may regulate population dynamics have become textbook knowledge. However, there is very little theory predicting how facilitation affects populations and how such population-level effects may propagate to a community-level. The missing of population-level consequences of facilitation may be caused by the dominance of the notion ‘a large plant helping a small one’, while the idea of reciprocal interactions has rarely been explored. In order to address the research gap, we conducted two reviews to find out evidence for intraspecific facilitation and facilitation mechanisms in various stressful habitats. We could show that intraspecific facilitation has been detected in almost all biomes, climate zones and across a range of stress factors, which indicates it may be underestimated. By combing evidence from the two reviews and analyzing whether facilitation mechanisms are reciprocal and symmetric, we are able to develop a conceptual framework about reciprocity and symmetry of facilitation. This framework could be used as the foundation for future studies which aim to explore intraspecific facilitation and reciprocal facilitation.

I. Introduction

Plant-plant interactions affect the structure and temporal dynamics of plant populations and communities. For example, competition for resources determines whether or not plant species may coexist (Grime 1973); Hautier *et al.* (2009), it leads to regular spatial pattern and is a key process in regulating population densities (Enquist *et al.* 1998; Stoll & Bergius 2005). Ever since Darwin, research about negative plant-plant interactions has dominated the literature. However, after the very early acknowledgement of facilitation as a driver of successional processes by Clements (1916), positive interactions among plants has also been intensively explored in stable communities in the past two decades (Brooker *et al.* 2008; McIntire & Fajardo 2014). These studies have indicated that plants may facilitate each other through a variety of mechanisms including, for example, shading (Bertness & Shumway 1993), hydraulic lift (Ludwig *et al.* 2003), cloud combing (Rigg *et al.* 2002), fertility islands (Callaway *et al.* 1991), mycorrhizal fungal networks (Van Der Heijden & Horton 2009), or protection from herbivory (Callaway *et al.* 2005).

Since the seminal paper by Callaway (1995), myriads of empirical studies have been conducted to address whether and where facilitation occurs in plant communities, i.e., under which conditions positive interactions could overwhelm competition and dominate. These have been reviewed several times by now (Bruno *et al.* 2003; Brooker *et al.* 2008; Maestre *et al.* 2009; He *et al.* 2013; He & Bertness 2014), with the aim of evaluating how facilitation may shape community structure and test the so-called Stress Gradient Hypothesis (SGH), a conceptual model that predicts a higher frequency of positive interactions in severer environments (Bertness & Callaway 1994; Brooker & Callaghan 1998). However, in contrast to studies on competition, facilitation studies are largely limited to a community-level, and intraspecific studies seem to be relatively rare. Existing theories also focus only on a community level. For example, facilitation has been put forward as a key mechanism promoting species coexistence and thus diversity (Gross *et al*. 2015, for recent review see McIntire & Fajardo 2014); driving community dynamics under abiotic stress and resource limitation (Butterfield 2009); or predicting patch-size distribution of vegetation (Kefi *et al.* 2007). Nevertheless, population-level consequences of facilitation remain unclear.

One reason for the bias towards community-level studies may be that the initial acknowledgement of facilitation in succession (Clements 1916) and later authors was driven by the aim of understanding mechanisms of species turnover (Connell & Slatyer 1977) or coexistence (Tanner *et al.* 1994). Another reason could be the dominance of the notion of 'a large plant helping a small one' in our current perception of facilitative interactions. Most research was conducted between species pairs or diverse species differing dramatically in their morphology and/or physiology, such as shrubs, tree seedlings and herbs (Callaway 1995; Callaway 2007). These may explain why the focus of facilitation research has been on interspecific case studies. Even if facilitation within species has been studied, it is often concerned with interactions among unequal individuals, e.g. large adults shading small seedlings (Eränen & Kozlov 2008; Cavieres & Penaloza 2012). In fact, most studies of facilitation only consider unidirectional relationships of benefactors facilitating beneficiaries (Bronstein 2009), and the idea of reciprocal interactions within equal-aged cohorts of the same species has rarely been addressed.

However, a few recent studies indicated that this intraspecific facilitation could co-occur with competition among even-aged plants and it may change classical patterns of density-dependence (Chu *et al.* 2008; Fajardo & McIntire 2011; Castro *et al.* 2013; Vogt *et al.* 2014). For example, Chu *et al.* (2008) reported that the relationship between mean individual biomass and density shifted from monotonic to humped-shaped with increasing stress in model simulations and field experiments. In that case, individuals in a population were able to benefit from each other even when they were very similar. Thus, these findings deviated from the classical ‘large benefactor-small beneficiary’ setting that characterizes most previous observations and experiments in facilitation research. Of course, these intraspecific studies themselves are important, because they found facilitation could overwhelm competition under very strong niche overlap (conspecific cohort) and exhibit net positive interactions. This is interesting, because the key role that competition plays in determining population dynamics has become textbook knowledge. For instance, classical population ecology has focused on negative density-dependence of survival (e.g. self-thinning law, Yoda *et al.* 1963), growth (e.g. law of constant final yield, Weiner & Freckleton 2010) or recruitment (e.g. logistic growth, Pearl & Reed 1920).

Compared to competition studies, we virtually have very little theory about how facilitation affects populations and how such population-level effects may propagate to communities. Therefore, these findings, which contradict classical competition theory (Bomze 1983; Begon *et al.* 2006), could provide the foundation for exploring how facilitation could regulate population dynamics thus incorporating facilitation into mainstream ecological theory based solely on resource competition.

In order to investigate population-level consequences of facilitation, an obvious prerequisite is figuring out under which circumstances intraspecific facilitation could happen. Namely, we should find out under which stress facilitation rely on the 'large benefactor-small beneficiary' setting and which do not require the size-discrepancy (reciprocal). For example, in northwestern Russia, Eränen and Kozlov (2008) evaluated both effects of adult-seedlings as well as seedling-seedlings interactions on mountain birch *Betula pubescens*. They found adults that were substantially larger could protect smaller seedlings from wind stress and exhibited facilitation, while competition was stronger for seedling-seedlings because individuals of similar size could hardly shelter each other. However, at New England marshes, Bertness and Yeh (1994) found seedling survivorship of perennial shrub *Iva frutescens* was higher when grown at high seedling densities, while solitary *Iva* seedlings suffered extremely high mortality. The main mechanism under salt stress is shading substrate by neighbouring plants, which could decrease evaporation thus reducing salinity in the soil. Then any individuals in the vicinity could contribute to the stress amelioration and receive benefit from each other. Therefore, the occurrence of intraspecific facilitation could be expected when size dependences are not required.

Nevertheless, qualitatively identifying whether intraspecific facilitation could happen in a certain harsh habitat might be insufficient for fully understanding its consequences. This is because size-hierarchies always exist even in an even-aged population and the size of individuals may determine how they alleviate stress and receive benefit quantitatively. For example, under salinity stress, a larger individual may shade more substrate area thus exerting strong facilitative effects, while a smaller individual could be more sensitive to stress amelioration. These unbalanced effects and/or responses could further affect population structure and dynamics. A recent empirical study, albeit on community-level, has reported that intermediate-sized individuals of *Agrostis magellanica* grass were most strongly facilitated by the cushion plant *Azorella selago*, which has led to a different size-class distribution compared with *A. magellanica* on the adjacent soil (le Roux *et al.* 2013). Recent models that have looked at facilitation alone also indicated that the manner in which facilitative interactions vary (or not) with the size of the individuals, may differ in affecting spatial pattern and structure of populations (Chu *et al.* 2009; Lin *et al.* 2012). Therefore, studying the size-symmetry of facilitation is crucial for completing our theoretical understanding of plant-plant interactions and their role in structuring plant populations and communities.

Similar to the concept of symmetry in competitive interactions (Weiner & Thomas 1986; Weiner 1990), we can define asymmetric facilitation as an interaction among plants whereby the larger plant exerts disproportionately larger facilitative effects compared to smaller neighbour. Symmetric facilitation could be understood as a scenario in which both larger and smaller individual contribute proportionally or even equally to stress amelioration according to their size. From this perspective, reciprocal facilitation could be either symmetric or asymmetric, while unidirectional facilitation is an extreme case of asymmetric interactions, i.e., completely asymmetric. However, knowledge about under which conditions facilitative interactions are symmetric or asymmetric is virtually missing. In fact, the concept of unbalanced benefits for plants with different size is only mentioned in some facilitation models (Lin *et al.* 2012) and it has not been systematically investigated before. Taking some guidance from competition research should be a good idea. This is because the bias towards community-level studies is not apparent in competition studies and much in competition theory has been written about whether or not the division of resources will be asymmetric or symmetric (Weiner 1990; Stoll & Bergius 2005; Bennett *et al.* 2013). A common perception is that below-ground competition is size-symmetric, i.e., each plant in a competitive interaction acquires resource amounts proportional to its size (Schwinning & Weiner 1998). *Vice-versa*, above-ground interactions such as competition for light has been modelled as size-asymmetric because as one plant is able to overgrow another, it will gain over proportional access to light (Weiner 1990). Here, we suggest that this could also apply to the symmetry of facilitative interactions. For example, if light acts as a stress factor and facilitation occurs via shading (e.g., Pages & Michalet 2006) then larger plants can facilitate their shorter neighbours. On the other hand, below-ground facilitation might be symmetric, e.g., Luo *et al*. (2010) found when stressed by inundation, two wetland species *Carex lasiocarpa* and *Deyeuxia angustifolia* showed greater biomass when grown with more conspecific neighbours by releasing oxygen into the soil. This could be rather symmetric if the released oxygen is proportional to their size.

Unfortunately, these ideas have not been explored because detecting direct empirical evidence for reciprocity or symmetry of positive interactions is very difficult. Firstly, competition and facilitation occur simultaneously and studies that are merely observations (i.e. the vast majority of studies) cannot distinguish purely facilitative interactions from net effects. Secondly, studying reciprocity often requires complex experimental approaches that manipulate both neighbor presence and the environmental factor simultaneously (Holzapfel & Mahall 1999). Thus, such studies are very rare. In addition, quantifying the extent to which such reciprocal interactions are symmetric or not would add another factor that needs to be manipulated. Not surprisingly, such studies are virtually missing. Finally, if facilitation and competition are for the very same resource, then separating them experimentally is impossible.

However, myriads of studies exist about facilitation mechanisms and there have been studies about intraspecific facilitation (even-aged population) and facilitation in adult-seedling systems. In this study, we attempted to utilize this wealth of empirical information to review our current knowledge of intraspecific facilitation and explore reciprocity and symmetry of facilitation. To do that, we

1) reviewed existing evidence for intraspecific facilitation to figure out under which circumstances it could be reciprocal or unidirectional by comparing intraspecific facilitation and facilitation in adult-seedling systems under certain stress. We assumed that in an intraspecific setting, the occurrence of unidirectional (completely asymmetric) facilitation could be expected in adult-seedling systems rather than even-aged populations or conspecific cohorts, where individuals are more similar to each other. So if facilitation could happen in even-aged populations under specific stress, then the stress factor should

be prone to generate reciprocal facilitation. Vice-versa, for other stress factors, if facilitation can only occur in adult-seedling systems, then they may be likely to generate unidirectional facilitation. Based on the review, we also evaluate how common intraspecific facilitation may be in major biomes and climate zones.

2) reviewed mechanisms in facilitation (including both intra- and interspecific studies) and found out reciprocal facilitation in interspecific studies. This was done because we found for a certain stressful habitat plants could have multiple mechanisms leading to different modes of facilitation. Also, many intraspecific studies were not designed for investigating facilitation mechanisms, which did not allow further analysis for the symmetry. Furthermore, reciprocal facilitation in interspecific studies could also reinforce our conclusions based on the first review.

3) developed, by using evidence from the two reviews, a conceptual framework about which mechanisms of facilitation are prone to be reciprocal than unidirectional and which of the reciprocal interactions may be more likely symmetric than asymmetric.

II. How common is intraspecific facilitation and where does it occur?

2.1 Search criteria and analyses for intraspecific facilitation studies

In order to find out the evidence for intraspecific positive interactions in different stress conditions, we initially searched the Web of Science (1970-2014) with strings as follows: Topic = (facilitation OR positive interaction) AND Topic = (stress* OR resource OR gradient OR light OR UV OR radiation OR irradiance OR snow OR salt OR salinity OR nutrient OR fertili* OR nitrogen OR grazing OR browsing OR trampling OR herbivor* OR predation OR water OR moisture OR disturbance OR exposure OR flooding OR tide OR wave OR burial OR wind OR cold OR thermal OR heat OR sedimentation OR temperature OR drought OR precipitation OR rainfall OR acidity OR hypoxia OR inundation OR waterlogging OR submergence OR pollution OR pollinator) AND Topic = (intraspecific OR conspecific OR cohort OR population) AND Topic = (plant). These keywords were defined after an initial assessment of the main possible mechanisms by which plants facilitate each other. This database was very large and yielded a total of 1189 studies. This initial list was then refined and condensed using the following criteria:

1. The study is empirical and facilitation should be restricted to intraspecific interactions because the search also yielded a number of interspecific studies.

2. The study should include a neighbour treatment, i.e., either amount or presence of neighbours should be manipulated or by using existing states in the field (e.g. with benefactor *vs*. without).

3. The study use fitness-related parameters such as survival, biomass, reproduction, growth rate and *etc.* as response variables of the beneficiary plants. Response measures are important because the outcome of plant interactions often differ based on different measures, e.g., positive effects of survival provided by shelter of benefactors may take a cost of photosynthesis for beneficiaries (Callaway *et al.* 1996). Also, many studies have used spatial pattern (positive spatial associations) as response variables, but it could also be the result of propagule accumulation or seed trapping and do not necessarily reflect genuine facilitation (Callaway 1995). We retained such studies only if they were supported by extra evidence from subsequent investigations or parallel studies (le Roux & McGeoch 2008; Fajardo & McIntire 2010; Cerfonteyn *et al.* 2011).

4. The study should have pronounced evidence for positive net effects. Studies that observed some signs of intraspecific facilitation but the net outcome of plant interactions was competition (Lu *et al.* 2010; Zhang *et al.* 2012; He *et al.* 2014) were not considered. This is because we cannot be certain that facilitation actually occurred in the case of net negative effects, although this may have led to the exclusion of studies where intraspecific facilitation was present.

5. We mainly focused on the amelioration of stress and/or low resource levels in pairwise benefactor-beneficiary interactions and did not consider population-level positive density-dependence such as in Allee effects (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Stephens *et al.* 1999) mediated by shortage of mates or inbreeding due to small population size. This was done because the definition of facilitation (Bronstein 2009; Brooker & Callaway 2009) is not unequivocal when it comes to such effects.

Finally, in accordance with different species and response measures, 79 intraspecific cases in 52 studies were retained. For a complete list of references see Appendix 1a.

In order to answer 'where does intraspecific facilitation occur', we identified the location of the studies and categorized them according to ecosystems and biomes. Then these studies were categorized according to biomes and climate zones (Appendix 1b). The categories for biomes were adopted from a previous review and a meta-analysis (Callaway 1995; He *et al.* 2013): arctic/alpine, coastal/marine, freshwater wetland, grassland/savanna (including desert and steppe), forest/woodland and old field. Note that for common garden and greenhouse experiments, biomes referred to the origin of study species. Climate zones were defined based on the classification of the Köppen–Geiger system (Kottek *et al.* 2006) and included tropical, arid, temperate, Mediterranean, snow, polar and control. Control was added because we included four manipulated greenhouse studies with strong evidence for facilitation in even-aged populations. Mediterranean was separated from temperate climate because Mediterranean climate is representative in facilitation research.

In order to understand in which harsh conditions intraspecific facilitation could occur, we used the stress factor (as a third category) whereby similar stressors (e.g. low temperature and severe winters) were combined into a single category (e.g. 'chill'). The final list of stressors included the 13 stressor, which were often opposite end points along environmental gradients: wave, wind, heat, chill, burial, drought, waterlogging, substrate mobility, salinity, snow cover, radiation, nutrient deficiency and herbivory (see also Appendix 1b). We assume that unidirectional facilitation may occur in adult-seedlings but hardly in even-aged populations or conspecific cohorts. Thus, if intraspecific facilitation could be found in even-aged populations or both study systems (even-aged population and adult-seedlings) for a specific stress factor, then we may conclude that facilitation in this stress should be reciprocal. Then we distinguished between cases where facilitation was detected among individuals within an even-aged population (reciprocal facilitation) or between plants that were largely different in size (mostly due to age). Whether the relative frequency of even-aged/adult-seedling was higher than expected by chance was also examined. Namely, we tested whether there were significantly more cases with even-aged than with an uneven-aged setting under certain stress, using simple chi-square test with total frequency of even-aged vs. uneven-aged as null model. The analysis was performed in R (R-project. 2016).

2.2 The occurrence of intraspecific facilitation

Results about biomes and climate zones indicate intraspecific facilitation may be ubiquitous in nature (Fig. 1A and B). Actually, the occurrence both facilitation in adult-seedling systems and intraspecific facilitation has been reported in almost all biomes and climate zones (except for old field). However, the analyses (Chi^2-tests) for stress factors showed the over-representation of facilitation in adult-seeding systems in certain harsh habitats (Fig. 1C). In fact, under stress such as radiation, wind and burial, facilitation has been reported to only occur in adult-seedling systems rather than even-aged populations. For example, Eränen and Kozlov (2008) conducted an experiment with mountain birch in northwestern Russia, where mean wind speeds in the high stress sites were up to 15 times higher than in the respective low stress sites. They found plant interactions were size-dependent: facilitation could dominate when the benefactors were substantially larger than the beneficiary, while competition may be stronger when the plants were of similar size because they could not protect each other from wind efficiently. Therefore, this above-ground stress and similar ones (e.g., radiation) are more likely to trigger unidirectional (completely size-asymmetric) facilitation.

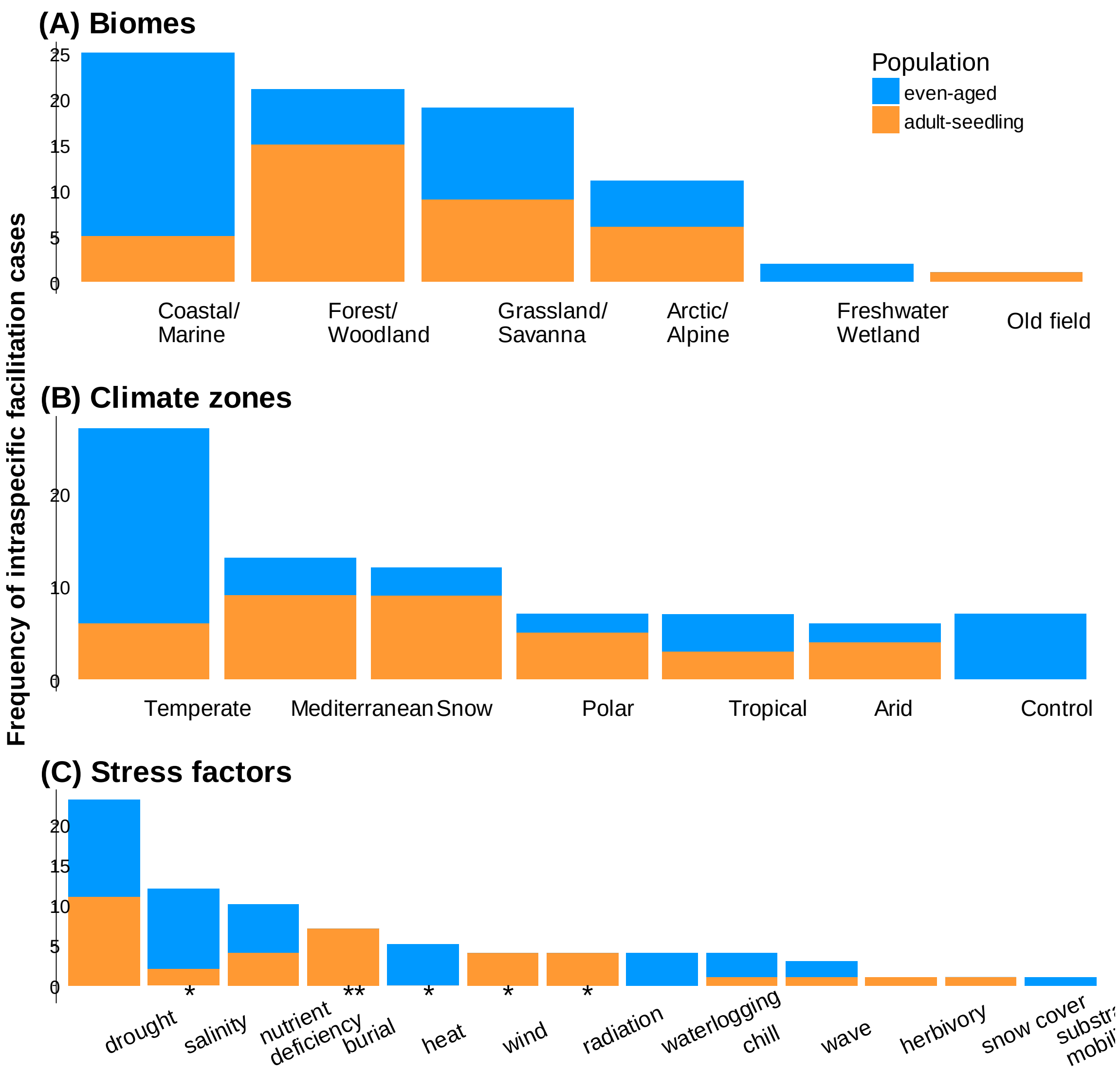

Figure.1 Frequency of facilitation (including intraspecific facilitation in even-aged population and facilitation in adult-seedling systems) across different biomes (A), climate zones (B) and stress factors (C). Totally, there are 79 facilitation cases in 52 studies.

However, the analyses for stress types also indicated intraspecific facilitation were particularly common for salinity and heat stress (Fig. 1C). For example, a representative case is salt marshes, one of the best documented systems in facilitation research. Here, Bertness and Yeh (1994) found in the upper zones, that both survival and growth of the shrub seedling *Iva frutescens* was significantly promoted both by their conspecific adults and high conspecific seedling densities. The species *Juncus gerardii* also exhibited a similar pattern. The main mechanism identified in such studies has been the shading of substrate by plants of any age or size, which could limit salt accumulation via a reduction in transpiration of water from the soil. A similar mechanism was also reported for heat stress, e.g., Goldenheim *et al.* (2008) found the annual forb *Suaeda linearis* performed much better when growing with more conspecific neighbours, because plant cover could greatly reduce the soil temperature. Consequently, the occurrence of facilitation under such stress does not rely on size differences among individuals and these stress factors may generate reciprocal and possibly symmetric facilitation.

The comparison between facilitation in even-aged populations and adult-seedling systems in a stressful habitat yielded a preliminary insight into whether this specific stress factor tends to generate reciprocal (e.g., salinity, heat and waterlogging) or unidirectional (e.g., radiation, wind and burial) facilitation. Nevertheless, the problem is that for a particular harsh habitat plants may have not only one mechanism for a certain stress factor, which could lead to different modes of facilitation. When looking at drought, the most frequently reported stress factor in intraspecific facilitation (Fig. 1) and facilitation for both even- and uneven-aged population has been found. However, the corresponding mechanisms may be quite different. For example, Bingham and Simard (2011) found facilitation under drought by means of mycorrhizal networks. Namely, *Pseudotsuga menziesii* seedlings with potential to mycorrhizal networks connected with nearby conspecific seedlings could receive water and had higher survival compared to solitary seedlings. Intraspecific facilitation through these mechanisms should be reciprocal because the transport of resources can be bidirectional for those connected individuals (Gorzelak *et al.* 2015), and because it is reasonable to assume that all individuals within a population share similar mycorrhizal. *Vice-versa*, the classical mechanism of drought facilitation is via shading, such as nurse plants, and there is a number of intraspecific studies that found this above-ground mechanism as the main one (Fuentes *et al.* 1986; Wied & Galen 1998; Otto *et al.* 2010). For these cases, facilitation should be unidirectional instead of reciprocal because beneficiary seedlings cannot shade adult neighbours.

These findings from the intraspecific survey indicate that it is important to consider the main mechanism in stressful environments rather than only focus on the stress factors alone. However, the number of case studies with intraspecific facilitation is limited and many of them are not designed to explore facilitation mechanisms. Therefore, we took the next step and included also interspecific studies to develop conceptual ideas about whether and why facilitation mechanisms are more prone to be reciprocal or symmetric. Furthermore, including interspecific studies and identifying reciprocity in interspecific studies may provide additional evidence for conclusions based solely on the first review.

III. Facilitation mechanisms : reciprocity and symmetry

3.1 A literature review for facilitation mechanisms

To do so, we started with searching articles published from 1970 to 2014 via Web of Science again by using items different from the first search Topic = (facilitation) AND Topic= (plant) AND Topic = (stress* OR resource OR gradient OR light OR UV OR radiation OR irradiance OR snow OR salt OR salinity OR nutrient OR nitrogen OR grazing OR browsing OR trampling OR herbivor* OR predation OR water OR moisture OR disturbance OR exposure OR flooding OR tide OR wave OR burial OR wind OR cold OR thermal OR heat OR sedimentation OR temperature OR fertili* OR drought OR precipitation OR rainfall OR acidity OR hypoxia OR inundation OR waterlogging OR submergence OR pollution). This survey yielded many more studies (1759 articles), which were then again flited by the following criteria:

1. The study should be empirical and facilitation should be restricted to a within-trophic-level to fulfil the general definition of facilitation in plants (Bronstein 2009; Brooker & Callaway 2009).

2. The study should include a neighbour treatment, i.e., either amount or presence of neighbours should be manipulated or by using existing states in the field (e.g. with benefactor *vs*. without).

3. The study should use fitness-related parameters such as survival, growth (e.g., biomass, growth rate, height, number of leaves or branches), fitness (e.g., seed production and

number of flowers) as indicator for positive interactions. Furthermore, some studies used ‘species richness’ as indicator (Howard *et al.* 2012; Becerra & Montenegro 2013). These studies were retained only if they had evidence that benefactor species can alleviate stress because increased diversity could be attributable to heterogeneity (McIntire & Fajardo 2014). In this case, beneficiary species were recorded as ‘mixed’.

4. The study should explore facilitation mechanism with a manipulative approach or consider the mechanism of facilitation explicitly based on parallel studies in similar habitats.

5. The study should either have pronounced evidence for positive net effects or distinguish purely facilitation from net interactions (Holzapfel & Mahall 1999).

6. Intraspecific studies in Appendix 1(a and b) that met the above criteria were also included.

In summary, 488 facilitation cases from 235 studies were retained that fulfilled the above criteria (see Appendix 2a for the literature list). We then classified the studies according to stress factor and identified whether or not reciprocal interactions were found to provide further evidence (section 3.2). We also found out the main facilitation mechanism in the study, and then similar stress factors and correlative mechanisms were combined (see Appendix 2b). Finally, for each mechanism, we reviewed evidence for them and discussed whether or not they could be reciprocal and symmetric (section 3.3).

3.2 Where does reciprocal facilitation occur in interspecific studies?

In fact, we can only find reciprocal facilitation in three case studies (Bertness & Hacker 1994; Pugnaire *et al.* 1996a; Holzapfel & Mahall 1999). Bertness and Hacker (1994) found a reciprocal positive association between the shrub *Iva frutescens* and perennial turf *Juncus gerardii*. Interestingly, the same authors also found intraspecific facilitation within *Iva* and *Juncus* in the same type of habitat (Bertness & Yeh 1994). This indicates that evidence for intraspecific facilitation could be indicative for the potential reciprocity of facilitation also between species. In semi-arid Spain, reciprocal facilitation related to soil nutrients was detected. Pugnaire *et al.* (1996a) reported the leafless leguminous *Retama sphaerocarpa* and understory herbs (e.g., *Marrubium vulgare*) can facilitate each other through improving nutrient availability. The soil fertility under shrubs was higher compared with plants growing on their own, which was interesting because *Marrubium* is not a legume. Thus, this study showed that in a classical 'island of fertility' situation (Callaway 1995), each partner can contribute and benefit, resulting in a mutualistic association. Facilitation under nutrient deficiency has also been found in intraspecific studies (Fig. 1), albeit via different mechanisms, and we suspect intraspecific facilitation might also occur if conspecifics could form island of fertility. The third reciprocal study was reported by Holzapfel and Mahall (1999), who found both canopy shading of desert shrub (*Ambrosia dumosa*) and ‘thatch effect’ of annuals increased soil water content thus facilitating each other. They separated pure positive and negative effects via simulating physical effects of neighbours and reciprocal removal of neighbours. However, the net effects of annuals on shrubs were still negative due to competition. Similar mechanisms were also found in intraspecific studies under drought or heat stress (Doran *et al.* 2001; Goldenheim *et al.* 2008).

Overall, there is very little evidence for reciprocity in interspecific studies (three). This does not mean, however, that reciprocity does not exist. In fact, we would interpret this fining as support to our initial assumption that the focus of most facilitation research has been on unidirectional interactions (large benefactors facilitating small beneficiaries), i.e., this is mainly the result of a bias in the study approach. Thus, we believe that the lack of evidence for reciprocity is due to the lack of explicit tests of reciprocity. This is also confirmed by the fact that the stress and corresponding mechanisms are consistent with conclusions from intraspecific studies. Namely, stress factors that could generate reciprocal facilitation have also been found to generate facilitation in even-aged populations. *Vice-versa*, we may also expect reciprocal interspecific facilitation in habitats in which intraspecific facilitation has been detected, e.g., salt, chill and heat. Therefore, reciprocity should be more common than what has been reported. Based on the two reviews and the following discussion (section 3.3) about mechanisms for each stress factor, we can build a concept framework about which mechanisms or stress are prone to be reciprocal and symmetric (Table 1).

Table 1. Summary of main facilitation mechanisms found in intra- and interspecific studies and expectations regarding reciprocity and symmetry. Numbers indicate the number of facilitation cases. “Y” and “N” means that reciprocity has been found in interspecific studies (Y) or not found (N), respectively. “R” and “U” indicate that we expect the mechanism should be reciprocal (R) or unidirectional (U). “S” and “A” indicate whether the reciprocal facilitation is more prone to be symmetric (S) or asymmetric (A). To be consistent, we use “CA” (completely asymmetric) to represent unidirectional facilitation in symmetry.

Type of facilitation	**Stress factors**	**Mechanisms**	**Even-aged**	**Adult-seedling**	**Reciprocal interspecific facilitation**	**Expected reciprocity**	**Expected symmetry**
Above-ground	Wind	shelter against wind	0	4	N	U	CA
	Snow cover	protection from snow	0	1	N	U	CA
	Radiation	shelter from radiation	0	4	N	U	CA
	Herbivory	biotic refuge	0	1	N	U	CA
		associational avoidance	0	0	N	R	S
	Chill	reduced convective heat loss	3	1	N	R	S
	Nutrient deficiency	soil nutrient enrichment (island of fertility)	0	0	***Y***	R	S
	Burial	protection from the weight of sediment	0	6	N	U	CA
	Drought	reduced water loss through shading	2	7	***Y***	R	A
		tap onto water resource (e.g., cloud combing)	0	1	N	U	CA
		increased water storage by neighbors	4	0	N	R	S

	Heat	decreased temperature under canopy	5	0	N	R	S
	Salinity	reduced salt accumulation via shading	10	2	***Y***	R	A
Below-ground	Salinity	salt uptake	1	0	N	R	S
	Drought	mycorrhizal networks and natural grafts	4	2	N	R	S
	Waterlogging	ground elevation	2	0	N	R	S
		oxygen leakage through aerenchyma	2	0	N	R	S
	Nutrient deficiency	mycorrhizal networks and natural grafts	5	0	N	R	S
	Wave	reduced wave velocity	2	1	N	R	S
	Substrate mobility	soil stabilization through plant structures	1	0	N	R	S
	Soil contamination	uptake of heavy metals from soil	0	0	N	R	S

3.3 Reciprocity and symmetry facilitative mechanisms

A. Drought (130 cases)

Facilitation in arid and semi-arid areas is one of the most investigated patterns. The associated mechanisms can be distinguished into four types which are discussed separately.

i) The most common mechanism against drought is via shading that decreases water loss from soil and from the tissues of a beneficiary (104 cases). This has been demonstrated by many studies conducted in arid and other water-limited systems, and it also has been suggested as being part of the so-called nurse plant syndrome (Fuentes *et al.* 1986; Callaway *et al.* 1996; Maestre *et al.* 2001; Gomez-Aparicio *et al.* 2008; Anthelme *et al.* 2014). In terms of this mechanism, the strength of facilitation would positively depend on plant size because the canopy would determine how much of the substrate is shaded.

This mechanism could be likely reciprocal because a target plant and it neighbours can both shade soil and facilitate each other. For example, Bacilio *et al.* (2011) found that the volume, hydration and water potential of the giant cacti (*Pachycereus pringlei*) and soil was increased by high densities of conspecific *P. pringlei*. They could show that this effect was due to shading of plants, i.e., direct evaporation from soil surface was much more than water loss from transpiration by cacti. In one of the few studies ever looking at reciprocal relationships, Holzapfel and Mahall (1999) used artificial structures to separate the competitive and facilitative interactions and found shading of both shrubs (*Ambrosia dumosa*) and understory annuals can increase soil moisture significantly. Nevertheless, it remains unclear, whether it is size-symmetric or not. For example, if the vicinity of an individual has been fully shaded, then extra plants may unlikely to add much to the decreased evaporation. Also, as larger plants overtop smaller ones, the positive effect imposed by the small plant could dwindle to a negligible effect. The evidence of Holzapfel and Mahall (1999) indicates this situation could be even more complex, due to the temporal dynamics in the system. Namely, annuals had no positive effect on shrubs in the wet season, when the shrub was green and much larger than the annuals. While positive effects by the dead annuals occurred once the shrub had shed its leaves and the only shading material was the annual plant litter. Therefore, we would expect this above-ground mechanism to be reciprocal but partly size-asymmetric.

ii) There are several manners by which plants can tap onto water resources and release them for other plants to use (14 cases). For example, there is evidence from arid ecosystems of hydraulic lift (Richards & Caldwell 1987; Prieto *et al.* 2010), capture of water from the atmosphere like fog precipitation (del-Val *et al.* 2006) or cloud combing (Rigg *et al.* 2002). For example, in coastal California grassland, Kennedy and Sousa (2006) found seedlings of tree species *Pseudotsuga menziesii* and *Lithocarpus densiflora* were greatly increased by adults. Using plastic trees and shading cloth treatment, they also proved that the mechanism was the input of fog precipitation rather than shading.

Due to the special characteristics of plants exhibiting this mechanism, it is highly likely to be species-specific (Ludwig *et al.* 2004a) and thus unlikely to be reciprocal in an interspecific case. For intraspecific studies, only facilitation in adult-seedling systems has been reported (Rigg *et al.* 2002). Furthermore, this mechanism might require size discrepancy, e.g., only plants whose roots can reach the deep, moist soil layers are able to facilitate others via hydraulic lift (Prieto *et al.* 2010). While if all individuals in a population could reach the moist layer, they will probably not be stressed by drought. Therefore, it could be unidirectional rather than reciprocal.

iii) Plants can also increase water storage through their structure or accruing soil organic matter (8 cases), especially for bryophyte species (Okland & Okland 1996; Pedersen *et al.* 2001). Tsai *et al.* (2010) also found the intraspecific facilitation in intertidal eelgrass (*Zostera japonica*) populations. They concluded the mechanism should be amelioration of desiccation stress when water can be held by a lawn of blades. We anticipate this mechanism is reciprocal and even symmetric because larger individuals with more leaves should hold more water thus excreting a greater facilitative effect.

iv) There is evidence that plants can share resources (water and nutrients) with others (4 cases). Plants may pass these resources between each other through mycorrhizal networks, stem-merging, root grafts and *etc.* to promote the growth of neighbours

(Bormann 1966; Graham & Bormann 1966; Christie *et al.* 1974; Keeley 1988; Navarro-Cano *et al.* 2015). For example, Bingham *et al.* (2012) found in a Canadian forest ecosystem that when drought stress was strong, survival of *Pseudotsuga menziesii* seedlings were lowest if they were unable to access ectomycorrhizal networks connected with adults. In a parallel lab experiment, they also reported *P. menziesii* seedlings with potential to form mycorrhizal networks with nearby conspecific seedlings had higher survival (Bingham & Simard 2011). This mechanism may also be symmetric because the transport of water or nutrients resources among connected plants can be bidirectional (for a recent review, see Gorzelak *et al.* 2015).

In summary, except for the second mechanism (tapping onto water resource), the other three have been found to occur in even-aged population (Table 1), thus, we hypothesize that tapping onto water resource is unidirectional while others should be reciprocal. However, the first mechanism (shading substrate), may be partly asymmetric because the facilitative effect is not always positively related to plant size. While others are expected to be symmetric, because increased water storage (mechanism 3) and resource sharing (mechanism 4) could be proportional to benefactors' size.

B. Herbivory (80 cases)

The terms such as "associational avoidances", "defense guilds", "biotic refuges" and "associational resistance" have been used in conjunction in the plant-herbivore literature and have led to some misunderstanding. To distinguish the concepts, we followed Milchunas' framework about external plant avoidances of herbivory (Milchunas & Noy-Meir 2002) and classified the mechanisms into two groups, refuges and associational avoidances. We excluded the 'indirect avoidance' mechanisms in Milchunas's framework because it involves herbivores and their predators rather than plants.

Refuges refer to physically impeded herbivore access, e.g., via thorns and dense canopy (40 studies). The mechanism could be highly species-specific (Rousset & Lepart 2000) and one prerequisite for the mechanism is that the benefactor should be large enough to harbor neighboring plants. Thus, it should be unidirectional because only benefactors can protect beneficiaries but not *vice versa*. Intriguingly, the mechanism may also depend on the size of herbivores. Namely, smaller plants could be benefactors and protect larger neighbors if grazing animals are also very small. For example, Bakker *et al.* (2004) found young spiny shrub *Prunus spinosa* (low branches) rather than old shrubs (higher, cannot hinder rabbits) can protect tree species *Quercus robur* from small herbivores. As a result, if plants suffer from both large and small herbivores, such as sheep and rodents, we might expect large and small thorny plants could protect each other.

The other mechanism, associational avoidance, may operate through influences on herbivore search behavior (visual, olfactory), diet selection (growing with palatables or unpalatables), or variable resource concentrations (40 cases). For example, Bossuyt *et al.* found several palatable species, such as *Cerastium fontanum* and *Holcus lanatus*, had a higher frequency, cover and/or flowering success when they grew with unpalatable species (Bossuyt *et al.* 2005). This mechanism is also species-specific (Hierro & Cock 2013), but for an intraspecific setting, it could be reciprocal because size disparities between benefactors and beneficiaries are not necessary. It is unclear whether associational avoidance is symmetric or not, and facilitative effects may closely related to the decision-making of herbivores. However, we might expect the symmetry if the deterrence (e.g., smell or toxic) would increase with their size.

For both mechanisms, we were not able to find reciprocal facilitation or intraspecific facilitation under herbivory. The first mechanism (biotic refuge) is expected to be unidirectional because it is usually species-specific and requires size differences between benefactors and beneficiaries. However, the second mechanism (associational avoidance) is also species-specific but it might be reciprocal because the mechanism does not rely on size differences. The degree of its symmetry uncertain, but suggest it might be symmetric if a large individual would be more deterrent.

C. Nutrients (55 cases)

Plants can directly enrich the nutrients in the soil and create islands of fertility via litterfall, leaching, trapping particles or vegetative residual and nitrogen fixation (45 studies). This mechanism has been mainly found for trees in savannas, shrubs in deserts, cushion plants in alpine areas (Callaway *et al.* 1991; Moro *et al.* 1997; Pugnaire *et al.* 2004; Anthelme *et al.* 2012). Nutrients enrichment could be reciprocal. As reported by Pugnaire *et al.* (1996a), the shrub *Retama sphaerocarpa* and understory herbs can facilitate each other through improving nutrient availability. They both contribute and benefit from the island of fertility. We also argue this mechanism might be proportional to plant size, because a large plant may take up more nutrients from deep soil (or intercept more particles outside the canopy) and deposit nutrients under them. This idea has also been confirmed by empirical studies. For instance, Ludwig *et al.* (2004b) found that *Acacia tortilis* trees can facilitate understory plants, while the soil nutrient availability increased with the age and size of *Acacia tortilis* trees. Pugnaire *et al.* (1996b) also reported the improvement of soil nutrient content under *Retama sphaerocarpa* shrub was most pronounced for the oldest age (size) classes. Therefore, facilitation via nutrient enrichment is more likely to be symmetric.

The nutrient facilitation may also operate indirectly by nutrient transfer via biological link, e.g., mycorrhizal networks with neighboring plants (10 cases). Dickie *et al.* (2005) showed the growth of *Quercus macrocarpa* was maximized at intermediate distances from adult tree *Quercus ellipsoidalis*. They found beneficial influences of trees on seedling growth were due to increased ectomycorrhizal infection (increased nitrogen uptake). Similar to resource sharing under drought stress, we also hypothesize it could be symmetric.

Both mechanisms have been found in reciprocal interspecific studies or intraspecific studies (Table 1) and are prone to be reciprocal. We further suggest they may be symmetric because the two mechanisms should be positively related to plant size.

D. Radiation (44 cases)

Intensive radiation could result in water loss, and the stress itself also limit the performance of plants by photoinhibition or damaging the tissues directly (e.g., energetic short-wavelength ultraviolet radiation), especially for those species with high shade tolerance (Callaway 1992; Aerts *et al.* 2006). The main facilitation mechanism is also shading, i.e., canopies of large plants may shade smaller neighbours and protect them from the harmful radiation. For example, Cuesta *et al.* (2010) found in a Mediterranean community, the photochemical efficiency (Fv ⁄Fm) of tree seedlings (*Quercus ilex*) grown under shrubs was higher compared to those in gaps. They also confirmed the mechanism was reduced radiation because soil water content and fertility were even lower or similar under the shrub canopy.

Facilitation under radiation stress is not limited to arid or semi-arid habitats. It can also alleviate cold-induced photoinhibition in frost-prone environments. For example, seedlings of tree species *Eucalyptus pauciflora* were found to be less photoinhibited and had higher photosynthetic rates when shaded by adults in winter (Ball *et al.* 1991; Egerton *et al.* 2000).

Intraspecific facilitation under strong radiation was found only in adult-seedling systems. This is not surprising, because radiation is 'preemption' and for vertical plants it seems unlikely that a small individual are able to intercept intensive radiation for neihgbours higher than them. We suggest this mechanism under radiation stress is typically unidirectional.

E. Salinity (37 cases)

Most studies detecting beneficial effects of neighbours in saline habitats found that the main mechanism operates via shading of the substrate and thus decreasing evaporation, which reduces salt concentrations in the soil. For example, studies have shown that many species can shade substrate and alleviate soil salinity (Bertness 1991; Bertness & Ewanchuk 2002; Poulter *et al.* 2009; Huxham *et al.* 2010; He *et al.* 2012). Facilitative effects should be stronger for larger plants, which can shade much more area than smaller ones. This is confirmed by the studies of Bertness and collaborators who found that large nurse plants imposed a stronger facilitative effect than conspecific seedlings. They also found turf morphology of plants (*Juncus gerardii*) were more facilitative than other species (Bertness & Yeh 1994; Hacker & Bertness 1999). While this above-ground mechanism for alleviating a below-ground stressor would be likely reciprocal, we suggest, similar to the shading effect under drought stress that was discussed above, this mechanism could be partly asymmetric instead of symmetric. This is because facilitative effects may be not proportional to plant size in some scenarios, e.g., in the case of a large plant shading the substrate, a small plant growing beneath may contribute to the stress alleviation.

However, a second mechanism exists by which plants alleviate salt stress which is prone to be size-symmetric. Namely, salt may be actively taken up by a benefactor and thus neighbours of such a plant are exposed to lower salt concentrations (Chapter 2, 3). There were also signs for reciprocity between different species in salt marshes (Bertness & Hacker 1994; Bertness & Ewanchuk 2002), even though these authors mainly capitalized on shading as the main mechanism. The salt uptake would be proportional to plant size because larger plants may be able to hold more salt. We conclude this below-ground mechanism tends to be symmetric.

In summary, both reciprocal interspecific facilitation and intraspecific facilitation have been found under salt stress (Table 1). We thus expect facilitation may be reciprocal. However, the degree of symmetry may depend on whether the stress amelioration is mainly mediated below-ground (symmetric) or above-ground (partly asymmetric) mechanism.

F. Heat (36 cases)

In semi-arid and arid habitats or cobble beaches, plants can ameliorate heat stress and protect neighbors from lethal soil temperature by shading (Bertness & Leonard 1997; Shumway 2000; Saccone *et al.* 2009; Caldeira *et al.* 2014). For instance, Good *et al.* (2014) also reported that perennial grasses could greatly decrease soil temperature ameliorating heat stress (30-40 °C to 15-25 °C) and increased survival of *Eucalyptus coolabah* seedlings. Heat and drought stress are often related and corresponding mechanisms are the same, i.e., shading. Similar to drought stress, intraspecific facilitation has also been reported in even-aged populations under heat stress. Goldenheim *et al.* (2008) found dense stands of *Suaeda linearis* can decrease soil temperature by 3–6°C on the shore and facilitate conspecific neighbours. Intriguingly, they found only soil temperature was reduced but soil moisture was generally unaffected. As the shading effect we discussed in drought stress, we suggest this mechanism in heat stress is also reciprocal and partly asymmetric.

G. Wind (28 cases) snow cover (1 case)

Larger neighbors can protect plants from direct physical damage of wind such as chafing tissues with blowing snow, ice, sand or other particulates in the air, battering leaves and branches or even uprooting (Callaway 1998b; Choler *et al.* 2001). For example, Arroyo *et al.* (2003) reported alpine cushions *Azorella monantha* could reduce wind velocity by 89% thus protecting plants within them. The mechanism of protection from winter snow is similar (Cavieres & Penaloza 2012). As what we have discussed for radiation stress, the mechanism under wind stress is also prone to be unidirectional because a small plant cannot shelter its neighbours. Actually, the idea that facilitation in wind is size-dependent been tested. In the Kola Peninsula, northwestern Russia, Eränen and Kozlov (2008) investigated the effects of both conspecific adults and seedlings (mountain birch *Betula pubescens*) in northwestern Russia, where plants are stressed by strong wind. They concluded that facilitation might dominate when the benefactor is substantially larger than the beneficiary (adult-seedling), while the facilitative effects were very weak when the plants were of similar size cannot protect each other (seedling-seedling). Also, this mechanism was only found to occur in interspecific cases and adult-seedling systems. We therefore expect it should be unidirectional instead of reciprocal.

H. Chill (27)

In alpine and arctic areas, surrounding vegetation may provide a warmer micro-environment by reducing conductive heat loss from substrate surface through creating a boundary layer and increasing net-incoming radiation at the large scale due to the lower albedo for ground covered by plants (Charney *et al.* 1975). For example, the macrolichen *Usnea antarctica* can act as nurse species to Antarctic flora in King George Island and increase soil temperature approximately 100% higher than bare ground (Molina-Montenegro *et al.* 2013). Guo *et al.* (2013) found salt marsh plants may protect black mangroves seedlings from fatal coldness (-5 °C) by creating a boundary layer of warmer temperatures. The facilitative effect (increased temperature) may depend largely on coverage of plants, e.g., dense vegetation should impose a stronger positive effect than sparse vegetation and a larger plant can cover more area. Then the strength of facilitation may be proportional to plant size. Besides, facilitation under chill can occur in even-aged populations (Chu *et al.* 2008). Consequently, we argue that this mechanism could be reciprocal and symmetric.

I. Waterlogging (22 cases)

In freshwater marshes and wetlands, anoxic soil caused by waterlogging often inhibits growth of plants. We found two main mechanisms in plants responding to this stress, namely, oxygen leakage (15 cases) and ground elevation (7 cases).

For plants in wetlands, transportation of gases from leaves to submerged roots is considered to be an important process and the oxygen may leak form roots and oxygenate soil in the rhizosphere (Callaway & King 1996). In the Sanjiang Plain, the largest freshwater marsh in China, Luo *et al*. (2010) reported the intraspecific facilitation in marsh species *Carex lasiocarpa* and *Deyeuxia angustifolia* via oxygen leakage. This below-ground mechanism is likely to be reciprocal and size-symmetric, if a larger plant could deliver more oxygen to below-ground tissues.

The other mechanism is ground elevation, e.g., raised rings created by facilitator plants and trapping effect in mangroves due to their complex root structure (Fogel *et al.* 2004; Wang *et al.* 2011). For example, in Puttalam Lagoon of Sri Lanka, Kumara *et al.* (2010) found surface elevation accretion was greater for mangrove *Rhizophora mucronata* at higher densities. The elevated ground level should be positively related to plant size because the size and/or number of roots might determine the amount of sediment they can trap. As a result, we suggest that this mechanism is also symmetric.

We conclude that facilitation under waterlogging stress should be reciprocal and symmetric because they are prone to be proportional to plant size (aerenchyma and roots). In fact, both below-ground mechanisms have been reported in even-aged populations. However, the first mechanism, leak oxygen is highly species-specific. Namely, plants may not be able to act as benefactors without the special aerenchyma, irrespective of their size.

J. Substrate mobility (16 cases) and burial (6 cases)

In sand dunes of deserts and beaches, plants are usually stressed by unstable substrate such as sand or cobbles. Vegetation in these scenarios can stabilize substrate by the presence of their physical structure, e.g., roots and dense assemblage (Bruno 2000; Bruno & Kennedy 2000; Zhao *et al.* 2007; Irving & Bertness 2009). Because physical structures of any species can stabilize the soil, this mechanism seems not to be species-specific. For example, Franks (2003) found survival of *Uniola paniculata* and *Iva imbricata* were enhanced by their neighbors and the facilitation was independent of neighbor identity (conspecific or heterospecific neighbors). The substrate stabilization should be proportional to the size of plants, i.e., the size or number of roots may determine how much area plants can stabilize and the strength of stabilization. Therefore, we conclude this mechanism is reciprocal and likely to be symmetric.

Burial disturbance and substrate instability often come up together in sand dunes of deserts. The stabilized substrate and reduced extremes in sand movement could also prevent the occurrence of burial. But if burial cannot be avoided, surrounding plants could share the weight of sand or sediment thus create a relatively benign micro-environment. Franks and Peterson (2003) used shoveling sand to mimic burial and found plants appeared to protect each other from the weight of the sand, and they had significantly greater survival and biomass when growing with more neighbours. This mechanism is more complicated than substrate stabilization, e.g., when growing beneath a large individual, roots small plants may still stabilize soil and contribute to the stress alleviation, but only the large plant can protect neighbours from heavy sediment while smaller plants could not share the weight. Considering this mechanism has not been reported for intraspecific facilitation, we suggest facilitation under such stress is more prone to be unidirectional.

K. Wave (4 cases)

The survival and growth of species in marine and coastal community or floodplain are often limited by the wave and flooding disturbance. Plants can alleviate the stress by reducing the velocity of waves through their physical structures. For instance, Bos and van Katwijk (2007) found high density of eelgrass *Zostera marina* can increase the survival rate, particularly at locations with high exposure to wave. They also reported the mechanism should be reduced drag force of wave due to the presence of neighbours. The positive effect is very likely to be proportional to plant size which could determine the strength of physical protection, e.g., a larger leaf may reduce drag force more efficiently. We hypothesize that the mechanism is reciprocal and more prone to be symmetric.

L. Soil contamination (2 cases)

In spite of the fact that some studies were conducted in polluted areas, the effects of pollution were usually not significant especially when compared to the strong natural environmental gradients. Consequently, pollution is usually neglected in analyses of plant-plant interactions (Zvereva & Kozlov 2007; Eränen & Kozlov 2009). There was also the situation that neighboring plants can even amplify the stress by trapping pollutants (Eränen & Kozlov 2007; Domínguez *et al.* 2015). Actually, we could only find two instances about the effects of facilitation in contaminated areas. For example, Frerot *et al.* (2006) reported the phytostabilization by metallicolous grasses. They found the grasses greatly enhanced the regeneration of legumes *Anthyllis vulneraria*. This mechanism, phytoremediation (e.g., phytostabilization and phytoextraction), might positively relate to plant size because a large plant may uptake and stabilize more metal. We conclude this below-ground mechanism is like to be symmetric.

3.4 Conclusion

Overall, our review indicates reciprocal intraspecific facilitation - though less frequently studied- is actually ubiquitous. It has been detected in major biomes (arctic/alpine, coastal/marine, freshwater wetland, grassland/savanna and forest/woodland), all climate zones (tropical, arid, temperate, Mediterranean, snow and polar), and across a range of stress factors (wave, heat, chill, drought, waterlogging, substrate mobility, salinity and nutrient deficiency). Therefore, this may imply the potential effects of intraspecific facilitation could be largely underestimated. These intraspecific studies are also important for enlightening and completing our theories based solely on resource competition.

Another major finding of our reviews is that symmetric facilitation seems more likely for below-ground interactions than above-ground (Table 1). However, we only discussed main facilitation mechanisms under certain stress. As we have mentioned above (session 3.3), some stress factors are closely related and different modes of facilitation may occur simultaneously in some scenarios. For example, intensive radiation could also increase soil temperature and evaporation, thus inducing or enhancing heat, drought or even salinity stress (Bertness *et al.* 1999). Protection from radiation should be typically unidirectional and asymmetric, but facilitation under other stress is more prone to be reciprocal and symmetric. In addition, plants in nature may be inhibited by multiple stress factors, e.g., alpine plants may be stressed by both strong wind (asymmetric), chill (symmetric) and/or nutrient availability (Cavieres & Sierra-Almeida 2012; Schöb *et al.* 2013). Therefore, there may be a more continuous method for understanding reciprocity and symmetry of facilitation, which is analogous to competition for different types of resources (e.g., light and nutrients). Namely, we can place facilitation along a continuum ranging from completely asymmetric (unidirectional facilitation) to completely symmetric (benefactor and beneficiary receive the same benefit from each other), with wind, radiation, burial, *etc.* at the asymmetric end while salinity, waterlogging, chill, *etc.* at the symmetric end (Schwinning & Weiner 1998; Lin *et al.* 2012). This approach might be more appropriate and quantitative for exploring and explaining how different types of facilitation may affect populations and communities, especially when plants are limited by different types of stress.

Reciprocal interspecific facilitation was detected much less than we expected, but this should be caused by focusing only on unidirectional interactions, which is a characteristic for most facilitation research. This is also confirmed in the results of reviewed mechanisms, which indicate we can expect reciprocity in most types of facilitative interactions. Namely, most facilitation at the symmetric end of the continuum, such as salinity, wave, soil contamination, waterlogging, *etc*., should be ideal for studying the reciprocity of positive interactions. Moreover, considering that plants in nature may suffer from multiple stress factors, different species may facilitate each though the ‘complementary’ mechanisms. For example, Frerot *et al.* (2006) found the metallicolous grasses (*Festuca arvernensis* and *Koeleria vallesiana*) in the abandoned polluted field greatly enhanced the regeneration of legume *Anthyllis vulneraria* via phytoremediation, while the legume improved soil nutrients for nutrients. Although this study was not strictly designed for detecting reciprocal facilitation, it indeed indicates these species may benefit each other, albeit via different mechanisms. Therefore, reciprocal facilitation is highly likely much more common than we have found.

Our review also indicates that in order to study reciprocal interactions, an intraspecific setting are also the method of choice. This is also supported by the fact that in the few cases where interspecific reciprocity was found, intraspecific facilitation among even-aged plants was detected as well. Thus, evidence for intraspecific facilitation, especially among even-aged plants, could be indicative for the general reciprocity of facilitation. We therefore advocate more intraspecific studies, not only when it comes to the question of reciprocity or size-symmetry but also for studying general mechanisms of positive interactions. This is because interspecific studies are always automatically confounded with the identity of the component species, e.g., species identity will be confounded with the focal trait we want to explore (Donovan & Richards 2000; Liancourt *et al.* 2005). Furthermore, experiments are dearly needed that study reciprocal positive interactions and that are designed to separate competitive and facilitative interactions. This could be done along a gradient of stress that is experimentally created to have control over the relative importance of facilitation vs. competition. Such experiments could also inform us about the generality of the stress gradient hypothesis (Bertness & Callaway 1994) in a much better manner than interspecific studies that are done in the field.

In summary, by reviewing intraspecific facilitation in various habitats and analyzing facilitation mechanisms, we build a conceptual framework regarding the reciprocity and size-symmetry of facilitation. We hope it could inspire future studies for exploring reciprocity of facilitation and lay the foundation for evaluating the consequences of facilitation at the population-level - both have been rarely investigated.

Chapter 3

Intraspecific facilitation: responses and effects of conspecific genotypes with different stress tolerance

Abstract

Positive interactions among plants often coincide with competitive interactions, and the importance of the resulting net-effects on survival and growth have been intensively studied in the past decades. In contrast to competition, facilitation research is dominated by an interspecific perspective. However, focus on interspecific interactions may have led to the multiple confounding of stress factors and species traits in existing field studies. Here, we present a novel approach to facilitation research whereby we use an intraspecific setting with genetically-defined plants to test a set of qualitative key predictions related to net plant-plant interactions at different stress levels. Using even-aged conspecifics with genetically defined stress tolerance (salt-sensitive mutants of *Arabidopsis thaliana vs.* relatively tolerant wildtypes), we tested for the trait-dependence of facilitative effect and response, looked at genetically-based trade-offs between stress tolerance and competitive ability, and derived data for predicting how net plant-plant interactions change along stress gradients. There was unequivocal and strong evidence for a shift from negative to positive interactions along a salinity gradient for all plant types and all response variables. In agreement with life-histroy theory, salt-sensitive genotypes exhibited a larger competitive ability and a stronger facilitative response than salt-tolerant genotypes. However, perhaps surprisingly, sensitive genotypes also imposed consistently stronger facilitative effects despite being smaller under high salinity. This indicates a novel 'suicidal' facilitation mechanism mediated via increased salt uptake from the soil. Our overall findings demonstrate that an intraspecific and genetically-controlled

setting is highly useful for generating predictions about trait specificity of interactions and changes of interactions along environmental gradients. We strongly advocate the use of similar approaches to inspire progress in quantitative theory and the mechanisms involved in facilitation research.

Introduction

Competition and environmental stress are two essential factors that may limit the performance of plants and determine both individual adaptations as well as distribution patterns (Grime 1977; Tilman 2009). Regarding competition, ecologists have proposed many theories to understand and predict distribution and abundance patterns of plant species such as niche theory (Hutchinson 1957), coexistence mechanisms and the Lotka-Volterra model (Bomze 1983), as well as population regulation via density-dependence (Hassell 1975). In the past two decades, an increasing number of studies demonstrated that not only competition but also facilitation, i.e. positive plant-plant interactions, are very common in plant communities, with facilitation especially important in stressful environments (Brooker *et al.* 2008). With the increasing popularity of facilitation research, a number of hypotheses have been developed to predict under which conditions facilitation would dominate over competition. The most popular of these concepts is the so-called Stress-Gradient-Hypothesis (SGH, Bertness & Callaway 1994), which states that the relative frequency and magnitude of plant interactions will shift from competition to facilitation along a gradient from benign to harsh conditions (including both stress and disturbance).

However, one prominent difference between competition and facilitation research is that the latter has been dominated by an interspecific perspective (McIntire & Fajardo 2014; Soliveres *et al.* 2015), i.e. most studies were conducted between pairs or more species that differ largely in their morphology and/or physiology. Namely, a classical species pair would be a large benefactor (e.g. a shrubs, trees or cushion plant) that ameliorates habitat conditions for a smaller herbaceous plant (Callaway 1995; Callaway 2007). This evokes the idea that facilitation is mostly asymmetric and unidirectional (i.e. from benefactor to beneficiary), and has come to dominate the literature. For these reasons, rarely has facilitation at the intraspecific level been considered worthy of testing.

There have been some empirical studies reporting intraspecific facilitation in nature (Chu *et al.* 2008; Goldenheim *et al.* 2008; Fajardo & McIntire 2011) and some development of the possibility, but in a very limited theoretical framework compared to interspecific facilitation. This is regrettable, because we can learn a lot from an intraspecific perspective. In fact, a main conceptual advancement in studies of competition stems from intraspecific competition, which has been crucial for explaining key ecological processes such as population dynamics and self-thinning (Weller 1987; Enquist *et al.* 1998; Li *et al.* 2013), the symmetry and reciprocity of competition (Weiner 1990; Weiner *et al.* 2001), or coexistence mechanisms (Chesson 2000; Adler et al. 2007; Kraft et al. 2015). Compared to the theoretical advancement in studies of competition, we have very little theory at hand that may predict how facilitation affects population or community dynamics (Michalet *et al.* 2006; Maestre *et al.* 2009; Malkinson & Tielbörger 2010).

A major disadvantage of interspecific studies is that species identity may be confounded with the factors that determine the very mechanisms we want to study. For example, it has been suggested that the intensity and importance of facilitation are dependent on beneficiaries' traits related to competitive ability and stress-tolerance (Maestre *et al.* 2009). Namely, stress tolerant species are less likely to benefit more from facilitation than species that are less tolerant (Liancourt *et al.* 2005; He *et al.* 2011). It has also been suggested that not only the facilitative response of beneficiaries but also the positive effects of potential benefactors depends on specific traits (Tielbörger & Kadmon 1995; Callaway & King 1996; Dickie *et al.* 2005). For example, the structure of the canopy may determine facilitative effects on understory (Tielbörger & Kadmon 1997; Schöb *et al.* 2013), symbioses with soil organisms may affect facilitative interactions (Dickie *et al.* 2002), or the ability of benefactors to deter herbivores affects their facilitative effect (Bossuyt *et al.* 2005). However, the trait-specificity of facilitative effect and response cannot be unequivocally determined in an interspecific setting, because species rarely differ in only a single trait. Therefore, facilitation is also species-specific (Callaway 1998a; Callaway 2007; Paterno *et al.* 2016) and species identity will always be confounded with effects of the focal trait. On such a level of trait specificity, an intraspecific approach is clearly superior to an interspecific setting because it may disentangle trait effects from species identity.

The idea of trait-specific facilitative effect and response is highly related to a popular idea in life history theory: the trade-off between competitive ability and stress tolerance (following the CSR theory of Grime 1977). For example, traits that can confer tolerance to harsh environmental conditions are usually associated with biological processes requiring extra costs (Smith & Stitt 2007; Munns & Tester 2008; Atkinson & Urwin 2012; Bita & Gerats 2013). Therefore, trade-offs related to resource allocation exist and the ability for competing with neighbors in benign conditions and maintaining metabolic performance in stressful habitats cannot be maximized simultaneously. In fact, plants have evolved distinct adaptive strategies, i.e., in benign conditions, competitive species appear to dominate, while stress tolerating plants have an advantage in harsh environments (Yoshida *et al.* 2004; Pierce *et al.* 2013; Pierce *et al.* 2016). However, this theory stems mostly from community ecology, and experimental tests of this evolutionary trade-off under genetic control are virtually missing. For example, the genetic resources (e.g., mutants vs. wildtypes) that are available for certain model species have been underutilized in ecological studies, though using plants with clearly genetically defined traits could separate competitive ability and stress tolerance from multiple confounding effects. *Vice-versa*, ecological theory has only very recently started to inspire studies in molecular biology. For example, with respect to the tolerance-competition trade-off, we could, by using very broad search criteria, detect only a single genetically-controlled study that used wild type *Arabidopsis thaliana* vs. transgenic genotypes (Cipollini 2007). However, this study did not yield much support for the competition-tolerance trade-off, i.e. the stress tolerant genotype did not exhibit higher competitive ability. The lack of studies may be attributable to the fact that molecular biologists are interested in mechanisms of tolerance (Munns & Tester 2008; Hasanuzzaman *et al.* 2013) but less so in their ecological and evolutionary consequences. Therefore, to combine these strengths of approach and fill this knowledge gap, in the current study we used salt tolerant and non-tolerant genotypes of *Arabidopsis thaliana* to investigate the competition-tolerance trade off and to further discover whether these two traits are related to both facilitative response and effect along stress gradients.

Unlike in competition studies, the differentiation between facilitative effect and response is another unexplored field in facilitation research. Borrowing the concept of response and effect in competition (Miller & Werner 1987; Goldberg 1996; Wang *et al.* 2010), we define the facilitative response as the positive response of the target plant to the presence of neighbours, and facilitative effect as the ability of a plant to ameliorate habitat conditions for potential beneficiaries, respectively. Thus, if we apply the above concepts from community-level studies (Liancourt *et al.* 2005; He *et al.* 2012) to an intraspecific level, tolerant genotypes deviate less from their optimum than non-tolerant ones in severe environments, and we expect them to respond less to facilitation than stress-sensitive plants. When looking at facilitative effects, we would expect that tolerant plants will exert larger positive effects on beneficiaries under stress, simply because they perform better and are thus able to provide more habitat amelioration than sensitive plants. For example, recent conceptual models (Michalet *et al.* 2006; Malkinson & Tielbörger 2010; Michalet *et al.* 2014) and empirical studies (Forey *et al.* 2010; Le Bagousse-Pinguet *et al.* 2012; Maalouf *et al.* 2012) have shown that in very severe habitats, benefactors may be too stressed to protect neighbors. Although the relationship between stress tolerance and facilitative effect ability has not been directly explored, it seems logical to predict that tolerant plants should be more facilitative at high stress. For example, Schöb *et al.* (2013) reported that the facilitative ability of a cushion species was positively related to its size and vigour. Compared to an interspecific approach, an intraspecific setting would also enable us to disentangle focal trait and species-specific effects, and thus look at facilitative effect and response simultaneously.

Intraspecific facilitation has been described relatively rarely, but of the few cases, most focus has been on seedling-nurse systems in which larger adult plants unidirectionally protect intraspecific seedlings (Weltzin & McPherson 1999). However, it is perceivable that similar to competition, facilitation also occurs among similar-sized individuals, e.g. in even-aged populations or cohorts, through mechanisms that apply irrespective of size-asymmetry (symmetric facilitation, Lin *et al.* 2012, chapter 2). In such a case, each individual would be both benefactor and beneficiary and response and effect can be studied simultaneously. However, reciprocity of facilitation is probably not ubiquitous across all types of stress factors, and thus the stressor needs to be selected with care. In the current study, we used salt stress, because salinity is a clear, quantitative stress factor limiting growth of all plants, and some level of salt tolerance is a relatively common trait in plants. More importantly, mechanisms of facilitation under salt stress, such as shading of neighboring plants that reduce evaporation have been well studied (Bertness 1991; Bertness & Shumway 1993; Bertness & Leonard 1997; He *et al.* 2011). This mechanism does not require size-asymmetry, i.e. it also works among small plants of similar size (Bertness & Yeh 1994) and is thus ideal for an intraspecific setting.

In this study, we used a greenhouse experiment with genotypes of *Arabidopsis thaliana* differing only in salt tolerance to provide a largely unconfounded test of ecological and evolutionary theories related to plant-plant interactions along stress gradients. We predicted on a population level that 1) the Stress-Gradient-Hypothesis applies to an intraspecific and even-aged setting, i.e. intraspecific facilitation dominates at the saline end of a salinity gradient while competition prevails at the benign end. On an individual level, we predicted that there is a trade-off between stress tolerance and competitive ability that would lead to the following patterns: 2a) sensitive genotypes profit more from facilitation by neighbours than tolerant genotypes, while they may respond less negatively to the presence of neighbours in benign conditions; and 2b) tolerant plants exert a larger facilitative effect in stressful environments than sensitive plants.

Methods

Study species

Our study species was *Arabidopsis thaliana*, an annual plant with small size, short life cycle (about 6 weeks), prolific seed production (several thousand seeds), a small genome and copious mutant lines. These characters have made this species a very popular model organism in plant biology. *A. thaliana* was also chosen because the genetic basis of salt tolerance mechanism has been well investigated in this species. For example, in *A. thaliana*, the SOS1 SOS2 and SOS3 (SOS: salt overly sensitive) genes are essential for intracellular Na^+ and K^+ homeostasis and tolerance to high Na^+ environments (Wu *et al.* 1996; Halfter *et al.* 2000). We used six genotypes for our experiment, three of which were from wildtypes with moderate salt tolerance and three were mutants derived from wildtypes that were highly sensitive to salt. Specifically, these non-tolerant genotypes (sos1-1, sos2-1, and sos3-1) are three genotypes from salt sensitive mutant lines with a mutation at the sos1, sos2 and sos3 loci, respectively. For tolerant lines, we selected three genotypes (Col/gl1, Col-5/gl1, and Col-6/gl1) from background wildtypes (Col/gl; stand for Columbia/ glabrous), which were also the parental ecotypes of SOS mutants (Wu *et al.* 1996; Chan *et al.* 2011). Under control conditions, the salt sensitive SOS-mutants exhibit no phenotypic differences to the wild types (Wu et al. 1996). All six genotypes were bought from Nottingham Arabidopsis Stock Centre (NASC, http://www.arabidopsis.info) and these genotypes were raised for one generation in the same greenhouse to obtain enough seeds before starting the experiment and to ensure all seeds have the same maternal history.

Experimental design

Previous studies have shown that contradictory results about SGH may due to the unverified gradient lengths, i.e., stress gradients were not ‘real’ and plants’ performance may not actually decrease along the gradients (Lortie & Callaway 2006; Eränen & Kozlov 2008). Also, the stress could be too low for differentiating between tolerant and sensitive genotypes. Therefore, we carried out a pilot study prior to the start of the full experiment to determine the appropriate stress levels. In the pilot study, *A. thaliana* were grown alone or with a neighbor in each pot, and targets and neighbours were paired in a fully factorial manner, i.e., solitary tolerant *vs*. tolerant-sensitive, solitary sensitive vs. sensitive- tolerant. Plants were watered with 0, 25, 50, 75 and 100 mM NaCl solution for ca. 6 weeks and there were 5 replicates for each pair in each salt treatment. Based on the results of that pilot, we selected three salt levels for the final experiment: no salt (control), 50 mM NaCl (visible growth reduction but mortality of wildtypes and mutants was similar) and 100 mM NaCl (mortality of mutants was higher).

In our experiment, there was one target genotype in each pot, grown either with two neighbors or without neighbors. The two neighbors always had the same genotype and maternal sibship. Each salt treatment included the fully-factorial combination of genotypes, with all 6 genotypes grown individually (target genotype - without neighbours, replicated 12 times) and each target genotype grown with the 6 possible neighbor identities (with neighbors, replicated 6 times) (see Fig. S1 for experimental design). The higher number of replicates for the “without neighbor” pots was chosen because the pilot study indicated higher mortality of plants growing alone. In total, the design yielded 36 (genotype combinations) × 6 (replicates) ×3 (salt levels) + 6 (single genotypes) × 12 (replicates) ×3 (salt levels) = 864 pots with 2160 plants. The experiment was set up in a roof-top greenhouse at Tübingen University, Germany, and lasted for almost 2 months (full lifespan of *A. thaliana*) from March to May, 2015. Day temperatures ranged from 20 ˚C to 35˚C during the experiment.

The detailed experimental process was as follows: Seeds were firstly washed with 70% ethanol for 2 minutes for sterilization and then were put in petri dishes and stratified at 4°C for 5 days in a refrigerator to break dormancy and induce synchronous germination (Grozinger et al. 2001). The stratified seeds were then transferred to pots (10×10×10cm) filled with potting soil (Einheitserde Classic, Gebr. Patzer Company). The location of pots with different treatments was fully randomized and the distance between pots was approx. 2cm. 4-6 seeds were sown for each target genotype and its neighbors at predefined locations in each pot (middle for target, opposite corners for neighbours) to ensure that we will obtain at least one seedling per target and neighbour. We also sowed the 6 genotypes (5-6 seeds for each genotype) to 30 additional pots as backup for failure of germination in the experimental pots. Seeds were kept moist during the germination period by spraying the soil surface. Most seeds germinated simultaneously within the first four days after sowing, i.e., the synchronization via stratification was successful. The experimental plants were selected at random and thinned three days after germination to leave one target, and where needed, two respective neighbor plants. After the removal, spare seedlings were transplanted from backup pots into pots without germination (62 plants). Based on our experience from the pilot study, the salt treatment was started ten days after germination; before that we kept soil moist by spraying. During the salt treatment application, pots were watered with solutions containing 0 mM NaCl, 50 mM NaCl, or 100 mM NaCl every 5-7 days. Each pot received the same amount of solution at each irrigation event, and this amount was increased with plant growth from 50ml at the start to 150ml by the end of the experiment. At the end of May 2015, we counted surviving individuals and for each surviving target, we determined the number of siliques per plant. The above-ground parts of target plants were then harvested, dried at 70 ℃for

24h and weighed. Salt treatments strongly decreased the lifespan of plants. Therefore, plants that died before harvest but produced seeds were also counted, weighed and included in the analysis as survived. Pots in which all neighbours died were excluded from the analyses (35 pots).

Data analysis

In order to test our hypotheses, we analyzed the data from different angles and by using different subsets. To test the differential response of plant tolerance and genotype to salt stress, we used the no-neighbour treatment only. Here, we tested whether non-tolerant types responded more negatively to salt stress than tolerant ones in the three response variables: survival (including plants survived until the end of experiment or plants that died before harvest but produced seeds), fecundity (number of siliques per plant, including dead plants with zero fecundity) and above-ground biomass. Generalized Linear Mixed Models (GLMM) were used for this test, and performed in R (R-project. 2016), using package ‘lme4’ (Bates *et al.* 2015). For survival a binomial distribution with logit link function was used; for fecundity Poisson distribution was used. For each GLMM the fixed factors tested were salt concentration, neighbour tolerance and target toleracne; and the random factors were neighbour genotype (nested within neighbour tolerance) and target genotype (nested within target tolerance). We used the corrected Akaike Information Criterion (AICc) for comparing all nested mixed models (Burnham & Anderson 2004).

To test the SGH and evaluate differential responses and neighbor effects of genotypes differing with tolerance under varying levels of salt stress, we used the full dataset to calculate the relative interaction index (RII), i.e. the relative change in performance when grown with *vs.* without neighbours (Armas *et al.* 2004):

$$RII = \frac{P_{W} - P_{S}}{P_{W} + P_{S}}$$

Where P_W is the performance of target plants with neighbors and P_S is the performance of single plants without neighbors. RII ranges from -1 to 1 with negative values indicating competition and positive values representing net facilitative interactions.

RII was calculated for survival, fecundity and biomass and data was averaged per genotype in each treatment combination (stress–neighbour–tolerance, including single plants) before RII calculation and statistical analyses (Al Hayek *et al.* 2015). We fitted Linear Mixed Models (LMM) for RIIs with the fixed factors salt concentration, neighbour tolerance and target tolerance. Significance of each fixed factor was assessed with a Wald *F-test* on the full models. . The statistical analysis was performed in package 'nlme' (Pinheiro *et al.* 2016). Student's t-test was used to check whether RII values were different from zero (i.e. no net neighbour effect).

Results

All performance measures decreased with increasing salt stress as indicated by the representation of salt stress (S) in all best models. Sensitive plants performed generally worse than tolerant plants, particularly at the stressful end (Table 1 and Fig. 1). The decrease in performance with increasing stress was stronger for sensitive plants in survival (significant target tolerance x salinity interaction), but not for biomass.

Table 1 Summary of AICc models and AICc differences for survival, fecundity and biomass of single plants (*Arabidopsis thaliana*) grown in benign (no salt), intermediate (50mM NaCl) and high salt stress (100mM NaCl) without conspecific neighbors. Plants were either non-tolerant genotypes or tolerant genotypes. Here we only displayed the best models and some related models. S = Salt Treatment; T= Target Tolerance; G = Target Genotype. Models with the lowest AICc value stand for the best model fitting the data and Δ AICc stands for differences in AICc (best models and values are in bold).

Plant Performance	Models	AICc	Δ AICc
Survival	T + G	219	43.3
	S + S × T + T + G	179.1	3.4
	S + S × T	**175.7**	**0**
Fecundity	S	2874	38.9
	S + G	2848.3	13.2
	S + S × T + G	**2835.1**	**0**
Biomass	S	-537.3	4.7
	T	-410.2	131.8
	S + T	**-542**	**0**

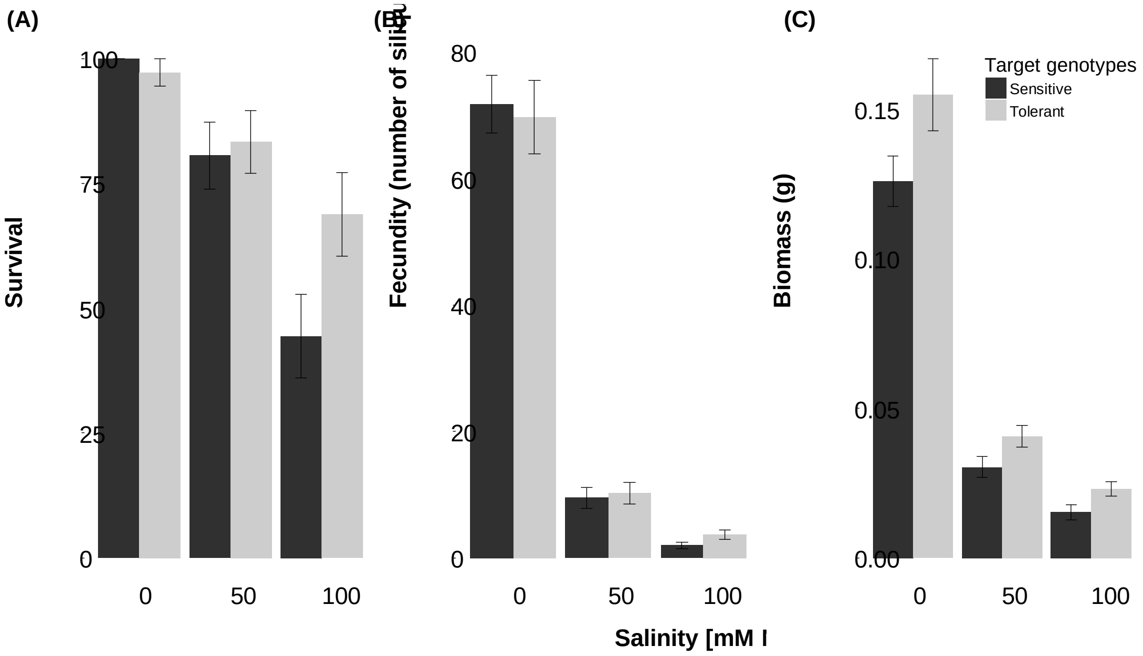

Figure 1 Survival (A), fecundity (B) and biomass (C) of single plants (*Arabidopsis thaliana*) in three salt treatments (Mean ±SE). Plants were either sensitive mutant genotypes (black bars) or relatively tolerant wild types (grey bars) and they were grown in benign (water), intermediate (50mM NaCl) and high salt stress (100mM NaCl) without conspecific neighbors.

Neighbour effects changed clearly and sequentially from negative to positive along the salt stress gradient for all performance measures (Figure 2), as indicated also by a significant effect of salt levels on all RIIs (Table 2). There was also a significant interaction between salt treatment and target tolerance for all performance measures (Table 2). This reflected the fact that the trend of increasingly positive interactions along the gradient was stronger for sensitive plants. Overall, sensitive plants seemed to be less negatively affected by neighbours, i.e. net interactions were either less negative at the benign end or more positive at the stressful end (Fig. 2). In general, facilitative interactions were much stronger for survival and fecundity than for growth, where negative to neutral interactions prevailed.

Table 2. Summary of linear mixed models for testing effects of salt stress, target tolerance, neighbour tolerance and their interactions on survival, fecundity and biomass of *Arabidopsis thaliana*. Plants were grown with or without conspecific neighbors in benign (water), intermediate (50mM NaCl) and high salt stress (100mM NaCl).

Target/Neighbor plants were either salt-sensitive mutants or tolerant wild types. P-values < 0.05 are reported in bold.

	RII for Survival			**RII for fecundity**			**RII for Biomass**		
Factors	**d.f./d.f.**	***F***	***P***	**d.f./d.f.**	***F***	***P***	**d.f./d.f.**	***F***	***P***
Salt	2/63	79.47	**<0.001**	2/63	131.27	**<0.001**	2/61	30.07	**<0.001**
Target Tolerance (TT)	1/4	5.39	0.08	1/4	3.34	0.14	1/4	0.14	0.73
Neighbor Tolerance (NT)	1/29	4.87	**0.04**	1/29	1.22	0.28	1/28	0.76	0.39
Salt × TT	2/63	8.17	**<0.001**	2/63	12.4	**<0.001**	2/61	8.23	**<0.001**
Salt × NT	2/63	0.04	0.97	2/63	0.28	0.76	2/61	0	1
TT × NT	1/29	0.04	0.84	1/29	0.65	0.43	1/28	0.53	0.47
Salt × TT × NT	2/63	0.12	0.89	2/63	1.71	0.19	2/61	1.41	0.25

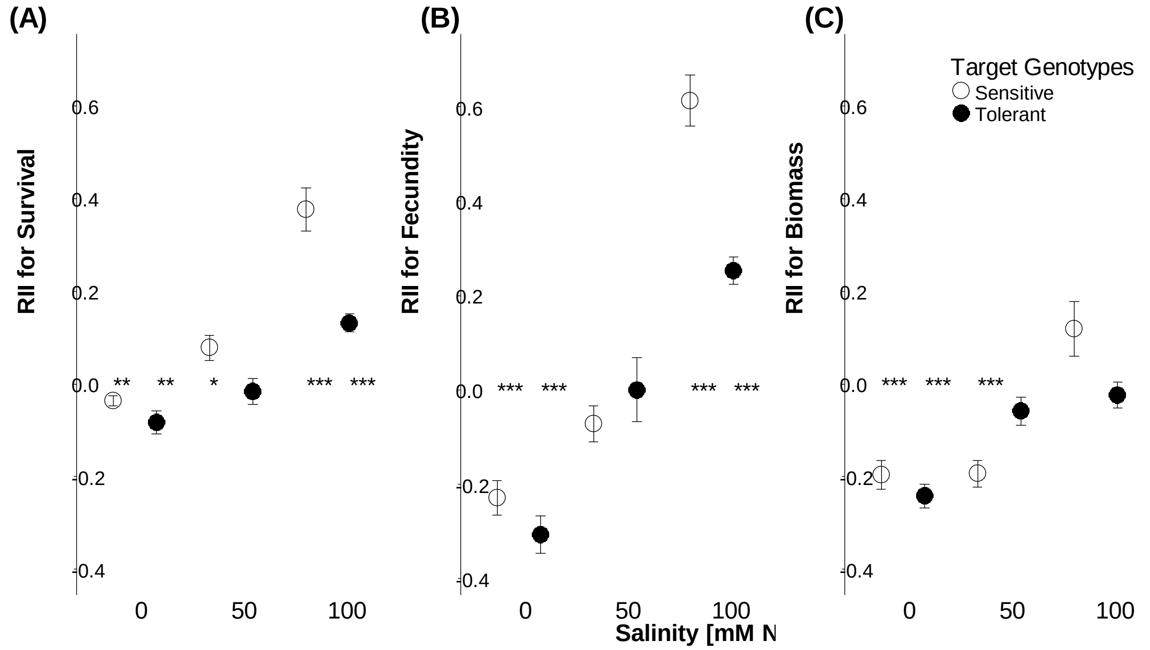

Figure. 2 Responses (Mean ±SE) of tolerant and sensitive genotypes (*Arabidopsis thaliana*) to neighbours based on the Relative Interaction Index (RII) for survival (A), fecundity (B) and above-ground biomass (C). Plants were grown with or without conspecific neighbors in benign (water), intermediate (50mM NaCl) and high salt stress (100mM NaCl). Target/Neighbor plants were either salt-sensitive mutants or tolerant wild types. Asterisks near x-axis indicate that the index is significantly different from zero. Levels of significance: *P < 0.05, **P < 0.01, ***P < 0.001.

The facilitative effects of neighbours increased with stress, and there was no strong difference between tolerance types in their effect on targets (Table 2). However, there was a trend towards stronger facilitative effects of non-tolerant plants for all performance measures and at all salinity levels (Fig. 3), and these stronger facilitative effects were significant for survival (Table. 2). Similar to the target response, the largest facilitative effects were observed for survival and fecundity, while biomass was not affected.

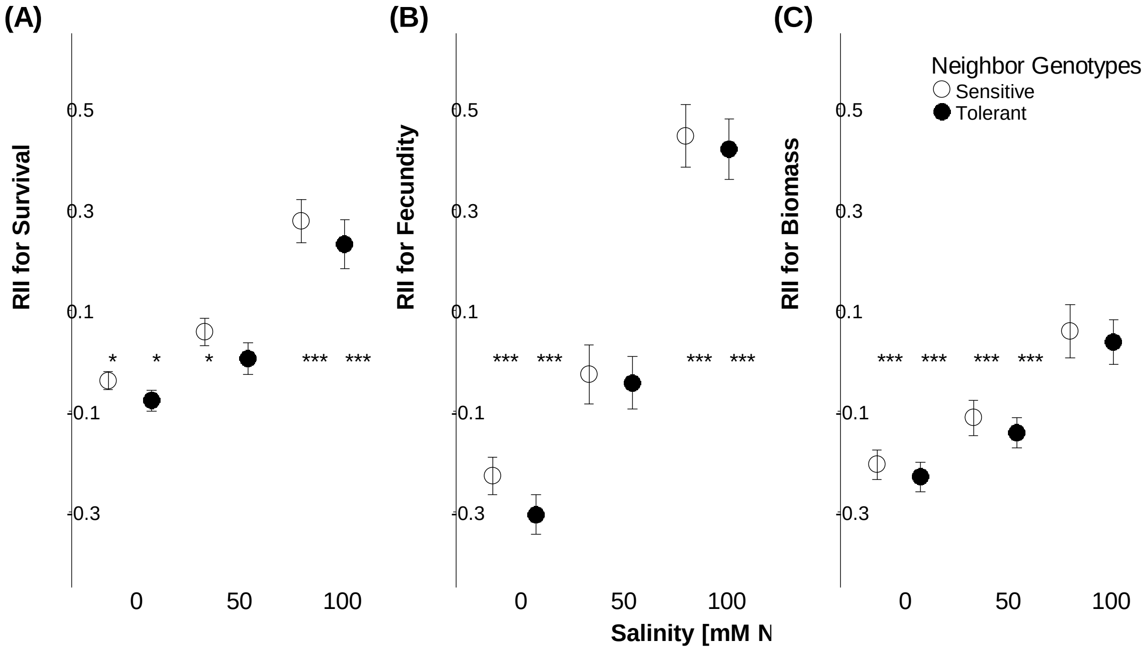

Figure. 3 Effects (Mean ±SE) of tolerant and sensitive genotypes of *Arabidopsis thaliana* based on Relative Interaction Index (RII) for survival (A), fecundity (B) and above-ground biomass (C). Plants were grown with or without conspecific neighbors in benign (water), intermediate (50mM NaCl) and high salt stress (100mM NaCl). Target/Neighbor plants were either sensitive mutants or tolerant wild types. Asterisks near x-axis indicate that the index is significantly different from zero. Levels of significance: *P < 0.05, **P < 0.01, ***P < 0.001.

Discussion

Our overall findings provide very strong support for the stress gradient hypothesis on an intraspecific level. Furthermore, this is the first study showing that life history trade-offs may explain the direction and strength of plant-plant interactions along stress gradients. Namely, differential stress response determined, to a large degree, the net outcome of competitive and facilitative interactions. In the following, we discuss our findings with respect to the initial hypotheses.

The stress gradient hypothesis (Bertness & Callaway 1994; Brooker & Callaghan 1998) predicts that facilitation dominates at the stressful end of an environmental gradient and competition is more important when conditions are benign and environments are productive (Bertness & Callaway 1994). For this hypothesis we found unequivocal support in our study, i.e. the net interactions shifted consistently and sequentially from competition to facilitation with increasing salinity for all response variables and all tolerance types. These results are new for even-aged cohorts of a single species and indicate that the SGH may actually be universally applicable once multiple sources of confounding are removed. Despite its intuitive logic, e.g. the fact that facilitative interactions can only occur when some stress exists, the SGH has so far not found unequivocal support and its general applicability has been strongly questioned (Maestre *et al.* 2009). Though a recent meta-analysis (He *et al.* 2013) indicated that more studies are in favour than against the SGH, there are still many studies that do not confirm or even contradict the idea of increasingly positive interactions with stress (Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Forey *et al.* 2010; Le Bagousse-Pinguet *et al.* 2012; Koyama & Tsuyuzaki 2013). These studies have either found continuously increasing negative interactions with increasing stress (e.g. Tielbörger & Kadmon 2000) or a breakdown of positive interactions at the extreme end of the gradient. One of the explanations put forward for such a unimodal response of facilitation intensity to stress is that at the stressful end, the benefactors themselves are too stressed to exhibit any facilitative effect (Michalet *et al.* 2006; Michalet *et al.* 2014). In these scenarios, benefactors are "too small" to help their neighbors, i.e. often differential size is an inherent assumption in studies of facilitation (e.g. Forey et al. 2010). It is therefore striking that the evidence from our intraspecific even-aged study was unequivocal and applied to all life stages equally despite the fact that our approach deviated from the classical 'large benefactor-small beneficiary' setting. In fact, facilitation among similar-sized conspecifics has been reported rather rarely compared to interspecific cases (Bertness & Yeh 1994; Chu *et al.* 2008; Fajardo & McIntire 2011; Castro *et al.* 2013;

Vogt *et al.* 2014) but interestingly, often in habitats with salt stress (Bertness & Yeh 1994; Castro et al. 2013; Vogt et al. 2014, our study). In these habitats, facilitative interactions are more prone to be size-symmetric and reciprocal (Chapter 2), i.e. future studies focusing on even-aged intraspecific settings should carefully select the stress factor of interest. The strength and ubiquity of facilitation detected in our study is also interesting because theory would predict large niche overlap among conspecifics and thus more intense competition (Connell 1983; Chesson 2000; Kraft *et al.* 2015). Our overall findings could therefore suggest that contradictory evidence for the SGH generated previously (Cavieres *et al.* 2008) may be the result of multiple confounding with species identity (Cavieres *et al.* 2006) or of multiple stress factors along the same spatial or temporal gradients (e.g. Tielbörger & Kadmon 2000).

Though the evidence for the SGH was strong for all response variables, facilitation was much stronger (more than three-fold higher) for survival and fecundity than for biomass. Previous studies have investigated the life-stage dependence of plant-plant interactions and it has been suggested that facilitation would dominate in early life stages, while competition takes over when plants grow taller (Goldberg *et al.* 2001; Schiffers & Tielbörger 2006). This idea has found some support in experiments done with annual plants (Schiffers & Tielbörger 2006), and shrubs (Miriti 2006; Armas & Pugnaire 2009; Alvarez-Yepiz *et al.* 2014). Though our study is compatible with these in that facilitative response was strong in early life stages (i.e. during survival), the variables fecundity and biomass were measured simultaneously. This indicates that under stress, more resources were allocated to reproduction than to growth when neighbours were present. Though stress has been shown to induce seed set in annuals and result in earlier reproduction (Stanton *et al.* 2000; Verhoeven *et al.* 2008), it is surprising that reproductive allocation increased in the presence of neighbours, where more vegetative biomass may infer a competitive advantage. However, in the absence of competitive net interactions at high salinity, this size benefit may be immaterial, especially in annuals which need to invest mainly into reproduction (Grime 1977; Pierce *et al.* 2013). At any rate, our findings indicate that the life stage at which an interaction is studied is of crucial importance for the outcome of net interactions (Schiffers & Tielbörger 2006; le Roux *et al.* 2013).

We also predicted that the two types of plants used in our study would respond differentially to salt stress and that this differential response would determine both their facilitative effect and response. Our initial assumption of differential salt tolerance was, not surprisingly, confirmed in that tolerant plants performed consistently better under high salinity compared to non-tolerant mutant lines (Wu *et al.* 1996; Halfter *et al.* 2000). Because of this, we hypothesized that non-tolerant plants would benefit much more from the presence of neighbours than tolerant plants, and our findings provide very strong support for this hypothesis for all three response variables. The idea that facilitative response of a species should be relative to the deviation from its ecological optimum is not new (Choler *et al.* 2001) but has been formulated for between-species settings. For example, Liancourt *et al.* (2005) found that under water limitation, two competitive grass species showed stronger facilitative response to neighbors than a coexisting drought tolerant species. Other studies that attempted to test this idea confirmed (Wang *et al.* 2008; Liancourt & Tielbörger 2011), but also contradicted (Donovan & Richards 2000) it. These studies again suffered from the fact that they were conducted for multiple species, i.e. the factor ‘stress response’ was confounded with species identity. Thus, our study is the first solid experimental evidence for the effect of stress tolerance alone on the outcome of facilitative interactions.

Interestingly, the observed sensitivity to salt stress was associated with larger competitive response ability, i.e. non-tolerant ecotypes responded less negatively to the presence of neighbours than tolerant plants. Though this could also be the result of stronger facilitation, the fact that competitive response was also smaller without salt stress indicates that there was a trade-off between stress tolerance and competitive ability. This trade-off has been postulated many times previously (Grime 1977; Suding *et al.* 2003; Pennings *et al.* 2005; Maestre *et al.* 2009), but so far, the idea has been pertinent to community ecology and not to proper evolutionary studies. Here, we demonstrate for the first time, by using salt-tolerant wildtypes and their salt-sensitive genetic derivatives that there is a genetically determined and physiologically active trade-off between stress tolerance and competitive ability. The only study designed to test the evolutionary trade-off under strict genetic control used herbivore resistant and sensitive plants of *Arabidopsis thaliana* (Cipollini 2007). However, the author did not find any evidence for a trade-off between competitive ability and defoliation tolerance (Cipollini 2007). This could be the result of methodological differences to our study (e.g. no replication- only one genotype; only one performance measure), but also, defoliation is not the same type of stress as abiotic stress. In our study, the similarity between tolerant and sensitive plants was also almost maximized (i.e. background variance reduced) in that the mutants and wildtypes were genetically similar and they differed in only a single trait of interest- salt tolerance. It is intriguing that these SOS-mutations were consistently associated with larger competitive response ability for all three variables. Thus, our results provided very clear and solid evidence for the trade-off between stress tolerance and competitive ability, one of the most basic paradigms in ecology.

A surprising result of our study was that tolerant plants exerted a weaker facilitative effect on the beneficiaries than sensitive plants. This contradicts our initial hypothesis which was based on the assumption that facilitative effects under salt stress should be positively correlated with size. Namely, a main mechanism by which facilitation under salt stress occurs which has been confirmed by many empirical studies is shading of the soil surface by neighboring plants (Bertness & Shumway 1993; He et al. 2011). Through shading, transpiration of water and thus salinity in the soil is reduced. This mechanism would imply that larger plants, which shade a larger area, should have a larger facilitative effect in severe environments (Bertness & Yeh 1994; Vogt et al. 2014). Therefore, we originally predicted tolerant genotypes to have greater positive effects, because they are able to grow larger than intolerant genotypes at high stress. Interestingly, we found exactly the opposite with non-tolerant plants imposing a consistently stronger facilitative effect on targets than tolerant plants, especially when looking at survival. The fact that we found the opposite pattern cannot be explained by shading, because sensitive plants were indeed considerably smaller than tolerant plants when grown under high salinity. One explanation may be that larger individuals also exert larger competitive effects (Weiner 1990; Goldberg & Landa 1991), i.e. tolerant genotypes could have had larger negative effects on neighbours (Emery *et al.* 2001), resulting in less positive net effects than for sensitive plants. Another explanation could lie in the mechanisms of salt tolerance (see Munns & Tester, 2008, for extensive review). Salt tolerance could be achieved by taking up salt and possessing a mechanism to avoid detrimental effects within the plant, e.g., tolerance of tissue to accumulated Na+ (Garthwaite *et al.* 2005; Munns 2005). Alternatively, tolerant types may be able to exclude salt and are thus not confronted with excessive intracellular salt levels whereas non-tolerant plants accumulate too much salt (Liu & Zhu 1998). Interestingly, in the second case, the facilitative effect could be explained by a larger uptake of salts by the sensitive plants. Considering we actually observed facilitation for survival at an early stage (individuals were not large enough for shading) in pilot and this experiment, this seems to be a highly likely explanation in our case. In fact, in *A. thaliana*, the SOS genes encode a number of proteins (Halfter *et al.* 2000; Shi *et al.* 2000), which in effect lead to a larger accumulation of Na+ under salt stress compared to the wild type (Liu & Zhu 1998). Thus, the larger facilitative effect of the sensitive plants can be explained by the removal of more salts from the soil when compared to the tolerant wildtype. Interestingly, this would imply a novel mechanism by which plants may facilitate each other, because most previous studies have assumed evaporation as the key to understanding positive interactions in saline habitats (Callaway 1995; He *et al.* 2011). In our case, this mechanism is the result of an artificial mutation (Wu *et al.* 1996; Zhu *et al.* 1998). However, it would be interesting to detect in naturally saline or in other systems, e.g. hyperaccumulators of heavy metals, (Zvereva & Kozlov 2007), whether such a 'suicidal' behaviour of a benefactor results in a facilitative effect on beneficiary plants.

To conclude, our study provides a combination of novel aspects that may serve to advance basic theory in facilitation research. By using an intraspecific approach with plants of similar age and genetically defined stress tolerance, we could demonstrate that facilitative response and effect are predictably determined, to a large degree, by stress tolerance. Furthermore, our findings provide new and solid evidence for the existence of a physiologically-based trade-off between competitive ability and stress tolerance. Finally, we could unequivocally support the predictions of the stress-gradient hypothesis. We therefore advocate the utilization of controlled and unconfounded intraspecific settings for advancing our knowledge about mechanisms of plant-plant interactions under varying environmental conditions.

Chapter 4

Density-dependence tips the balance between facilitation and competition along stress gradients

Abstract

Positive plant-plant interactions have usually been studied qualitatively by comparing plant with and without neighbours, and the number of neighbours has been neglected. However, recently, density-dependent effects of facilitation have been found with maximum positive effects of neighbours at intermediate densities. Yet, these findings have not been incorporated into classical theories about how plant-plant interactions will shift with environmental changes. Here, we propose a conceptual model to predict how density-dependence change along stress gradients and how it may alter the balance between facilitation and competition. Using an intraspecific setting with the model species *Arabidopsis thaliana* grown under different densities and salinity levels, we tested our model experimentally. Both of the following model predictions were strongly supported: (1) facilitation peaks at a higher density with increasing stress; (2) the stress-gradient hypothesis (SGH) which predicts the highest intensity of positive interactions under highest stress is only confirmed when densities are high. Under low density, it breaks down and negative interactions among neighbours prevail. This is the first quantitative evidence for a mechanism explaining a prominent deviation of the SGH found in previous studies. Also, we could show that neither stress nor density acts alone in determining individual fitness but that they are closely interrelated. We advocate the quantitative consideration of the density for investigating the balance between competition and facilitation and the interactions between density and environmental stress.

Introduction

Exploring plant-plant interactions is crucial for predicting the structure and dynamics of plant populations and communities. Plants compete for resources and space, but they may also facilitate each other in harsh environments, mainly through stress amelioration and often via increasing resource availability (Callaway 1995; Brooker *et al.* 2008). In the past two decades, many studies have greatly improved our knowledge about the role of positive interactions for ecological and evolutionary processes. For example, facilitation can increase species richness (Callaway et al. 2005; Cavieres et al. 2014), restore phylogenetic diversity (Butterfield et al. 2013; Navarro-Cano et al. 2016), support additional ecosystem services (Badano & Marquet 2009; Brooker et al. 2016) or drive community dynamics (Kefi et al. 2007; Butterfield 2009). However, the literature about facilitation is largely dominated by case studies, and the theoretical progress related to when and where facilitation should dominate or what the mechanisms are has far lagged behind. Most theory around facilitative interactions has remained conceptual, such as the most studied stress-gradient-hypothesis (SGH, Bertness and Callaway) that predicts dominance of facilitation over competition when stress levels are high. Only few quantitative models exist (Travis et al. 2005; Butterfield 2009), and these have not dealt with the general conditions or mechanisms driving facilitative interactions. One reason for the lack of theoretical progress could be that facilitation has been studied qualitatively, while very few quantitative models have been put forward to predict the relative importance of positive interactions for structuring populations and communities (but see Butterfield 2009). For example, most studies evaluate facilitation by comparing performance of target plants ‘with neighbors’ and ‘without neighbors’ (Sthultz *et al.* 2007; Louthan *et al.* 2014), and ignore the fact that neighbours have also a certain density, and that this density may vary across environments, too.

Negative density-dependence has been studied intensively and it is paramount for a number of widely accepted ecological rules. For instance, on a community level, the density of neighbours is crucial for modeling and predicting the outcome of competition among species (Adler *et al.* 2007; Adler *et al.* 2010; Kraft *et al.* 2015). On a population level, well-established theories such as the law of constant final yield (Weiner &

Freckleton 2010) and the related competition-density relationship on an individual level are based on the fact that as plants grow denser, individuals will be smaller or eventually die (known as self-thinning) due to competition for resources (Yoda *et al.* 1963; Ford 2014). Unfortunately, density-dependence of facilitation has been studied only very rarely (Dickie *et al.* 2005; Bishop *et al.* 2013), and simple target-neighbour designs prevail. This is surprising because the balance between competition and facilitation should clearly be altered by the amount and density of neighbours as well (Chapin *et al.* 1994; Callaway & Walker 1997), either through classical negative density-dependence acting via competition, or via density-dependent processes that are characteristic of positive interactions. For example, if facilitation occurs and densities of potential benefactors are very low, distances among plants may be insufficient to alleviate environmental stress (Dickie *et al.* 2005; Bishop *et al.* 2012). Therefore, facilitative effects should become stronger as densities increase (e.g. Allee effects, sensu Courchamp *et al.* 1999) . However, as facilitative and competitive interactions always co-occur (Callaway 1995; Callaway & Walker 1997), competitive effects may dominate at very high densities. As a consequence, we may predict that facilitation should prevail at intermediate densities. In fact, recent empirical studies involving two or more species have supported this idea and showed that benefactor species are more facilitative at intermediate densities, whereas benefactors at either low or high densities can only exert weak positive effects (Dickie *et al.* 2007; Bishop *et al.* 2012; Linstädter *et al.* 2016). Similar findings, i.e., dominance of positive interactions at intermediate density, have been obtained in an intraspecific setting, albeit only in harsh conditions (Chu *et al.* 2008; Duffy & Stout 2011; Xi *et al.* 2016).

While these studies have challenged our view of the ubiquity and dominance of net negative density-dependence, their findings have not been related to general theory about interactions along environmental gradients. This is very surprising, because stress experienced by plants and density of benefactors are not independent. As outlined above, densities may affect the likelihood for net facilitative interactions to occur and thus the level of stress experienced by plants that are growing with neighbours. The lack of studies relating density-dependence to stress is even more surprising when considering the most studied theory in facilitation research - the stress gradient hypothesis (Bertness

& Callaway 1994; Brooker & Callaghan 1998). This theory (the SGH) deals with the importance of facilitation along stress gradients and predicts more frequent and/or intense positive interactions among plants as environmental harshness increases. Based on the above considerations, the outcome of this hypothesis should itself be a function of density, which means that the SGH might not be generally applicable. Indeed, the fact that increasing stress does not always lead to increasing occurrence and/or intensity of positive interactions, has been acknowledged and found many times (Maestre *et al.* 2005; Malkinson & Tielbörger 2010), and this was also confirmed in a recent meta-analysis (He *et al.* 2013). Though that study and similar ones (Bertness & Ewanchuk 2002; Callaway *et al.* 2002; Saccone *et al.* 2010) showed more evidence in favour than against the SGH across many ecosystems, a large number of studies showed no sign of increasingly positive interactions under harsh conditions, or even a shift towards negative interactions when conditions were very stressful (Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Forey *et al.* 2010; Le Bagousse-Pinguet *et al.* 2012; Koyama & Tsuyuzaki 2013). Case-specific models have been put forward to explain these patterns but there is yet no clear and quantitative theoretical framework for predicting under which conditions facilitation would dominate over competition. Here, we argue that the lack of focus on density-dependence of facilitation could be a main reason for the equivocal support that the SGH has received.

One important prerequisite for simultaneously studying stress and density effects of benefactors is therefore not to focus unilaterally on the beneficiary species and their traits, which is characteristic for most empirical studies (Choler *et al.* 2001; Liancourt *et al.* 2005; He *et al.* 2013). More recent conceptual models and empirical research suggested that benefactors and their traits are also crucial for determining the net outcome of plant interactions (Michalet *et al.* 2006; Schöb *et al.* 2013). For example, it has been hypothesized that when environmental conditions are very harsh, the benefactors themselves are too stressed, thus exhibiting weak facilitative effects (or even negative via resource competition) on the beneficiary species (Michalet et al. 2006). Subsequent empirical studies have supported this idea (Baraza *et al.* 2006; Forey *et al.* 2010; Le Bagousse-Pinguet *et al.* 2012). Consequently, we can hypothesize that more neighbors will be required at high stress levels compared to benign conditions to provide similar habitat amelioration. In other words, the previously detected peak of facilitative effects at intermediate densities (Chu et al. 2008; Linstädter et al. 2016) should be highest in low-stress conditions, whereas no facilitation or weak facilitation may be observed in very severe conditions. If benefactors grow at relatively high densities, they may have weak facilitative effects on beneficiaries under low stress due to competition. The humped-shaped relationship between intensity and/or frequency of plant-plant interactions will move to the right along a density gradient and facilitative interactions will peak at a higher density, as stress levels increase (Fig. 1). As a consequence, at high densities, net interactions should become consistently more positive as environmental harshness increases, consistent with the SGH (Bertness & Callaway 1994). However, at low densities, net plant-plant interactions will be less positive or even negative, i.e. the SGH will not apply. In summary, we may expect that while the direction of net plant-plant interaction is predictable, it will be strongly density-dependent.

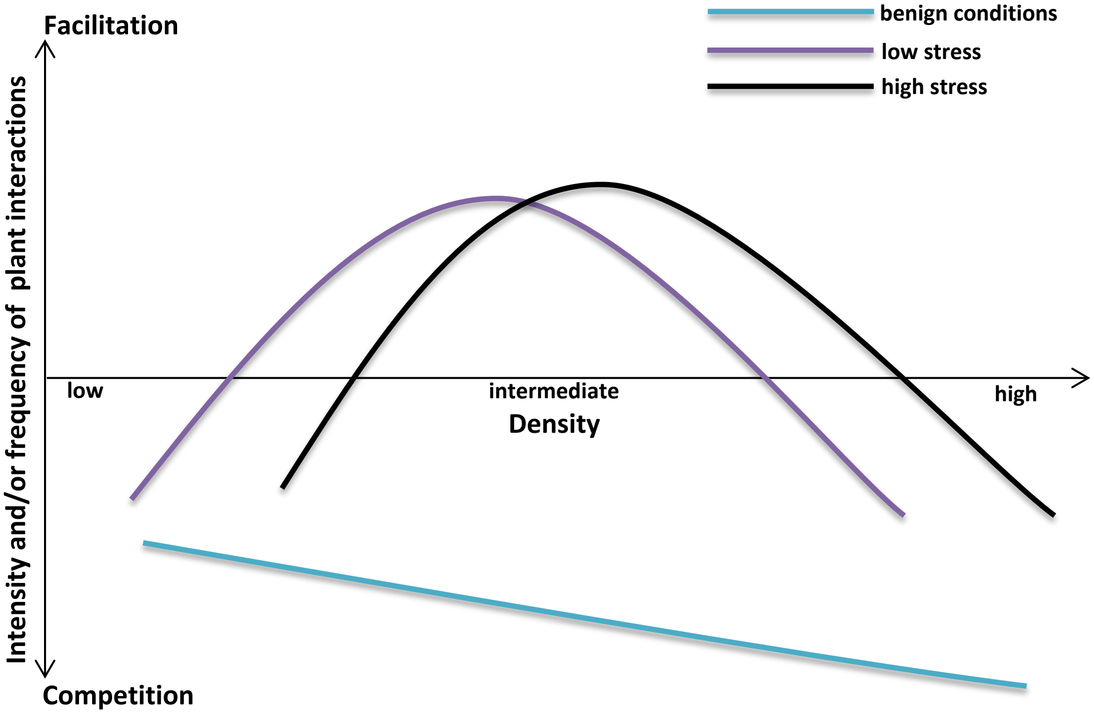

Figure 1. A conceptual model for the way the frequency and/or intensity of plant-plant interactions (competition and facilitation) may shift along a stress gradient and be modified by the density of benefactors.

We selected a study system that exhibits a number of desirable properties for addressing density-dependence along a stress gradient. In order to exclude confoundings caused by species-specific effects (Chapter 3), we used an intraspecific setting with a single study species. Thus, we can ensure that both benefactors and beneficiaries are strongly inhibited by the same stress factor and that the interactions among plants are not confounded by species-specific traits. We used *Arabidopsis thaliana* as model species and salinity as stress factor, because facilitation under salinity is easy to manipulate quantitatively and reciprocal facilitation among even-aged plants has been reported before in salt marshes (Bertness & Yeh 1994; Castro *et al.* 2013; Vogt *et al.* 2014). Furthermore, we could show in a parallel study that intraspecific facilitation occurs within *Arabidopsis thaliana* (Chapter 3).

By growing plants in a full-factorial density and salinity gradient, we tested the following hypotheses: 1) Facilitation under stressful conditions will be density-dependent with a peak of plant performance at intermediate densities; 2a) Along a salinity gradient, facilitation will peak at higher densities when salinity are high than when salinity are low; 2b) The SGH will be confirmed for high densities, while under low densities, it may break down when salinity is high.

Methods

Study species and system

The study species was *Arabidopsis thaliana*, an annual plant with small size, short life cycle (about 6-8 weeks), prolific seed production (several thousand seeds), a small genome and copious mutant lines. These characters have made this species a very popular model organism in plant biology. *A. thaliana* was also chosen because intraspecific facilitation under salt stress for this species has been observed in our previous study and the mechanism is ideal for testing our predictions (chapter 3). Seeds of *A. thaliana* (the most widely used wildtypes, *Columbia*) were bought from Nottingham Arabidopsis Stock Centre (NASC, http://www.arabidopsis.info) and raised for one generation to obtain enough seeds before starting the experiment and to ensure that all plants in the experiment experiences the same maternal growing conditions.

Experimental design

Plants were sown with a varying number of *A. thaliana* seeds to obtain a density gradient, i.e., 1, 2, 3, 5, 7, 10, 15, 20 individuals per pot. The single plants served as control, i.e. the plants were grown without competition. Four salinity levels were applied based on a previous experiment (Chapter 3). All salinity levels caused a visible decrease in plant performance, with the highest level having large detrimental effects on growth and fecundity but not too high mortality, in order to obtain sufficient replicate pots for final data analyses. In the experiment, plants were watered with 0 mM NaCl (tap water, controls), 50 mM NaCl (low), 100 mM NaCl (intermediate) and 150 mM NaCl (high) solution. There were 50 replicates for controls, 30 replicates for 2 and 3 plants per pot, respectively, and 20 replicates for higher densities because according to our own (Chapter 3) and previous studies, plants growing with fewer neighbours may suffer more from stress (Bos & van Katwijk 2007; Fajardo & McIntire 2011). We therefore set more replicates of plants at low densities to obtain enough plants for subsequent analyses. The experiment was set up in an air conditioned greenhouse at Tübingen University in early October 2015. The light intensity in the greenhouse was 130-150 µmol/m^2/s for 16 hours per day and temperatures ranged from 15 ˚C (night) to 20˚C (day) during the experiment. Plants were harvested at seed set in mid-December 2015.

Prior to setting up the experiment, the seeds were sterilized in 70% ethanol for 2 minutes and then transferred to petri dishes and stratified at 4°C for 5 days in a refrigerator to break dormancy and induce synchronous germination (Grozinger et al. 2001). The stratified seeds were then transferred to pots (10×10×10cm) filled with potting soil (Einheitserde Classic, Gebr. Patzer Company). The location of pots assigned to the different salinity and density treatments was fully randomized and distance between pots was approx. 4cm. We sowed an excess (twice the number) amount of seeds in each pot to ensure that we will obtain enough germinating plants for the density gradient. The position of seeds in each pot was random. We also sowed seeds to 40 additional pots (10 seeds per pot) as backup for failure of germination in the experimental pots. Seeds were kept moist by spraying the soil surface and most seeds germinated simultaneously within the first four days after sowing, i.e., the synchronization via stratification was successful. Three days after germination, a 10×10cm cardboard (with a 8.5 cm hole in the middle) was used to exclude plants which might be affected by the border of pots and surplus plants were also removed. Spare seedlings (approx. 60 seedlings) were transplanted from the backup pots into pots without or with far too little germination. The salt treatment started eight days after germination. During the salt treatment, pots were watered every 5-7 days depending on soil conditions. Each pot received the same amount of solution at each irrigation event, and this amount was successively increased (from 50 to 150 ml) as plants grew bigger.

Measurements

At the end of the experiment, we counted the number of surviving plants for all pots. For each plant, we determined the number of siliques as fitness parameters. Totally, 3530 plants survived. As single plants suffer more from stress (Bos & van Katwijk 2007; Fajardo & McIntire 2011), we had more replicates of low densities. In total, we had 25 survivals for single plants under the highest stress levels, i.e. almost the same number of pots remained for final measurements as in the highest densities. After the final measurements, the above-ground parts of all plants were harvested, dried at 70 °Cfor 24h and weighed. Salt treatments decreased the lifespan of plants strongly. Therefore, we included in the analyses only those that survived to seed set. Plants that died before harvest but produced seeds were also counted, weighed and recorded as survival.

Data analysis

The relative interaction index (RII) was used to evaluate the strength and direction of net plant-plant interactions (Armas *et al.* 2004): RII = $(P_w – P_s) / (P_w + P_s)$, where P_W is the performance of target plants with neighbors and P_S is the performance of single plants without neighbors. RII ranges from -1 to 1 with negative values indicating competition and positive values representing net facilitative interactions. Since we had an intraspecific setting, we did not distinguish between benefactors and beneficiaries and we calculated P_W and P_S as the average individual biomass in each population within a pot without and with interactions (2 to 20 plants per pot), respectively (Chu *et al.* 2008; Lin *et al.* 2012). RII was calculated separately for different densities. Note that following similar designs (Lortie & Turkington 2002; Weiner & Freckleton 2010) and the fact that survival itself is density-dependent, density here refers to sowing density (initial density) and not of surviving density.

Results

The salt stress strongly affected the relationship between population density and plant performance. All performance measures-density relationships were similarly; thus, we show only biomass here (see Fig. S2 and Fig. S3 for survival and fecundity, respectively). In controls and low salt stress, mean biomass decreased monotonously with increasing density (Fig. 2A and 2B). However, the shape of this curve gradually shifted to hump-shaped with increasing salt stress, i.e. the largest mean biomass was observed at intermediate densities for the two higher salinity levels(Fig. 2C and 2D). Furthermore, the mean biomass of populations peaked at a higher density with the increase of stress (Fig. 2C and 2D). Correspondingly, the curve of the RII changed from monotonic decreasing to hump-shaped and the unimodal facilitation-density relationship shifted to the right with increasing stress (Fig. 3A).

At high densities (e.g., 10 individuals/pot), intraspecific interactions always exhibited monotonically decreasingly negative or increasingly positive interactions along the stress gradient. However, at relatively low densities (e.g., 2 and 4 individuals/pot), facilitation under intermediate stress was higher than that under high stress (Fig. 3B), i.e. the balance between positive and negative interactions responded in a unimodal fashion to increasing stress levels.

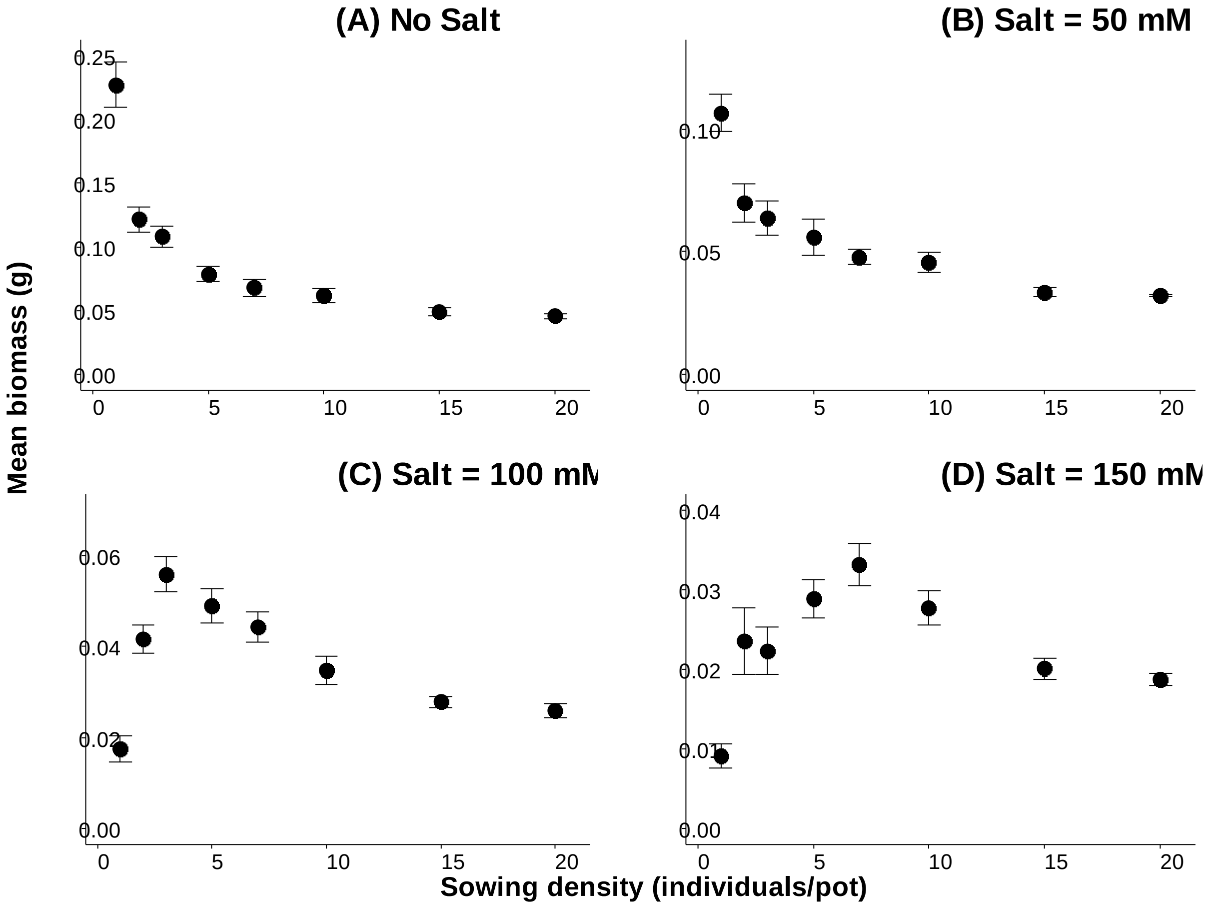

Figure 2. Relationship between sowing density and mean individual biomass (± SE) for *Arabidopsis thaliana* populations grown along a salt gradient: no salt (A), low salt stress (50mM, B), intermediate salt stress (100mM, C) and high salt stress (150mM, D). Note that due to large plant size differences among salinity levels, the scales of the y-axes are not the same to facilitate interpretation.

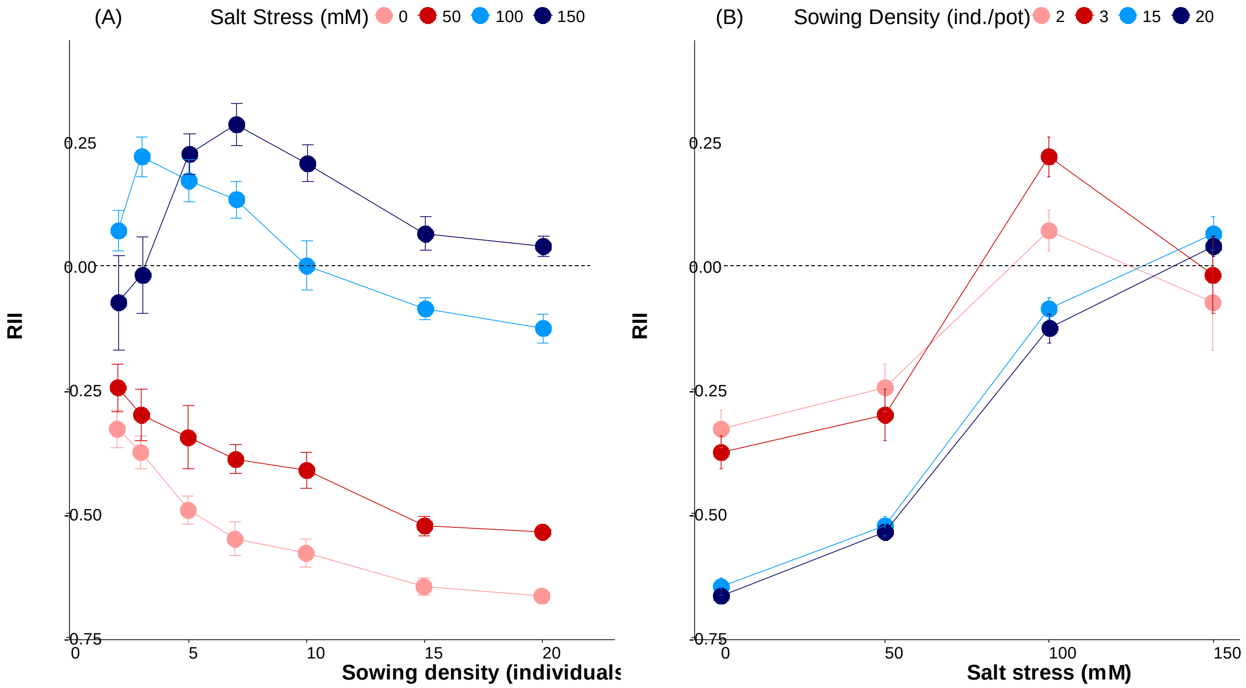

Figure 3. Relationship between sowing density and average Relative Interaction Index (± SE) for *Arabidopsis thaliana* populations grown along a salt gradient (panel A): no salt, low salt stress (50mM), intermediate salt stress (100mM) and high salt stress (150mM); and relationship between stress and average Relative Interaction Index (± SE) for *A. thaliana* populations grown along a salt gradient (panel B): 2, 3, 5, 7, 10, 15, 20 individuals/pot. Note that panel B is only used for displaying how plant-plant interactions change with the stress gradient and information in panel B (we only show the two lowest and two highest densities) is exactly the same as in panel A.

Discussion

Our overall findings suggest that density and abiotic stress strongly interact to determine the balance between competitive and facilitative interactions in plants. We could show, by means of an unconfounded approach, that this balance is predictable but follows the stress gradient hypothesis only under low stress and high densities. In the following, we discuss our novel findings with respect to our initial hypotheses.

Density-dependence of facilitation

The results about density-dependence of plant-plant interactions indicate that the relationship between plant performance and population density shifted to a humped shape as environmental stress increased. In relatively benign conditions, it was not surprising to find the classical negative association between individual fitness and density, which has long been considered a cornerstone of population biology (Watkinson 1980; Bruno *et al.* 2003; White *et al.* 2007). Nevertheless, under intermediate and high stress, all three response measures (biomass, survival and fecundity) were maximized at intermediate densities rather than the lowest densities. This challenges the view of competition as the main driver of intraspecific population regulation.

Indeed, facilitation can occur if neighbors are able to ameliorate environmental stress through various mechanisms (Callaway 1995), even in the intraspecific case (Goldenheim *et al.* 2008; Fajardo & McIntire 2011). However, intraspecific facilitation was only observed at intermediate densities. Negative interactions still dominated at the crowded end of the density gradient, which can be explained by competition due to increasing number of neighbors. At the sparse end, facilitation was also quite weak probably because plants can hardly receive benefit if neighboring plants were too few (or too far away) to moderate stress. This idea has been suggested also by previous studies conducted under high stress levels (Bos & van Katwijk 2007; Bishop *et al.* 2012; Bishop *et al.* 2013), and these considerations were the basis for our initial hypothesis, namely, that just as competition, facilitation is also density-dependent. This hypothesis found very strong support in the experiment. Though our findings challenge models and theories based solely on competition (Enquist *et al.* 1998; White *et al.* 2007), they are consistent with very recent studies involving facilitation in stressful habitats (Dickie *et al.* 2005; Chu *et al.* 2008; Bishop *et al.* 2012; Linstädter *et al.* 2016; Xi *et al.* 2016). For example, in an intraspecific setting, Chu et al. (2008) and Xi et al. (2016) found strong support for a unimodal biomass-density and fecundity-density relationship, respectively. Furthermore, interspecific studies also corroborated the idea of a hump-shaped response in performance to neighbours, e.g., Linstädter et al. (2016) reported that positive effects of four East African tree species on understory plants were strongest at intermediate tree density. Similar findings were obtained by Dickie et al. (2005) with seedling growth of beneficiary trees (*Quercus macrocarpa*) being reduced at both low and high densities of benefactor trees (*Quercus ellipsoidalis*). Taken together, previous studies and our results indicate that facilitative interactions must be taken into account in density-dependent demographic processes.

A shift in the peak of the RII along the density gradient

Although the hump-shaped response of facilitative interactions to density has been observed before, our findings about how density-dependence shift with stress levels and how this shift may influence the balance between facilitation and competition are completely new. In general, we detected purely negative density-dependence at benign and low salinity levels and a change to a unimodal shape at intermediate and high salinity. However, there were also complex interactions between density-dependence and salinity that represent the two most intriguing findings of our study. The first one was that when salinity increased from intermediate to high, the peaks of the RIIs moved to the right along the density gradient, i.e., facilitation peaked at larger densities when stress increased. This was consistent with our initial predictions and can, according to our conceptual model, be interpreted as follows: due to increased stress and the associated decreased facilitative ability of benefactors, more neighbours are required under higher salt levels for generating facilitative interactions than at benign conditions and low salinity.

Our conceptual model actually depends on the idea that the strength of facilitation should be determined by not only facilitative responses of beneficiaries (Liancourt *et al.* 2005), but also facilitative effects of benefactors (Schöb *et al.* 2013). For example, when benefactors are extremely tolerant to the very stress factor under consideration and facilitative traits are not affected by stress, we would expect the RII-density relationship could simply move upward instead of moving to the right along the density gradient. In fact, if net facilitative effects were not decreased by increasing stress, the SGH might always hold because plants deviating further from their optimum are more sensitive to stress amelioration (chapter 3, Liancourt *et al.* 2005; He *et al.* 2012). However, benefactors can be (too) stressed in harsh environments (Michalet *et al.* 2006; Malkinson & Tielbörger 2010; Le Bagousse-Pinguet *et al.* 2012) as well. Previous studies that investigated both benefactor and beneficiary species have found functional traits and facilitative ability of neighbors are greatly decreased in severe conditions (Baraza *et al.* 2006; Maestre *et al.* 2009; Le Bagousse-Pinguet *et al.* 2012; Schöb *et al.* 2013). This is also true for our study, therefore, more neighbours are needed for maintaining stress amelioration. Furthermore, our study is the first to demonstrate the interaction between density-dependence and stress-dependence of facilitation.

When considering mechanisms by which neighbours may ameliorate salt stress, the finding is consistent with previous studies in salt marshes (Bertness & Yeh 1994; Bertness & Ewanchuk 2002). One mechanism under salt stress is shading of the substrate by neighbours which reduces evaporation from the soil thus alleviating salt content (Bertness 1991; He *et al.* 2012). This facilitative effect should become stronger with more neighbours present, until the canopy is closed and the vicinity of beneficiaries is completely shaded. In our study, performance of benefactors/beneficiaries was greatly decreased by salinity, which apparently led to the requirement of more neighbors to impose the same level of stress amelioration. Therefore, the peak of facilitation was observed at larger densities with increasing stress. The same should apply to the second mechanism, active salt uptake by plants (Liu & Zhu 1998; Munns 2005), which was reported in a parallel study with the same study organism (chapter 3). The second mechanism seems more likely to lead to the positive density-dependence of facilitation because it is reciprocal for benefactors and beneficiaries.

Density-dependent facilitation and the SGH

As a result of the above interaction between density-dependence and stress, the peak of the RII moved to the right with increasing stress. This led to the second main finding, which is even more intriguing. Namely, the very applicability of the SGH (sensu Bertness & Callaway 1994) is density and stress-dependent. More specifically, the SGH holds for high densities but may not apply for low densities, especially under high stress. Under these conditions, i.e. few plants and harsh conditions, we observed that facilitative interactions broke down and became neutral (i.e. breakdown of facilitation only) to negative (i.e. competition dominated). At low densities, interactions were more negative among plants exposed to the high salinity than those growing under intermediate salt. Such a breakdown has also been found in several observational field studies (Maestre &

Cortina 2004; Le Bagousse-Pinguet *et al.* 2012). One explanation put forward has been that benefactors themselves suffer from stress and thus are not able to exert any net facilitative effects on neighbouring plants (Michalet *et al.* 2006). Our results provide experimental evidence for this idea, i.e., the performance of plants were greatly reduced by salinity. Furthermore, low densities could have aggravated the conditions because plants growing at low densities were much smaller than those growing at intermediate densities. Plant performance at high densities and high salt levels were also decreased perhaps due to both competition and stress. However, they still had enough neighbours for ameliorating the harsh conditions, even when these neighbours were small. Therefore, when focusing on relatively high densities (or only looking at low stress levels), our findings actually corroborate the stress gradient hypothesis in that competitive interactions dominate at the benign end and facilitation at the harsh end of a stress gradient (Bertness & Callaway 1994, Brooker & Callaghan 1998). The findings are even remarkably strong for an intraspecific setting, for which the SGH has been rarely tested compared to intraspecific cases. Very strong support for the SGH has been found in an intraspecific study of our own, too (Chapter 3), supporting the idea that intraspecific experiments are a more powerful setup for investigating general models about plant-plant interactions.

Most previous empirical research has only looked at the ‘presence’ (with/without neighbors) and investigated facilitation qualitatively (Sthultz *et al.* 2007; Louthan *et al.* 2014). However, missing the quantitative consideration could have led to the lack of theoretical progress in facilitation research. *Vice-versa*, only few studies have considered how the abundance of benefactor neighbors (or the distance) may influence the direction of plant-plant interactions (Dickie *et al.* 2005; Bishop *et al.* 2012; Linstädter *et al.* 2016). However, these studies looked only at a single stress level and did not relate their findings to the most prominent hypothesis about facilitation and stress, i.e., SGH. Despite much debate about the SGH (Maestre & Cortina 2004; Maestre *et al.* 2009; Malkinson & Tielbörger 2010; He *et al.* 2013), there is still no consensus on whether plant–plant interactions change predictably along environmental gradients. Here, we could demonstrate that by ignoring the effects of the ‘amount’ of benefactor plants, it is impossible to make general predictions about how plant–plant interactions change along environmental gradients and, related to that, to environmental change. Furthermore, explanations of deviations from the SGH are often case-study specific, and they may suffer from confounding of the stress factor of interest with other underlying environmental gradients and/or confounding of species identity with species traits (Kadmon & Tielbörger 1999; Liancourt *et al.* 2005; Cavieres *et al.* 2006; Schöb *et al.* 2013). Our study had the advantage of an intraspecific setting with a single stress factor and the clear factorial manipulation of density and salinity. We therefore believe that our conceptual model is likely to be more generally applicable than conceptual models developed for complex plant communities.

Our findings also provide a novel conceptual component to the facilitation research because they demonstrate the co-occurrence of direct stress effects and indirect effects, i.e. those operating via the amount of neighbours. We provide quantitative evidence for this novel mechanism, i.e., when adding density-dependence to the idea that benefactors also suffer from strong stress and positive interactions may breakdown (Michalet *et al.* 2006; Le Bagousse-Pinguet *et al.* 2012), an interesting indirect effect of stress emerges. If the facilitative effect of a benefactor is reduced by stress, fewer plants will be able to survive in its vicinity and thus the benefactor itself will suffer even more from stress. In other words, a positive feedback loop may lead to a rapid breakdown of facilitative interactions due to stress-induced mortality at very low densities. This mechanism relies strongly on the idea that facilitation is reciprocal, namely, benefactors could receive benefit from intra- and/or interspecific neighbors. It is obviously true for intraspecific facilitation because benefactors are also beneficiaries. However, for interspecific situations, the reciprocity of facilitation has been only rarely studied (Holzapfel & Mahall 1999; Bronstein 2009; Schöb *et al.* 2014), and none of these studies addressed densities. We therefore advocate the explicit consideration of density-dependence in future studies of interactions along gradients.

Conclusions

Our intraspecific setting and the clear results suggest that plant-plant interactions may change predictably- but differently than suggested by the SGH- along stress gradients. However, the degree to which our suggested model is universal should ideally be tested by additional studies in the future. Overall our study highlights the need to include density as a factor determining positive plant-plant interactions and to investigate facilitation quantitatively. We also advocate for more studies looking at both direct stress effects as well as indirect effects operating via neighbor density, as these may yield insight into the very basic mechanisms determining density-dependence of facilitative interactions among plants.

Chapter 5

Facilitation alters allometric responses of plants to density

Abstract

The negative density-dependent pattern is the cornerstone of population ecology. However, studies of facilitation have challenged our view of it. Recent studies have found that the density-dependence of plant interactions could actually shift with environmental gradients. In stressful conditions, the strength of net facilitation may firstly increase but then decrease with density, which could lead to a hump-shaped performance-density relationship. Therefore, this indicates that many patterns based on the negative density-dependence among plants might be reverted. One of the well-studied responses to increased population density is the shade avoidance syndrome. The shade avoidance is triggered by a reduction in the red to far-red ratio in wavelengths due to the preferential absorption of neighbouring plants. A main feature of shade avoidance is an enhanced vertical growth, while plants forming rosettes may elongate their petioles in response to competition and build a larger rosette. These responses could enable plants to avoid being suppressed in light competition and are thought to be adaptive in dense populations. However, in stressful environments, increased population density could provide facilitation, which is crucial for survival and growth of plants. In this scenario, suppressing or even excluding neighbours might not be advantageous. In this study, we tested whether plants deviate from the shade avoidance responses when intraspecific facilitation occurs and plants exhibit a positive density-dependence pattern. We grew *Arabidopsis thaliana* in a full-factorial density and salinity gradients and measured their morphology. The results were interesting. In benign and low stress conditions where competition dominated, as indicated by the allometric relationship between rosette-

diameter and biomass, plants could build a relatively larger rosette to compete with neighbours. This is consistent with the classical shade-avoidance response. However, allometric relationships were reversed when facilitation dominated under high stress levels. This may indicate that plants could decrease allocation to competitive traits in reciprocal intraspecific facilitation. However, mechanisms behind the observed pattern are not clear and should be subject to further studies.

Introduction

Interactions among plants are crucial for determining of plant population and community dynamics. These interactions can be negative, but plants can also facilitate each other in harsh environments. For example, neighbours can alleviate stress or increase resource levels when environmental conditions are stressful (Callaway 1995; Brooker *et al.* 2008). In the past two decades, many studies have greatly improved our knowledge about the role of positive interactions for ecological and evolutionary processes, and there have been several reviews about where and under which conditions facilitation dominates over negative plant-plant interactions (Maestre *et al.* 2009; Malkinson & Tielbörger 2010). However, there is a prominent difference between the abundant literature about competition and facilitation in that the latter has been studied mostly on a community level (i.e. interspecific), and population-level consequences of facilitation have been rarely addressed (but see Chapter 2). In fact, an intraspecific perspective has been crucial for establishing a number of key theories in ecology. For example, the shade avoidance response (Ballare *et al.* 1990; Dudley & Schmitt 1996), the law of constant final yield (Weiner & Freckleton 2010), population dynamics and self-thinning (Yoda *et al.* 1963; Enquist *et al.* 1998), the symmetry and reciprocity of competition (Weiner 1990; Weiner *et al.* 2001), or coexistence mechanisms (Chesson 2000; Adler *et al.* 2007) are all based on a population level or originate from a population perspective. However, very few attempts have been made to incorporate facilitation within these mainstream theories due to the narrow focus on community dynamics.

A cornerstone of population ecology is the negative density-dependence (Watkinson 1980; Bruno et al. 2003; White et al. 2007). However, studies of facilitation have challenged our view of the ubiquity and dominance of net negative density-dependence. A recent study (chapter 4) has found that density of benefactors can interact with stress and density-dependence of plant interactions could actually shift with environmental gradients. For example, when densities of potential benefactor species are very low, distances between neighbours may be insufficient to alleviate environmental stress (Bishop *et al.* 2012; Bishop *et al.* 2013). Therefore, facilitative effects should become stronger as densities increase, up to a certain density at which competition starts to overwhelm facilitation. This can lead to a hump-shaped performance-density relationship rather than simple negative density-dependence (Dickie *et al.* 2005; Dickie *et al.* 2007; Bishop *et al.* 2012; Linstädter *et al.* 2016). Similar relationship has also been reported for single species populations in stressful environments (Chu et al. 2008; Xi et al. 2016). Namely, competition dominates at very high population densities, but at low to intermediate densities intraspecific facilitation may prevail and its strength increases with densities (Bos & van Katwijk 2007; Kumara *et al.* 2010). These studies may indicate facilitation that can change or even revert many patterns based on the negative density-dependence among plants.

It has been suggested and shown that the outcome of both competitive and facilitative interactions depends on the traits of the interacting plant individuals (Liancourt *et al.* 2005; Maestre *et al.* 2009; Schöb *et al.* 2013; Kraft *et al.* 2015; Kunstler *et al.* 2016). For example, a recent study has showed that the morphology of benefactors may determine their facilitative effects (Schöb *et al.* 2013) and non-tolerant plants are more sensitive to facilitation, i.e., they have stronger facilitative response (Liancourt *et al.* 2005, chapter 3). Also, competition is trait-dependent and plants may adapt to competition by a range of morphological or physiological traits, e.g., it has been universally accepted that being taller confers plants stronger competitive ability through prior access to light when neighbours are present (Weiner 1990; Westoby *et al.* 2002). However, these traits are not fixed and plants can also plastically respond by reversibly adjusting these traits according to the presence or the density of neighbours (Ballare *et al.* 1990; Schmitt & Wulff 1993; Sultan 2000; Callaway *et al.* 2003). The most prominent of these plastic responses is the so-called shade avoidance syndrome which is triggered by shading and a reduction in the red to far-red ratio in wavelengths (Ballare *et al.* 1990; Smith 2000; Pierik *et al.* 2004; de Wit *et al.* 2012), indicating larger densities of competitors for light. A main feature of shade avoidance is an enhanced vertical growth (Schmitt & Wulff 1993; Schmitt *et al.* 2003; Vandenbussche *et al.* 2005; Franklin 2008). This response enables a plant to simultaneously escape the competition but also to enhance its competitive effect (Weiner & Thomas 1992; Ford 2014) or its 'confrontational behaviour' (sensu Novoplansky 2009). Plants that are predominantly forming rosettes and thus cannot lift their leaves to larger heights may elongate their petioles in response to competition and build a larger rosette (Callahan & Pigliucci 2002; Franklin 2008). All these responses enable plants to avoid being suppressed in light competition (Weiner 1990) and are thought to be adaptive in dense populations (Dudley & Schmitt 1996; Franklin & Whitelam 2005; Weijschedé *et al.* 2006).

However, will plants also show shade avoidance responses in a situation where net facilitation occurs and they can benefit from each other? For example, in stressful environments, increased population density might indicate facilitation instead of intensified competition (Bertness & Yeh 1994; Castro *et al.* 2013), at least between relatively low densities and intermediate densities (Chu *et al.* 2008; Xi *et al.* 2016). Therefore, under harsh environmental conditions, it may not necessarily be advantageous for a plant to exhibit a behaviour that enables it to suppress its neighbours, when they actually act as potential benefactors. In this scenario, suppressing or even excluding conspecific neighbours may be harmful, when stress amelioration provided by neighbours is crucial for survival. Consequently, enhancing traits fostering competitive ability (e.g., height and/or rosette size) might not be favoured. It may thus be hypothesized that in conditions where facilitation is important and/or intense, plants might not exhibit shade avoidance under high density. Instead, they may alter their morphology to decrease allocation for competitive traits. Such morphological responses to density in the presence of facilitation and its interaction with stress have never been investigated before. With our study, we want to fill that gap.

Our study system is well suited to simultaneously address density-dependence of positive and negative interactions and individual plastic responses. Firstly, we used an intraspecific setting with a single study species to ensure that facilitation is reciprocal. Namely, plants in the population are both benefactors and beneficiaries and they respond equally to the stress imposed. Secondly, we used a species, *Arabidopsis thaliana*, which we have used successfully before and for which we have demonstrated clear stress- and density-dependence of intraspecific facilitation (Chapter 3). It is also easy to grow and manipulate. As stress factor, we selected salinity, because of ease to manipulate in a quantitative manner and because facilitation under salt stress tends to be symmetric (chapter 1, Bertness & Yeh 1994; Castro *et al.* 2013; Vogt *et al.* 2014).

By growing plants of *A. thaliana* in a full-factorial density and salinity gradient and measuring their morphology, we tested whether plants deviate from the expected shade avoidance syndrome at high densities. Namely, when intraspecific facilitation occurs under high salinity stress, we expect plant morphology will be less promotive of competitive ability than under low stress or benign conditions.

Methods

Study species and system

The study species was *Arabidopsis thaliana*, a small annual plant which has become a popular model organism in plant physiology. *A. thaliana* was also chosen because it has proven ideal in our own previous studies for investigating stress and density effects simultaneously (Chapter 3 and 4). In these studies, we could demonstrate that the response to density is unimodal at high stress levels and negative when stress is low (Chapter 4). These findings also informed us about the ideal salinity and density levels to use for our allometric measurements. Seeds of the most commonly used *A. thaliana* accession (i.e. *Columbia*) were bought from Nottingham Arabidopsis Stock Centre (NASC, http://www.arabidopsis.info). The seeds were raised for one generation to obtain enough seeds before starting the experiment and to ensure that all plants in the experiment experiences the same maternal growing conditions.

Experimental design

Plants were sown at three densities of *A. thaliana*. Based on our own previous and parallel studies (Chapter 3 and 4), two and three individuals were sown per pot, respectively. Higher densities were used in a previous study (Chapter 4) which indicated that the main effects of density on performance are -dependent on stress level- detectable between the single and 2-plant or the 2-plant and 3-plants per pot level, i.e. higher densities were not necessary to ensure both facilitative and competitive interactions in the entire setup. Furthermore, higher densities led to largely overlapping plant rosettes, which did not allow measuring the rosette characteristics in an undestructive manner.

The single plants served as control, i.e., the plants were grown without competition. Four salinity levels were applied based on a parallel experiment (Chapter 4). All salinity levels caused a visible decrease in plant performance, with the highest level having large detrimental effects on plant performance without causing excessive mortality. In the experiment, plants were watered with 0 mM NaCl (controls), 50 mM NaCl (low), 100 mM NaCl (intermediate) and 150 mM NaCl (high) solution. There were 50 replicates for controls and 30 replicates for 2 and 3 plants per pot, respectively because single plants suffer more from stress (Bos & van Katwijk 2007; Fajardo & McIntire 2011) and exhibit higher mortality (Chapter 3, Chapter 4). The experiment was conducted in an air conditioned greenhouse at Tübingen University in early October 2015 and lasted until mid-December (seed set). Light intensity in the greenhouse was 130-150 $\mu mol/m^2/s$ for 16 hours per day and temperatures ranged from 15 ˚C (night) to 20˚C (day).

The seeds were sterilized following a protocol by Grozinger et al (2001) to induce synchronous germination: they were imbibed in 70% ethanol for 2 minutes and then transferred to petri dishes and stratified at 4°C for 5 days. The stratified seeds were then transferred to pots (10×10×10cm) filled with potting soil (Einheitserde Classic, Gebr. Patzer Company). The location of pots assigned to the different treatments of density and salinity was fully randomized in the greenhouse with a maximum distance between pots of 4cm. We sowed twice the number of seeds in each pot to ensure that we will obtain enough germinating plants. In addition, backup pots were prepared with seedlings to complement pots without germination. To germinate the seeds, they were kept moist by spraying the soil surface. Most seeds germinated simultaneously within four days after sowing. Three days after that, surplus plants were removed and backup seedlings were transplanted (ca. 60 plants). The salt treatment started eight days after germination. During the salt treatment, pots were watered every 5-7 days depending on soil conditions.

Each pot received the same amount of solution at each irrigation event, and this amount was successively increased (from 50 to 150 ml) as plants grew bigger.

Measurements

We measured, for each plant in the three density treatments the rosette diameter as a measure for the predicted shade avoidance response in rosette plants (Callahan & Pigliucci 2002; Franklin 2008). We also measured plant height and count the number of siliques. At the time of seed set, we harvested all plants and measured their above-ground biomass by harvesting the above-ground parts of all plants, drying them at 70 ℃for 24h and weighing them. We only included those plants in the analyses that survived to the end of experiment. Plants that died before harvest but produced seeds were also counted, weighed and recorded as survival.

Data analysis

Many phenotypic traits are size-dependent, i.e. leaf size and plant size could be positively related such that differences in leaf size can be simply due to size differences of plants (McConnaughay & Coleman 1999). We therefore standardized the rosette size by plant biomass, and used this measure to identify the 'apparent plasticity' (Weiner 2004). This is also the measure most directly related to our hypothesis. The allometric relationship between rosette-diameter and biomass was then analyzed with respect to the independent variables salinity (4 levels) and density (3 levels). For the density 2 and 3 (2 and 3individuals/pot), pots in which one or two plants died were excluded from the analyses (44 pots).

The slopes of rosette diameter–biomass relationship were estimated by the standardized major axis (SMA) regression (Li *et al.* 2013) on log–log-transformed data, i.e., log(x+1). Linear regression was used to estimate fit lines because previous studies have demonstrated that the height- and diameter-biomass relationship is most commonly linear (Weiner & Thomas 1992; Weiner & Fishman 1994). Slopes of fitted lines of different densities in each salt treatment were compared by a heterogeneity test (Warton *et al.* 2006) whereby slopes were assumed to be different if $P <$ critical value (0.05). All these analyses were performed in R (R-project. 2016), package 'smatr' (Warton *et al.*

2012). Furthermore, to illustrate the occurrence of intraspecific facilitation, we also analyzed how the density-dependency of biomass could shit along the salt gradient with a two-way ANOVA (density and salt as fixed factors).

Results

The salt stress strongly affected the relationship between density and biomass (Table 1). Specifically, the plant biomass always decreased with density in benign or low stress conditions (Fig. 1 A and B). However, under intermediate and high stress, the biomass increased with the density (Fig. 1 C and D).

Table 1. Two-way ANOVA results for shoot biomass with salt stress and density as fixed factors. *** indicates significant effect (*P*<0.001)

Source	***df***	***MS***	***F***	***P***
salt	3	0.39	156.30	<0.001 ***
density	2	0.04	14.63	<0.001 ***
salt * density	6	0.05	20.92	<0.001 ***
Error	526	0.00		

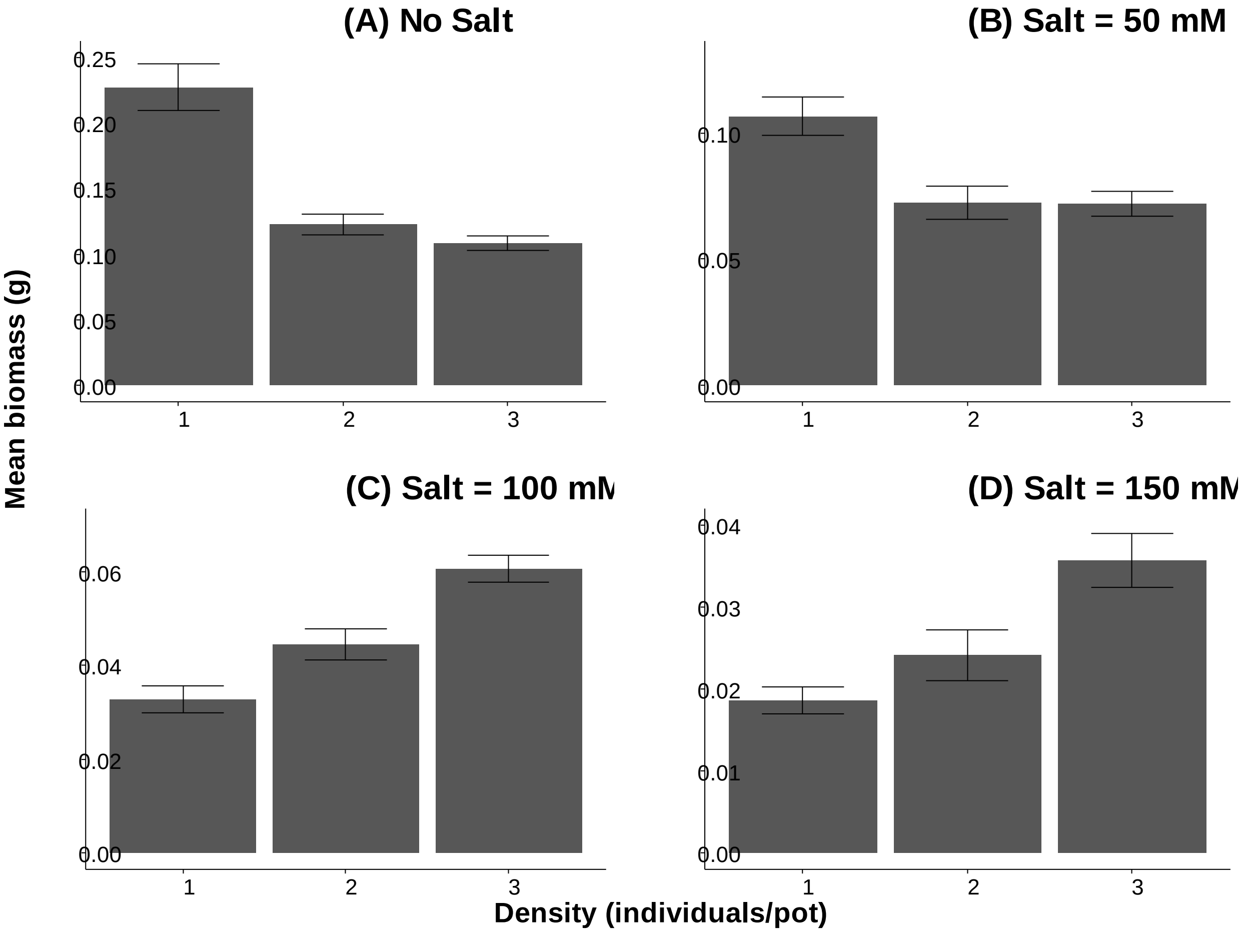

Figure 1. Mean biomass (±SE) of *Arabidopsis thaliana* grown alone (1 individual/pot), with one neighbor (2 individual/pot) and with two neighbours (3 individual/pot) along a salt gradient: benign condition (just water, no salt), low salt stress (50mM), intermediate salt stress (100mM) and high salt stress (150mM). Note that due to large plant size differences among salinity levels, the scales of y-axis are not the same.

The slope of the allometric relationship between log diameter and log biomass was significantly changed by three densities and slope also varied with increasing stress (Table 2). Specifically, the difference of slope was always significant between the single plants and the competitive scenarios (2 or 3ind./pot) but it was not significant between the two competitive settings (Table 2). In benign and low-stress conditions in which competition dominated, the slope increased with increasing density, i.e., rosette size of plants grown at higher densities increased faster with biomass, thus, plants at higher densities generally had a larger rosette for a given biomass (Fig. 2). But in intermediate and high stressful conditions, the trend was completely opposite (Fig. 2).

Table 2. Regression parameter of log rosette diameter–biomass relationships of *Arabidopsis thaliana* grown along a salt gradient (benign condition, low, intermediate, and high stress) at three sowing densities (1, 2 and 3 ind./pot, as estimated by the SMA regression. Different letters in the 'Slope' column indicate slopes of fitted lines of different densities in each salt treatment are significantly different from each other ***P < 0.001.

Stress (salt)	**Density (ind./pot)**	**r^2**	**Slope**
benign condition	1	0.53 ***	1.94 a
	2	0.52 ***	3.97 b
	3	0.51 ***	4.36 b
low (50 mM salt)	1	0.52 ***	2.98 a
	2	0.52 ***	4.42 b
	3	0.62 ***	5.35 b
intermediate (100mM salt)	1	0.64 ***	11.01 a
	2	0.53 ***	7.09 ab
	3	0.60 ***	8.33 b
high (150mM salt)	1	0.62 ***	22.23 a
	2	0.71 ***	14.03 b
	3	0.80 ***	11.48 b

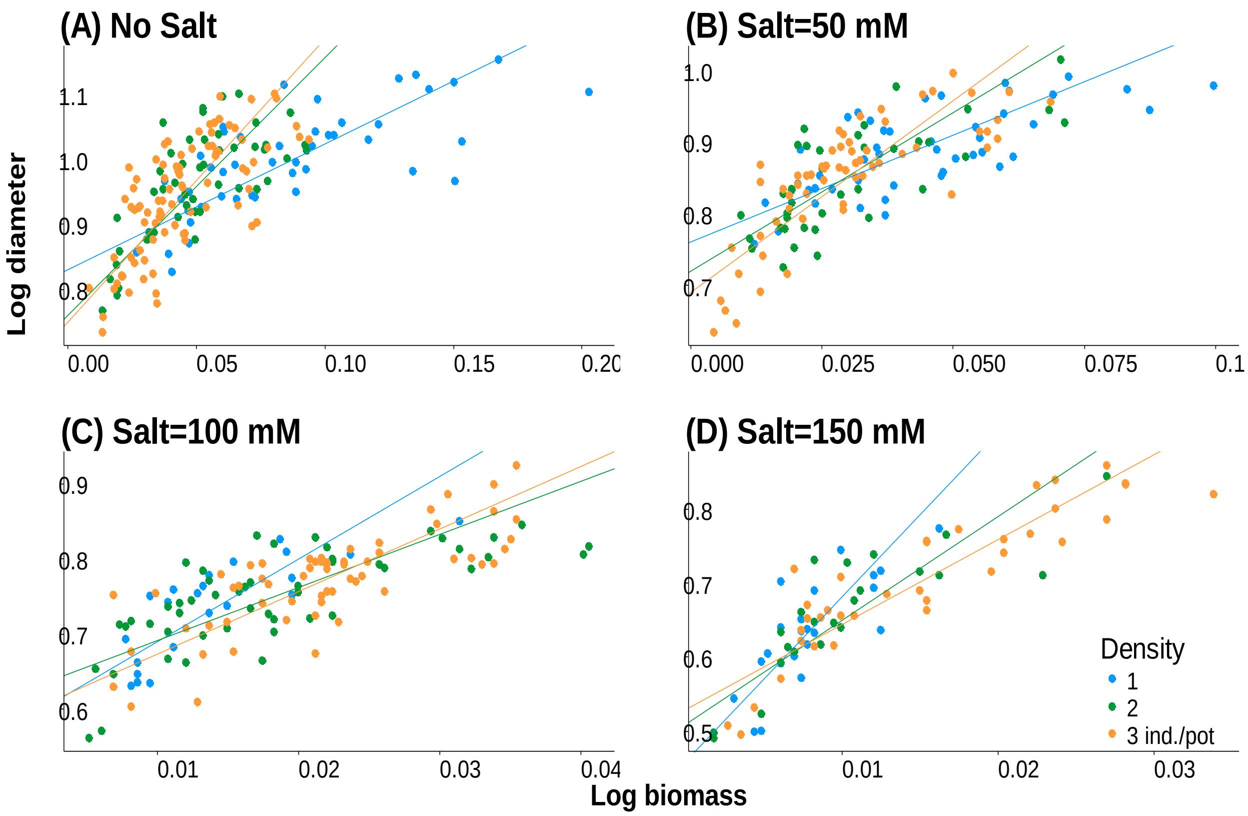

Figure 2. Allometric relationship between log rosette-diameter and log biomass for *Arabidopsis thaliana* growing alone (1 individual/pot), with one neighbor (2 individual/pot) and with two neighbours (3 individual/pot) along a salt gradient: benign condition (just water, no salt), low salt stress (50mM), intermediate salt stress (100mM) and high salt stress (150mM). Parameters of the linear regression (SMA) are shown in Table 1. Note that due to large plant size differences among salinity levels, the scales of axes are not the same.

Discussion

Our overall findings suggest that allometric relationships in plant morphology change in response to increased neighbours and that plants avoid suppressing their neighbours when depending on facilitation by them. Namely, the classical shade-avoidance syndrome was not found when plants were grown under intermediate and high stress levels when facilitation dominated.

One way of enabling tolerance of plants to stressful biotic or abiotic conditions is by plastically responding to these conditions. For example, we predicted that at low stress, increasing densities would lead to the shade avoidance syndrome, i.e. an elongation of petioles and/or rosette leaves (Schmitt *et al.* 2003; Kahlen & Stützel 2011; Ford 2014). Our results demonstrated that competition dominated in benign conditions and under low stress. In fact, there was also clear evidence for an increased ratio between rosette size and biomass in the control plants and plants grown under low salinity. This is consistent with previous studies on rosette plants which could show that shade avoidance in such species is mainly limited to leaves and involves the elongation of petioles or larger rosettes (Callahan & Pigliucci 2002; Franklin 2008; de Wit *et al.* 2012). This plastic response has been shown to increase competitive ability and fitness of plants through enhanced light interception capacity in dense stands (Dudley & Schmitt 1996; Schmitt *et al.* 2003). We therefore interpret the observation of relatively larger rosettes under high density and low stress as an adaptive response to competition.

The most intriguing finding in that context was that these allometric relationships that corroborate theory and previous studies were tipped by salt stress. In fact, when salinity was high (i.e. the two highest salt levels), higher densities led to *lower* instead of *higher* allocation to rosette growth, i.e. the pattern was exactly the opposite. It should be noted that because we used the relationship between rosette size and biomass as response variable in order to account for allometry (Weiner 2004; Berner 2011; Poorter *et al.* 2012), i.e. smaller rosettes cannot be the result of smaller biomass due to stress. Such a finding would be interpreted as 'apparent plasticity' rather than true plasticity (McConnaughay & Coleman 1999; Valladares *et al.* 2007). In our case, plants reduced their relative investment into rosette size (and thus into competitive ability, Dudley & Schmitt 1995, 1996; Schmitt *et al.* 2003, Ford 2014) when plant performance exhibited positive density-dependence due to facilitation. Under such conditions, it is advantageous to have many neighbours, i.e. allocation into competitive traits would be detrimental for the plants. This conclusion is also consistent with the idea that competition and facilitation always occur simultaneously and greater positive interactions could be attributed either to a decrease of competition intensity or increasing facilitative effects (Callaway 1995; Callaway & Walker 1997). Our results thus indicate a novel mechanism of plastic allometry in response to facilitative, rather than competitive interactions, which certainly deserves attention in future studies.

It must be noted that the switch in allometry under stress may not be universal but depend on the very mechanism by which plants ameliorate their environment for other plants. It should be noted that in most previous studies, the mechanism by which plants ameliorate salt stress is by shading of the substrate and decreasing evapotranspiration (Bertness & Shumway 1993; He et al. 2011). Therefore, in a rosette plant like *Arabidopsis thaliana*, shade avoidance response manifested in a larger rosette (Callahan & Pigliucci 2002; Franklin 2008) could actually simultaneously enhance facilitation. In that case, there should be selection for a shade avoidance syndrome even if this also enhances competition. However, in a parallel study we could show that a main mechanism by which *A. thaliana* alleviates soil salt content is via salt uptake and accumulation by neighbors (chapter 3). This below-ground mechanism enables us to disentangle facilitation from above-ground competition, albeit not completely.

One explanation might be the trade-off between stress-tolerance and competitive ability (Grime 1977). In stressful habitats, less allocation of resource to competitive ability may confer plants higher tolerance for the very stress (Yoshida *et al.* 2004; Pierce *et al.* 2013). Then decreased relative rosette size of plants growing with neihgbours may indicate more allocation to tolerance rather than increased of lower suppression of beneficial neighbours. However, for plants growing without neighbours, the relative size of rosettes always increased rather than decreased along the salinity gradient, implying the trade-off between competitive traits (rosette size) and tolerance might not be important for single plants. Although the trade-off may play out when stress and competition co-occur, i.e. under high density and high stress, it is not sufficient for explaining the whole results. Indeed, it is hard to image that plants increased allocation to tolerance when environmental stress is actually alleviated by neighbours.

However, understanding mechanisms behind such a behaviour is difficult and was not the focus of our study. Much has been done on the physiology behind shade avoidance, e.g., photoreceptors such as phytochromes and how they regulate shade avoidance are well studied (Nagatani *et al.* 1991; Reed *et al.* 1993). However, the phytochrome signaling could interact with other environmental cues to elicit plant responses, e.g., chill (Franklin & Whitelam 2007), drought and nutrients deficiency (Page *et al.* 2011). Recently, Galvan-Ampudia *et al.* (2013) also reported the halotropism, a response of plant altering direction of roots to avoid salinity stress, and this below-ground response could also interact with the above-ground shade-avoidance though plant hormones (Wolters & Jurgens 2009; Pierik & Testerink 2014). Yet little is known about the crosstalk of these physiological mechanisms and how the allocation to above- and below-ground structures may be affected when facilitation is involved. This is an open field of research and was beyond the scope of our study. It is also important to notice that we used the static intraspecific allometric relationship (rosette-size and biomass) to represent plant responses. However, salt stress may decrease the lifespan of plants strongly (Griffith & Watson 2005; Castro *et al.* 2013), while facilitation among plants at high densities may reduce the impact of stress. Therefore, further studies should also investigate the allometric growth trajectories (Weiner & Thomas 1992; Weiner *et al.* 2009), which could provide more information to evaluate to what extend rosette differences of plants at different densities may be affected by size.

In summary, we showed that plants might demonstrate relatively decreased rosette size with increasing density when intraspecific facilitation occurred under high stress. This was completely opposite with their response in benign conditions. We argue this response may be advantageous in a scenario where the facilitation by neighbours is crucial for plants survival and growth. Further studies are needed to explore mechanisms of the pattern and whether a particular plant trait (here: shade avoidance traits) may affect facilitative and competitive effects simultaneously.

Chapter 6

General conclusions

Compared to many core patterns based on intraspecific competition, the intraspecific facilitation has been largely overlooked. The main objective of this thesis was to find evidence for intraspecific facilitation, figure out in which conditions it may occur and use the intraspecific approach to address research gaps such as confounding effects caused by species identity and density-dependence of facilitation. In the following, considerations on my results about the generality, mechanisms and potential of intraspecific facilitation are set forward.

Generality and mechanisms (Chapter 2)

The first review in Chapter 2 indicates intraspecific facilitation may be ubiquitous in nature. Actually, the occurrence facilitation in even-aged populations (reciprocal intraspecific facilitation) or adult-seedling systems has been found in almost all biomes (arctic/alpine, coastal/marine, freshwater wetland, grassland/savanna and forest/woodland) and climate zones (tropical, arid, temperate, Mediterranean, snow and polar). However, further analysis (Chi^2-tests) for stress factors showed the over-representation of facilitation in adult-seeding systems in certain harsh habitats. Namely, under stress such as radiation, wind and burial, facilitation has never been reported to occur in even-aged populations. However, I also detected that the reciprocal intraspecific facilitation were particularly common under salinity and heat stress.

I assume unidirectional facilitation may occur in adult-seedlings but hardly in even-aged populations or conspecific cohorts. Thus, if facilitation could be found in even-aged populations or both study systems for a specific stress factor, then it may be reciprocal. This comparison yielded a preliminary insight into whether this specific stress factor tends to generate reciprocal (e.g., salinity, heat and waterlogging) or unidirectional (e.g., radiation, wind and burial) facilitation. Nevertheless, the problem is that for a particular harsh habitat plants may have multiple mechanisms for a certain stress factor (e.g., drought stress), which could lead to different modes of facilitation. Therefore, it is important to consider the main mechanism in stressful environments rather than only focus on the stress factors alone.

However, the number of case studies with intraspecific facilitation is limited and many of them are not designed to explore facilitation mechanisms. In order to find out under which conditions reciprocal facilitation might be expected, I included also interspecific studies and conducted the second review. Through this review, I identified main mechanisms under various stressors and then discussed whether or not they could be reciprocal and symmetric. Based on the synthesis of two reviews, I developed a conceptual framework about reciprocity and symmetry of facilitation (Chapter 1), which could be used as the foundation for future studies which aim to explore consequences of facilitation on the population-level.

Life history trade-off in facilitation and the advantage of an intraspecific approach (Chapter 3)

Using even-aged conspecifics and genetically defined stress tolerance (salt-sensitive mutants of *Arabidopsis thaliana* vs. relatively tolerant wildtypes), I found salt-sensitive genotypes exhibited a stronger facilitative response than tolerant genotypes. This is not surprising because non-tolerant plants are farther from their optimum and they should be more sensitive to the stress amelioration. This idea has been formulated before (Choler et al. 2001; Liancourt et al. 2005). Interspecific studies confirmed (Wang *et al.* 2008; Liancourt & Tielbörger 2011), but also contradicted (Donovan & Richards 2000) it. These studies suffered from the fact that they were conducted for multiple species, i.e., the factor ‘stress response’ was confounded with species identity. Thus, my study is the first solid experimental evidence for the effect of stress tolerance alone on the outcome of facilitative interactions.

Intriguingly, I found sensitive genotypes also imposed consistently stronger facilitative effects despite being smaller under high salinity. The explanation could lie in the mechanisms of salt tolerance, which could be achieved by developing tolerance of tissue to accumulated Na+ (Garthwaite *et al.* 2005; Munns 2005) or excluding salt to avoid excessive intracellular salt levels (Liu & Zhu 1998). In fact, it has been reported that in *A. thaliana*, the SOS genes encode a number of proteins (Halfter *et al.* 2000; Shi *et al.* 2000), which in effect lead to a larger accumulation of Na+ under salt stress compared to the wild type (Liu & Zhu 1998). Non-tolerant plants may accumulate more salt and demonstrate a larger facilitative effect because they cannot exclude salt due to the mutation of SOS genes.

Furthermore, the sensitivity to salt stress was associated with larger competitive response ability. The fact that competitive response was also smaller in benign conditions indicates that there was a trade-off between stress tolerance and competitive ability. This trade-off has been postulated many times previously (Grime 1977; Suding *et al.* 2003; Pennings *et al.* 2005; Maestre *et al.* 2009), but so far, the idea has been pertinent to community ecology and not to proper evolutionary studies. The only study specifically designed to test the evolutionary trade-off under strict genetic control used herbivore resistant and sensitive plants of *Arabidopsis thaliana* (Cipollini 2007). However, the author did not find any evidence for a trade-off between competitive ability and defoliation tolerance (Cipollini 2007). This could be the result of methodological differences to my study (e.g. no replication- only one genotype; only one performance measure), but also, defoliation is not the same type of stress as abiotic stress. In our study, the mutants and wildtypes were genetically similar and they differed in only a single trait of interest- salt tolerance. Thus, my results provided very clear and solid evidence for the trade-off between stress tolerance and competitive ability, one of the most basic paradigms in ecology.

Density-dependence of facilitation (Chapter 4 & 5)

Using a similar study system in Chapter 3 (*Arabidopsis* and salt stress), I tested my conceptual model about how density-dependence may shift along environmental gradients and how the shift may influence the balance between competition and facilitation. Results (Fig. 3 Chapter 4) strongly supported model predictions.

The first novel finding was facilitation peaked at larger densities when stress increased. This was consistent with my initial predictions and can be interpreted as follows: due to increased stress and the associated decreased facilitative ability of benefactors, more neighbours are required under higher salt levels for generating facilitative interactions than at benign conditions and low salinity. My conceptual model actually depends on the idea that the strength of facilitation should be determined by not only facilitative responses of beneficiaries (Liancourt *et al.* 2005), but also facilitative effects of benefactors (Schöb *et al.* 2013). For example, when benefactors are extremely tolerant to the very stress factor under consideration and facilitative traits are not affected by stress, I would expect the RII-density relationship could simply move upward instead of moving to the right along the density gradient. In fact, if net facilitative effects were not decreased by increasing stress, the SGH might always hold because plants deviating further from their optimum are more sensitive to stress amelioration (chapter 2, Liancourt *et al.* 2005; He *et al.* 2012). However, benefactors can be (too) stressed in harsh environments (Michalet *et al.* 2006; Malkinson & Tielbörger 2010; Le Bagousse-Pinguet *et al.* 2012) as well. Previous studies that investigated both benefactor and beneficiary species have found functional traits and facilitative ability of neighbors are greatly decreased in severe conditions (Baraza *et al.* 2006; Maestre *et al.* 2009; Le Bagousse-Pinguet *et al.* 2012; Schöb *et al.* 2013). This is also true for my study. Therefore, more neighbours are needed for maintaining the stress amelioration.

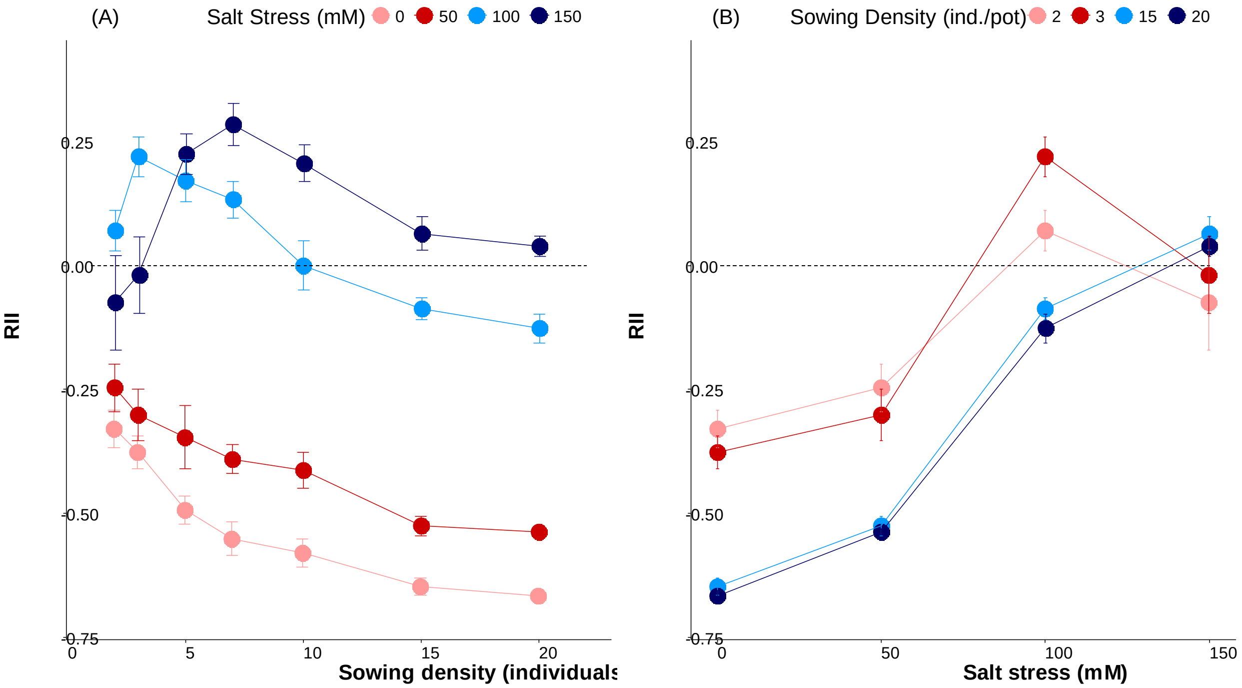

Figure 3 (Chapter 4). Relationship between sowing density and average Relative Interaction Index (± SE) for *Arabidopsis thaliana* populations grown along a salt gradient (panel A): no salt, low salt stress (50mM), intermediate salt stress (100mM) and high salt stress (150mM); and relationship between stress and average Relative Interaction Index (± SE) for *A. thaliana* populations grown along a salt gradient (panel B): 2, 3, 5, 7, 10, 15, 20 individuals/pot. Note that panel B is only used for displaying how plant-plant interactions change with the stress gradient and information in panel B (I only show the two lowest and two highest densities) is exactly the same as in panel A.

Because the RII-density relationship is not linear, moving to the right has led to the second main finding, which is even more intriguing (Fig. 3 Chapter 4). Namely, the very applicability of the SGH (sensu Bertness & Callaway 1994) is density and stress-dependent. More specifically, the SGH holds for high densities but may not apply for low densities, especially under high stress. Under these conditions, i.e. few plants and harsh conditions, I observed that facilitative interactions broke down and net interactions became neutral or negative. As I have mentioned above, one explanation put forward has been that benefactors themselves suffer from stress and thus are not able to exert any net facilitative effects on neighbouring plants (Michalet *et al.* 2006). Furthermore, low densities could have aggravated the conditions because plants growing at low densities were much smaller than those growing at intermediate densities. Plant performance at high densities was also decreased perhaps due to both competition and stress, but they still had enough neighbours for ameliorating the harsh conditions.

Since I found plants demonstrated a positive density-dependent pattern at relatively densities, I was curious about whether individual responses of plants could also be influenced (Chapter 4). For example, on classical plastic response to increased neighbours is the so-called shade avoidance syndrome (Ballare *et al.* 1990; Smith 2000; Pierik *et al.* 2004; de Wit *et al.* 2012). A main feature of shade avoidance is an enhanced vertical growth (Schmitt & Wulff 1993; Schmitt *et al.* 2003; Vandenbussche *et al.* 2005; Franklin 2008). Plants that are predominantly forming rosettes and thus cannot lift their leaves to larger heights may elongate their petioles in response to competition thus building a larger rosette (Callahan & Pigliucci 2002; Franklin 2008). All these responses enable plants to avoid being suppressed in competition (Weiner 1990) and are thought to be adaptive in dense populations (Dudley & Schmitt 1996; Franklin & Whitelam 2005; Weijschedé *et al.* 2006). However, in stressful environments, increased population density might indicate facilitation instead of intensified competition (Bertness & Yeh 1994; Castro *et al.* 2013), at least between relatively low densities and intermediate densities (Chu *et al.* 2008; Xi *et al.* 2016). Therefore, under harsh environmental conditions, it may not necessarily be advantageous for a plant to exhibit a behaviour that enables it to suppress its neighbours, when they actually act as potential benefactors. In this scenario, suppressing or even excluding conspecific neighbours may be harmful, when stress amelioration provided by neighbours is crucial for survival. Then I looked at the allometric relationship (rosette size-body mass) for plants growing at relatively low densities (1, 2 and 3 individuals/pot). Indeed, I found in benign and low stress conditions where competition dominated, plants could build a relatively larger rosette to compete with neighbours, which is consistent with the classical shade-avoidance response. However, the shade-avoidance syndrome was not found and the allometric relationship changed oppositely when facilitation dominated under high stress levels. Form an evolutionary point of view, this may be explained by the fact that it is advantageous for plants to avoid suppressing their neighbours when depending on facilitation by them.

However, mechanisms, especially the physiological mechanism behind the observed pattern is not clear and should be subject to further studies.

Open questions and future studies

My reviews also indicate that in order to study reciprocal interactions, an intraspecific setting is also the method of choice. The importance and shortage of reciprocal facilitation has been reviewed several times (Bronstein 2009; Soliveres *et al.* 2015). However, I found the few cases where interspecific reciprocity (via the second review) was found, intraspecific facilitation among even-aged plants was detected as well. Thus, evidence for intraspecific facilitation, especially among even-aged plants, could be indicative for the general reciprocity of facilitation. I advocate the utilization of intraspecific settings also because it is unconfounded with species identity.

Future studies should explicitly consider the density-dependence of interactions along gradients, because by ignoring the effects of the ‘amount’ of benefactor plants, it is impossible to make general predictions about how plant–plant interactions change along environmental gradients and, related to that, to environmental change. More quantitative studies are also necessary for making theoretical progress. Furthermore, although I may explain why the plants exhibited an opposite pattern in harsh conditions, i.e., decreased allocation for competitive ability in reciprocal intraspecific facilitation is more advantageous. However, mechanisms behind such a behaviour remains unclearly and need further research.

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Appendices

Appendix 1a Literature list for intraspecific facilitation studies

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Appendix 1b The categories of biomes, climate zones, stress factors and populations for cases of intraspecific facilitation

Authors and Year	Location of studies	Biomes	Climate zones	Stress factors	Species	Response variables	Populations
Parker (1982)	Bernalillo watershed, USA	Grassland/Savanna	Arid	herbivory	*Gutierrezia microcephala*	survival	adult-seedling
Fuentes et al. (1986)	Los Dominicos, Chile	Forest/Woodland	Mediterranean	drought	*Quillaja saponaria*	survival	adult-seedling
	Los Dominicos, Chile	Forest/Woodland	Mediterranean	drought	*Lithraea caustica*	survival	adult-seedling
Bertness and Yeh (1994)	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Iva frutescens*	survival	even-aged
	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Iva frutescens*	growth	even-aged
	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Iva frutescens*	survival	adult-seedling
	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Iva frutescens*	growth	adult-seedling
	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Juncus gerardii*	survival	even-aged
	Rhode Island, USA	Coastal/Marine	Temperate	salinity	*Juncus gerardii*	growth	even-aged
Okland and Okland (1996)	Norway	Arctic/Alpine	Snow	drought	*Hylocomium splendens*	growth	even-aged
Bertness and Leonard (1997)	New England, USA	Coastal/Marine	Temperate	heat	*Ascophyllum nodosum*	survival	even-aged
	New England, USA	Coastal/Marine	Temperate	heat	*Ascophyllum nodosum*	growth	even-aged
	New England, USA	Coastal/Marine	Temperate	heat	*Fucus distichus*	survival	even-aged
Wied and Galen (1998)	Mosquito Range of Colorado, USA	Grassland/Savanna	Arid	drought	*Frasera speciosa*	survival	adult-seedling
	Mosquito Range of Colorado, USA	Forest/Woodland	Arid	drought	*Cirsium scopulorum*	survival	adult-seedling
Weltzin and McPherson (1999)	southeastern Arizona, USA	Forest/Woodland	Arid	radiation	*Quercus emoryi Torr*	survival	adult-seedling
Worm and Reusch (2000)	Friedrichsort, Germany	Coastal/Marine	Temperate	wave	*Zostera marina L.*	growth	even-aged
Pedersen et al. (2001)	growth chambers, Norway	Arctic/Alpine	Control	drought	*Dicranum majus*	growth	even-aged
	growth chambers, Norway	Arctic/Alpine	Control	drought	*Rhytidiadelphus loreus*	growth	even-aged

Doran et al. (2001)	Nelder plots, USA	Forest/Woodland	Snow	drought	*Picea glauca*	growth	even-aged
Rigg et al. (2002)	Mont Do, New Caledonia	Forest/Woodland	Tropical	radiation	*Araucaria laubenfelsii*	growth	adult-seedling
Franks and Peterson (2003)	Rookery Bay, USA	Coastal/Marine	Tropical	burial	*mixed*	survival	adult-seedling
	Rookery Bay, USA	Coastal/Marine	Tropical	burial	*mixed*	growth	adult-seedling
Franks (2003)	Florida and Georgia, USA	Coastal/Marine	Temperate	substrate mobility	*Uniola paniculata*	survival	even-aged
Matthies (2003)	Zurich, Switzerland	Grassland/Savanna	Temperate	nutrient deficiency	*Rhinanthus alectorolophus*	fitness	even-aged
Gomez-Aparicio et al. (2005)	southern Spain	Forest/Woodland	Mediterranean	drought	*Acer opalus ssp. granatense*	survival	adult-seedling
Kennedy and Sousa (2006)	Bolinas Ridge, USA	Grassland/Savanna	Temperate	drought	*Pseudotsuga menziesii*	survival	adult-seedling
Dickie et al. (2007)	Anoka County, USA	Grassland/Savanna	Temperate	nutrient deficiency	*Quercus ellipsoidalis E.J. Hill*	survival	adult-seedling
	Anoka County, USA	Old field	Temperate	nutrient deficiency	*Quercus ellipsoidalis E.J. Hill*	survival	adult-seedling
Reisman-Berman (2007)	Lahav Nature Reserve, Israel	Forest/Woodland	Mediterranean	drought	*Sarcopoterium spinosum*	survival	adult-seedling
Eränen and Kozlov (2007)	Kola Peninsula, Russia	Grassland/Savanna	Snow	wind	*Betula pubescens ssp. Czerepanovii*	survival	adult-seedling
	Kola Peninsula, Russia	Grassland/Savanna	Snow	wind	*Betula pubescens ssp. Czerepanovii*	growth	adult-seedling
Bos and van Katwijk (2007)	Balgzand, Netherlands	Coastal/Marine	Temperate	wave	*Zostera marina*	survival	even-aged
Espeland and Rice (2007)	California, USA	Grassland/Savanna	Mediterranean	nutrient deficiency	*Plantago erecta*	growth	even-aged
Teste et al. (2008)	British Columbia, Canada	Forest/Woodland	Snow	nutrient deficiency	*Pseudotsuga menziesii var.glauca*	growth	adult-seedling
	British Columbia, Canada	Forest/Woodland	Snow	nutrient deficiency	*Pseudotsuga menziesii var.glauca*	survival	adult-seedling
van Wesenbeeck et al. (2008)	Westerschelde, the Netherlands	Coastal/Marine	Temperate	wave	*Spartina anglica*	growth	adult-seedling
Eränen and Kozlov (2008)	Kola Peninsula, Russia	Grassland/Savanna	Snow	wind	*Betula pubescens ssp. Czerepanovii*	survival	adult-seedling

	Kola Peninsula, Russia	Grassland/Savanna	Snow	wind	*Betula pubescens ssp. Czerepanovii*	growth	adult-seedling
Chu et al. (2008)	Qing-Hai Tibetan Plateau, China	Arctic/Alpine	Polar	chill	*Elymus nutans*	growth	even-aged
Goldenheim et al. (2008)	New England, USA	Coastal/Marine	Temperate	heat	*Suaeda linearis*	growth	even-aged
	New England, USA	Coastal/Marine	Temperate	heat	*Suaeda linearis*	fitness	even-aged
le Roux and McGeoch (2008)	Marion Island, South Africa	Arctic/Alpine	Polar	burial	*Azorella selago*	space pattern	adult-seedling
	Marion Island, South Africa	Arctic/Alpine	Polar	burial	*Agrostis magellanica*	space pattern	adult-seedling
	Marion Island, South Africa	Arctic/Alpine	Polar	burial	*Blechnum penna-marina*	space pattern	adult-seedling
	Marion Island, South Africa	Arctic/Alpine	Polar	burial	*Acaena magellanica*	space pattern	adult-seedling
Armas and Pugnaire (2009)	Almerı´a, Spain	Grassland/Savanna	Mediterranean	drought	*Juniperus phoenicea*	survival	adult-seedling
Chu et al. (2009a)	Qing-Hai Tibetan Plateau, China	Arctic/Alpine	Polar	chill	*Elymus nutans*	growth	even-aged
Teste et al. (2009)	British Columbia, Canada	Forest/Woodland	Snow	drought	*Pseudotsuga menziesii var.glauca*	growth	adult-seedling
Otto et al. (2010)	Anaga Massif, Spain	Forest/Woodland	Mediterranean	drought	*Juniperus turbinate*	space pattern	adult-seedling
Tsai et al. (2010)	Willapa Bay, USA	Coastal/Marine	Mediterranean	drought	*Zostera japonica*	growth	even-aged
Jiang et al. (2010)	Weishan County, China	Coastal/Marine	Temperate	nutrient deficiency	*Hydrilla verticillata*	growth	even-aged
Luo et al. (2010)	wetland in Sanjiang Plain, China	Freshwater Wetland	Temperate	waterlogging	*Carex lasiocarpa*	growth	even-aged
	wetland in Sanjiang Plain, China	Freshwater Wetland	Temperate	waterlogging	*Deyeuxia angustifolia*	growth	even-aged
Huxham et al. (2010)	Sri Lanka and Kenya	Coastal/Marine	Tropical	waterlogging	*Rhizophora mucronata*	survival	even-aged
	Sri Lanka and Kenya	Coastal/Marine	Tropical	salinity	*Avicennia marina*	survival	even-aged
Fajardo and McIntire (2010)	Patagonia, Chile	Forest/Woodland	Temperate	drought	*Nothofagus pumilio*	space pattern	even-aged
Kumara et al. (2010)	Puttalam Lagoon, Sri Lanka	Coastal/Marine	Tropical	waterlogging	*Rhizophora mucronata*	survival	even-aged

Leger and Espeland (2010)	California, USA	Grassland/Savanna	Control	nutrient deficiency	*Plantago erecta Morris*	survival	even-aged
	California, USA	Grassland/Savanna	Control	nutrient deficiency	*Erodium brachycarpum Thell*	survival	even-aged
	California, USA	Grassland/Savanna	Control	nutrient deficiency	*Geranium dissectum L.*	survival	even-aged
Bingham and Simard (2011)	growth chamber, Canada	Forest/Woodland	Control	drought	*Pseudotsuga menziesii*	survival	even-aged
Bacilio et al. (2011)	growth chambers, Mexico	Grassland/Savanna	Control	drought	*Pachycereus pringlei*	growth	even-aged
Cerfonteyn et al. (2011)	Marion Island, South Africa	Arctic/Alpine	Polar	burial	*Azorella selago*	space pattern	adult-seedling
Fajardo and McIntire (2011)	Patagonia, Chile	Forest/Woodland	Temperate	drought	*Nothofagus pumilio*	survival	even-aged
McIntire and Fajardo (2011)	Patagonia, Chile	Forest/Woodland	Temperate	drought	*Nothofagus pumilio*	survival	even-aged
Bingham and Simard (2012)	Canada	Forest/Woodland	Snow	drought	*Pseudotsuga menziesii*	survival	adult-seedling
Cavieres and Penaloza (2012)	Santuario de la Naturaleza Yerba Loca, Chile	Forest/Woodland	Mediterranean	snow cover	*Kageneckia angustifolia*	survival	adult-seedling
Rolo, V., et al. (2013)	Extremadura region of central-western Spain	Forest/Woodland	Mediterranean	radiation	*Quercus ilex*	survival	adult-seedling
	Extremadura region of central-western Spain	Forest/Woodland	Mediterranean	radiation	*Quercus ilex*	growth	adult-seedling
Castro et al. (2013)	California, USA	Grassland/Savanna	Mediterranean	salinity	*Medicago truncatula*	growth	even-aged
	California, USA	Grassland/Savanna	Mediterranean	salinity	*Medicago truncatula*	fitness	even-aged
Long et al. (2013a)	Hainan Island, China	Arctic/Alpine	Snow	chill	*mixed*	space pattern	adult-seedling
Sheley and James (2014)	Burns, USA	Grassland/Savanna	Arid	drought	*Elymus elymoides [Raf.] Swezey*	growth	even-aged
	Burns, USA	Grassland/Savanna	Arid	drought	*Taeniatherum caputmedusae L.*	growth	even-aged
Yu et al. (2014)	Hangzhou Bay,	Coastal/Marine	Temperate	salinity	*Conyza canadensis L.*	growth	even-aged

	China						
	Hangzhou Bay, China	Coastal/Marine	Temperate	salinity	*Funaria hygrometrica L.*	growth	even-aged
Biswas and Wagner (2014)	Jokers Hill, Canada	Forest/Woodland	Snow	chill	*Alliaria petiolata*	survival	even-aged
Vogt et al. (2014)	Ajuruteua peninsula, Brazil	Coastal/Marine	Tropical	salinity	*Avicennia germinans*	growth	even-aged

Appendix 2a Literature list for facilitation studies with mechanisms

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Appendix 2b Main mechanisms in both intra- and interspecific studies

Authors and Year	Benefactor species	Benefactor growth forms	Beneficiary species	Beneficiary growth forms	Response variables	Stress factors	Main mechanisms
Harris and Brock (1972)	*Lolium perenne*	graminoid	*Trifolium repens*	herb	growth	herbivory	associational avoidance
Tahvanai and Root (1972)	*mixed*	mixed	*Brassica oleracea*	herb	growth	herbivory	associational avoidance
Christie et al. (1974)	*Plantago lanceolata*	herb	*Lolium perenne*	graminoid	growth	nutrient deficiency	mycorrhizal networks and natural grafts
Mcnaughton (1978)	*mixed*	graminoid	*Themeda triandra*	graminoid	growth	herbivory	associational avoidance
Jaksic and Fuentes (1980)	*Colliguaja odorifera*	shrub	*Solenomelus peduncularis*	herb	growth	herbivory	biotic refuge
	Colliguaja odorifera	shrub	*Solenomelus peduncularis*	herb	fitness	herbivory	biotic refuge
	Colliguaja odorifera	shrub	*Pasithea coerulea*	herb	growth	herbivory	biotic refuge
	Colliguaja odorifera	shrub	*Pasithea coerulea*	herb	fitness	herbivory	biotic refuge
Parker (1982)	*Gutierrezia microcephala*	shrub	*Gutierrezia microcephala*	shrub	survival	herbivory	biotic refuge
Fuentes et al. (1984)	*mixed*	shrubs	*Quillaja saponaria*	shrub	survival	drought	reduced water loss through shading
	mixed	shrubs	*Lithraea caustica*	shrub	survival	drought	reduced water loss through shading
	mixed	shrubs	*Maytenus*	shrub	survival	drought	reduced water loss through shading
Harris et al. (1984)	*mixed*	nonvascular	*mixed*	nonvascular	survival	herbivory	biotic refuge
Schat (1984).	*Juncus maritimus*	rush	*Centaurium Iittorale*	herb	survival	waterlogging	oxygen leakage through aerenchyma
	Juncus maritimus	rush	*Centaurium Iittorale*	herb	growth	waterlogging	oxygen leakage through aerenchyma
	Juncus maritimus	rush	*Plantago coronopus*	herb	survival	waterlogging	oxygen leakage through aerenchyma
	Juncus maritimus	rush	*Plantago coronopus*	herb	growth	waterlogging	oxygen leakage through aerenchyma

Kellman (1985)	*mixed*	mixed	*Xylopia frutescens*	tree	survival	nutrient deficiency	soil nutrient enrichment
	Byrsonima crassifolia	tree	*Calophyllum brasiliense*	tree	survival	nutrient deficiency	soil nutrient enrichment
Fuentes et al. (1986)	*Baccharis spp.*	shrub	*Quillaja saponaria*	tree	survival	drought	reduced water loss through shading
	Baccharis spp.	shrub	*Lithraea caustica*	tree	survival	drought	reduced water loss through shading
	Quillaja saponaria	tree	*Quillaja saponaria*	tree	survival	drought	reduced water loss through shading
	Quillaja saponaria	tree	*Lithraea caustica*	tree	survival	drought	reduced water loss through shading
	Lithraea caustica	tree	*Quillaja saponaria*	tree	survival	drought	reduced water loss through shading
	Lithraea caustica	tree	*Lithraea caustica*	tree	survival	drought	reduced water loss through shading
Pfister and Hay (1988)	*Sargassum filipendula*	nonvascular	*Gracilaria tikvahiae*	nonvascular	survival	herbivory	biotic refuge
Holmes and Jepsoninnes (1989)	*Aristida spp*	graminoid	*Bouteloua gracilis*	graminoid	growth	herbivory	associational avoidance
Williams (1990)	*mixed*	nonvascular	*mixed*	nonvascular	growth	nutrient deficiency	soil nutrient enrichment
Callaway et al. (1991)	*Quercus douglasii*	tree	*mixed*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
Carlsson and Callaghan (1991)	*Cassiope tetragona*	shrub	*Carex bigelowii*	graminoid	growth	wind	shelter against wind by larger neighbors
	Empetrumh ermaphroditu	shrub	*Carex bigelowii*	graminoid	growth	wind	shelter against wind by larger neighbors
	Racomitriuml anuginosum	nonvascular	*Carex bigelowii*	graminoid	growth	wind	shelter against wind by larger neighbors
	Cassiope tetragona	shrub	*Carex bigelowii*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
	Empetrumh ermaphroditu	shrub	*Carex bigelowii*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
Valientebanuet and Ezcurra (1991)	*Mimosa luisana*	shrub	*Neobuxbaumia tetetzo*	tree	survival	radiation	shelter from radiation by taller neighbors
Walker and Vitousek	*Myrica faya*	tree	*Metrosideros polymorpha*	tree	survival	radiation	shelter from radiation by

(1991)							taller neighbors
Bertness (1991)	*Spartina patens*	graminoid	*Juncus gerardi*	graminoid	survival	salinity	limited salt accumulation by shading substrate
Callaway (1992)	*Salvia leucophylla*	shrub	*Quercus douglasii*	tree	survival	radiation	shelter from radiation by taller neighbors
	Artemisia californica	shrub	*Quercus douglasii*	tree	survival	radiation	shelter from radiation by taller neighbors
Kellman and Kading (1992)	*Quercus rubra*	tree	*Pinus strobus*	tree	survival	radiation	shelter from radiation by taller neighbors
	Quercus rubra	tree	*Pinus resinosa*	tree	growth	radiation	shelter from radiation by taller neighbors
Bertness and Shumway (1993)	*Spartina patens*	graminoid	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
	Distichlis spicata	graminoid	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
Hjalten et al. (1993)	*Betula pubescens*	tree	*Alnus incana*	tree	growth	herbivory	associational avoidance
	Betula pubescens	tree	*Alnus incana*	tree	growth	herbivory	associational avoidance
Dawson (1993)	*Acer saccharum*	tree	*Podophyllum peltatum*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Asarum canadense*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Smilacina racemosa*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Fragaria virginiana*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Thalietrum dioieum*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Trillium grandiflorum*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Solidago flexicaulis*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Vaccinium vacillans*	herb	growth	drought	increased water availability
	Acer saccharum	tree	*Holcus lanatus*	graminoid	growth	drought	increased water availability
Aguiar and Sala (1994)	*Mulinum spinosum*	shrub	*Bromus pictus*	graminoid	survival	wind	shelter against wind by

							larger neighbors
Chapin et al. (1994)	*Dryas drummondii*	tree	*Picea sitchensis*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Alnus sinuata	tree	*Picea sitchensis*	tree	growth	nutrient deficiency	soil nutrient enrichment
Bertness and Yeh (1994)	*Iva frutescens*	shrub	*Iva frutescens*	shrub	survival	salinity	limited salt accumulation by shading substrate
	Iva frutescens	shrub	*Iva frutescens*	shrub	growth	salinity	limited salt accumulation by shading substrate
	Iva frutescens	shrub	*Juncus gerardi*	graminoid	survival	salinity	limited salt accumulation by shading substrate
	Iva frutescens	shrub	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Iva frutescens*	shrub	survival	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Iva frutescens*	shrub	growth	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Juncus gerardi*	graminoid	survival	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
Bertness and Hacker (1994)	*Iva frutescens*	shrub	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Iva frutescens*	shrub	growth	salinity	limited salt accumulation by shading substrate
Callaway (1994)	*Arthrocnemum subterminale*	shrub	*Hutchinsia procumbens*	herb	survival	salinity	limited salt accumulation by shading substrate
	Arthrocnemum subterminale	shrub	*Parapholis incurva*	graminoid	survival	salinity	limited salt accumulation by shading substrate
	Arthrocnemum subterminale	shrub	*Hutchinsia procumbens*	herb	growth	salinity	limited salt accumulation by shading substrate
	Arthrocnemum subterminale	shrub	*Parapholis incurva*	graminoid	growth	salinity	limited salt accumulation by shading substrate
Berkowitz et al. (1995)	*mixed*	mixed	*Acer saccharum*	tree	survival	radiation	shelter from radiation by taller neighbors
Hacker and Bertness (1995)	*Juncus gerardi*	shrub	*Iva frutescens*	graminoid	growth	salinity	limited salt accumulation by shading substrate

Okland and Okland (1996)	*Hylocomium splendens*	nonvascular	*Hylocomium splendens*	nonvascular	growth	drought	increased water storage by neighbors
Callaway et al. (1996)	*Artemisia tridentate*	shrub	*Pinus monophylla*	tree	survival	drought	reduced water loss through shading
Callaway and King (1996)	*Typha latifolia*	herb	*Salix exigua*	shrub	survival	waterlogging	oxygen leakage through aerenchyma
	Typha latifolia	herb	*Myosotis laxa*	herb	growth	waterlogging	oxygen leakage through aerenchyma
Pugnaire et al. (1996a)	*Retama sphaerocarpa*	shrub	*Marrubium vulgare*	herb	growth	nutrient deficiency	soil nutrient enrichment
	Marrubium vulgare	herb	*Retama sphaerocarpa*	shrub	growth	nutrient deficiency	soil nutrient enrichment
Bertness and Leonard (1997)	*Ascophyllum nodosum*	nonvascular	*Ascophyllum nodosum*	nonvascular	survival	heat	decreased temperature under canopy
	Fucus distichus	nonvascular	*Fucus distichus*	nonvascular	survival	heat	decreased temperature under canopy
	Ascophyllum nodosum	nonvascular	*Ascophyllum nodosum*	nonvascular	growth	heat	decreased temperature under canopy
Moro et al. (1997a)	*Retama sphaerocarpa*	shrub	*mixed*	herb	growth	nutrient deficiency	soil nutrient enrichment
	Retama sphaerocarpa	shrub	*mixed*	herb	growth	drought	reduced water loss through shading
Moro et al. (1997b)	*Retama sphaerocarpa*	shrub	*Barley*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
	Retama sphaerocarpa	shrub	*Barley*	graminoid	growth	drought	reduced water loss through shading
Callaway (1998)	*Pinus albicaulis*	tree	*Abies lasiocarpa*	tree	growth	wind	shelter against wind by larger neighbors
Raffaele and Veblen (1998)	*Schinus patagonicus*	shrub	*mixed*	herb	survival	drought	reduced water loss through shading
	Berberis buxifolia	shrub	*mixed*	herb	survival	drought	reduced water loss through shading
Wied and Galen (1998)	*Frasera speciosa*	herb	*Frasera speciosa*	herb	survival	drought	reduced water loss through shading
	Cirsium scopulorum	herb	*Cirsium scopulorum*	herb	survival	drought	reduced water loss through shading
Weltzin and	*Quercus emoryi Torr*	tree	*Quercus emoryi Torr*	tree	survival	radiation	shelter from radiation by

McPherson (1999)							taller neighbors
Hacker and Bertness (1999)	*Juncus gerardi*	graminoid	*Atriplex patula*	herb	survival	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Solidago sempervirens*	herb	survival	salinity	limited salt accumulation by shading substrate
	Juncus gerardi	graminoid	*Iva frutescens*	shrub	survival	salinity	limited salt accumulation by shading substrate
Holzapfel and Mahall (1999)	*Ambrosia dumosa*	shrub	*mixed*	herb	survival	drought	reduced water loss through shading
	Ambrosia dumosa	shrub	*mixed*	herb	growth	drought	reduced water loss through shading
	Ambrosia dumosa	shrub	*mixed*	herb	fitness	drought	reduced water loss through shading
Levine (2000)	*Carex nudata*	herb	*Juncus covillei*	graminoid	survival	substrate mobility	soil stabilization through plant structures
	Carex nudata	herb	*Conocephalum conicum*	nonvascular	survival	substrate mobility	soil stabilization through plant structures
	Carex nudata	herb	*Mimulus guttatus*	herb	growth	herbivory	associational avoidance
	Carex nudata	herb	*Epipactis gigantean*	herb	growth	herbivory	associational avoidance
Worm and Reusch (2000)	*Zostera marina L.*	herb	*Zostera marina L.*	herb	growth	wave	reduced wave velocity
Bruno (2000)	*Spartina alterniflora*	graminoid	*Suaeda linearis*	herb	survival	substrate mobility	soil stabilization through plant structures
	Spartina alterniflora	graminoid	*Salicornia europaea*	herb	survival	substrate mobility	soil stabilization through plant structures
Callaway et al. (2000)	*Cirsium obvalatum*	herb	*mixed*	mixed	fitness	herbivory	biotic refuge
	Veratrum lobelianum	herb	*mixed*	mixed	fitness	herbivory	biotic refuge
Rousset and Lepart (2000)	*Buxus sempervirens*	shrub	*Quercus humilis*	tree	survival	herbivory	biotic refuge
	Juniperus communis	shrub	*Quercus humilis*	tree	survival	herbivory	biotic refuge
Bruno and Kennedy (2000)	*Spartina alterniflora*	graminoid	*Suaeda linearis*	herb	survival	substrate mobility	soil stabilization through plant structures
	Spartina alterniflora	graminoid	*Salicornia europaea*	herb	survival	substrate mobility	soil stabilization through plant structures
Carrillo-Garcia et al.	*Prosopis articulate*	shrub	*Pachycereus pringlei*	tree	survival	nutrient	soil nutrient enrichment

(2000)						deficiency	
	Prosopis articulate	shrub	*Pachycereus pringlei*	tree	survival	heat	decreased temperature under canopy
	Prosopis articulate	shrub	*Pachycereus pringlei*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Prosopis articulate	shrub	*Pachycereus pringlei*	tree	growth	heat	decreased temperature under canopy
Gerdol et al. (2000)	*Vaccinium liginosum*	shrub	*Empetrum hermaphroditum*	shrub	growth	wind	shelter against wind by larger neighbors
Kennedy and Bruno (2000)	*Spartina alterniflora*	graminoid	*Salicornia virginica*	herb	survival	substrate mobility	soil stabilization through plant structures
	Spartina alterniflora	graminoid	*Suaeda linearis*	herb	survival	substrate mobility	soil stabilization through plant structures
	Spartina alterniflora	graminoid	*Salicornia europaea*	herb	survival	substrate mobility	soil stabilization through plant structures
Kitzberger et al. (2000)	*mixed*	shrub	*Austrocedrus chilensis*	tree	survival	radiation	shelter from radiation by taller neighbors
Shumway (2000)	*Myrica pensylvanica*	shrub	*Solidago sempervirens*	herb	growth	heat	decreased temperature under canopy
	Myrica pensylvanica	shrub	*Solidago sempervirens*	herb	growth	nutrient deficiency	soil nutrient enrichment
	Myrica pensylvanica	shrub	*Ammophila breviligulata*	herb	growth	heat	decreased temperature under canopy
	Myrica pensylvanica	shrub	*Ammophila breviligulata*	herb	growth	nutrient deficiency	soil nutrient enrichment
	Myrica pensylvanica	shrub	*Solidago sempervirens*	herb	fitness	heat	decreased temperature under canopy
	Myrica pensylvanica	shrub	*Solidago sempervirens*	herb	fitness	nutrient deficiency	soil nutrient enrichment
	Myrica pensylvanica	shrub	*Ammophila breviligulata*	herb	fitness	heat	decreased temperature under canopy
	Myrica pensylvanica	shrub	*Ammophila breviligulata*	herb	fitness	nutrient deficiency	soil nutrient enrichment
Tielbörger and Kadmon (2000)	*mixed*	shrub	*Senecio glaucus*	herb	fitness	nutrient deficiency	soil nutrient enrichment
	mixed	shrub	*Rumex pictus*	herb	fitness	nutrient deficiency	soil nutrient enrichment

	mixed	shrub	*Erodium laciniatum*	herb	fitness	nutrient deficiency	soil nutrient enrichment
Pedersen et al. (2001)	*Dicranum majus*	nonvascular	*Dicranum majus*	nonvascular	growth	drought	increased water storage by neighbors
	Rhytidiadelphus loreus	nonvascular	*Rhytidiadelphus loreus*	nonvascular	growth	drought	increased water storage by neighbors
Doran et al. (2001)	*Picea glauca*	tree	*Picea glauca*	tree	growth	drought	reduced water loss through shading
Rubio-Casal et al. (2001)	*Arthrocnemum macrostachyum*	herb	*Salicornia ramosissima*	herb	survival	salinity	limited salt accumulation by shading substrate
Anderson et al. (2001)	*Quercus fusiformis*	tree	*mixed*	shrub	survival	heat	decreased temperature under canopy
Chambers (2001)	*Pinus monophylla*	tree	*Pinus monophylla*	tree	survival	drought	reduced water loss through shading
	Juniperus osteosperma	tree	*Pinus monophylla*	tree	survival	drought	reduced water loss through shading
	Artemisia tridentate	shrub	*Pinus monophylla*	tree	survival	drought	reduced water loss through shading
Maestre et al. (2001)	*Stipa tenacissima*	graminoid	*Medicago arborea*	shrub	survival	drought	reduced water loss through shading
	Stipa tenacissima	graminoid	*Quercus coccifera*	shrub	survival	drought	reduced water loss through shading
	Stipa tenacissima	graminoid	*Pistacia lentiscus*	shrub	survival	drought	reduced water loss through shading
	Stipa tenacissima	graminoid	*Medicago arborea*	shrub	growth	drought	reduced water loss through shading
Rigg et al. (2002)	*Araucaria laubenfelsii*	tree	*Araucaria kzubenfikii*	tree	growth	radiation	shelter from radiation by taller neighbors
	Araucaria laubenfelsii	tree	*Rapanea diminuta*	shrub	growth	radiation	shelter from radiation by taller neighbors
	Araucaria laubenfelsii	tree	*Scaevola beckii*	shrub	growth	radiation	shelter from radiation by taller neighbors
	Araucaria laubenfelsii	tree	*Dracophyllum verticillatum*	shrub	growth	radiation	shelter from radiation by taller neighbors
	Araucaria laubenfelsii	tree	*Wikstroemia viridifolia*	shrub	growth	radiation	shelter from radiation by taller neighbors
	Araucaria	tree	*Myodocarpus fraxinifolius*	shrub	growth	radiation	shelter from radiation by

	laubenfelsii						taller neighbors
Bertness and Ewanchuk (2002)	*mixed*	graminoid	*Spartina patens*	graminoid	growth	salinity	limited salt accumulation by shading substrate
	mixed	graminoid	*Juncus gerardi*	graminoid	growth	salinity	limited salt accumulation by shading substrate
	mixed	graminoid	*Atriplex patula*	herb	growth	salinity	limited salt accumulation by shading substrate
	mixed	graminoid	*Solidago sempervirens*	herb	growth	salinity	limited salt accumulation by shading substrate
	mixed	graminoid	*Iva frutescens*	shrub	growth	salinity	limited salt accumulation by shading substrate
Carino and Daehler (2002)	*Chamaecrista nictitans*	herb	*Pennisetum setaceum*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
Castro et al. (2002)	*Salvia lavandulifolia*	shrub	*Pinus sylvestris L.*	tree	survival	drought	reduced water loss through shading
	Salvia lavandulifolia	shrub	*Pinus nigra Arnold*	tree	survival	drought	reduced water loss through shading
Cavieres et al. (2002)	*Bolax gummifera*	shrub	*mixed*	mixed	species richness	wind	shelter against wind by larger neighbors
Maestre et al. (2002)	*Stipa tenacissima*	graminoid	*Quercus coccifera*	shrub	survival	drought	reduced water loss through shading
Franks and Peterson (2003)	*mixed*	mixed	*mixed*	mixed	survival	burial	protection from the weight of sediment or sand
	mixed	mixed	*mixed*	mixed	growth	burial	protection from the weight of sediment or sand
Franks (2003)	*Uniola paniculata*	graminoid	*Uniola paniculata*	graminoid	survival	substrate mobility	soil stabilization through plant structures
	Iva imbricate	shrub	*Iva imbricate*	shrub	survival	substrate mobility	soil stabilization through plant structures
Matthies (2003)	*Rhinanthus alectorolophus*	herb	*Rhinanthus alectorolophus*	herb	survival	nutrient deficiency	mycorrhizal networks and natural grafts
Arroyo et al. (2003)	*Azorella monantha*	shrub	*mixed*	herb	species richness	wind	shelter against wind by larger neighbors
Egerova et al. (2003)	*Spartina alterniflora*	graminoid	*Baccharis halimifolia*	shrub	survival	salinity	limited salt accumulation by shading substrate
	Spartina alterniflora	graminoid	*Baccharis halimifolia*	shrub	growth	salinity	limited salt accumulation by shading substrate

Lenz and Facelli (2003)	*Atriplex vesicaria*	shrub	*Orbea variegate*	herb	growth	radiation	shelter from radiation by taller neighbors
Maestre et al. (2003)	*Stipa tenacissima*	graminoid	*Pistacia lentiscus*	shrub	survival	drought	reduced water loss through shading
Martinez (2003)	*Chamaecrista chamaecristoides*	shrub	*Trachypogon plumosus*	graminoid	survival	wind	shelter against wind by larger neighbors
	Chamaecrista chamaecristoides	shrub	*Schizachyrium scoparium*	graminoid	survival	wind	shelter against wind by larger neighbors
Rodriguez-Echeverria and Perez-Fernandez (2003)	*Retama sphaerocarpa*	shrub	*mixed*	herb	growth	nutrient deficiency	soil nutrient enrichment
Garcia and Obeso (2003)	*Ilex aquifolium*	shrub	*Taxus baccata*	tree	survival	herbivory	biotic refuge
	Crataegus monogyna	shrub	*Taxus baccata*	tree	survival	herbivory	biotic refuge
Ross et al. (2003)	*mixed*	graminoid	*Ulmus rubra*	tree	survival	drought	reduced water loss through shading
Singh et al. (2003)	*Calligonum polygonoides*	shrub	*Cassia angustifolia*	shrub	survival	drought	reduced water loss through shading
	Calligonum polygonoides	shrub	*Cassia angustifolia*	shrub	growth	drought	reduced water loss through shading
Pugnaire et al. (2004)	*mixed*	shrub	*mixed*	herb	growth	nutrient deficiency	soil nutrient enrichment
Castro et al. (2004a)	*Berberis hispanica*	shrub	*Pinus sylvestris*	tree	survival	drought	reduced water loss through shading
	Prunus ramburii	shrub	*Pinus sylvestris*	tree	survival	drought	reduced water loss through shading
Castro et al. (2004b)	*Salvia lavandulifolia*	shrub	*Pinus sylvestris*	tree	survival	drought	reduced water loss through shading
	Salvia lavandulifolia	shrub	*Pinus nigra*	tree	survival	drought	reduced water loss through shading
Fogel et al. (2004)	*Triglochin maritime*	graminoid	*mixed*	herb	species richness	waterlogging	ground elevation
Maestre and Cortina (2004)	*Stipa tenacissima*	graminoid	*Pistacia lentiscus*	shrub	survival	drought	reduced water loss through shading
Martinez et al. (2004)	*Chamaecrista chamaecristoides*	shrub	*Trachypogon plumosus*	graminoid	survival	wind	shelter against wind by larger neighbors

	Chamaecrista chamaecristoides	shrub	*Schizachyrium scoparium*	graminoid	survival	wind	shelter against wind by larger neighbors
	Chamaecrista chamaecristoides	shrub	*Trachypogon plumosus*	graminoid	fitness	wind	shelter against wind by larger neighbors
	Chamaecrista chamaecristoides	shrub	*Schizachyrium scoparium*	graminoid	fitness	wind	shelter against wind by larger neighbors
Nara and Hogetsu (2004)	*Salix reinii*	shrub	*Salix reinii*	shrub	growth	nutrient deficiency	mycorrhizal networks and natural grafts
Bakker et al. (2004)	*Prunus spinosa*	shrub	*Quercus robur*	tree	survival	herbivory	biotic refuge
	Prunus spinosa	shrub	*Quercus robur*	tree	growth	herbivory	biotic refuge
Oesterheld and Oyarzabal (2004)	*mixed*	graminoid	*Bromus pictus*	graminoid	growth	herbivory	associational avoidance
	mixed	graminoid	*Bromus pictus*	graminoid	fitness	herbivory	associational avoidance
Olofsson (2004)	*mixed*	shrub	*Carex bigelowii*	graminoid	growth	wind	shelter against wind by larger neighbors
Bossuyt et al. (2005)	*Senecio jacobaea*	herb	*mixed*	mixed	growth	herbivory	associational avoidance
	Senecio jacobaea	herb	*mixed*	mixed	fitness	herbivory	associational avoidance
	Iris pseudacorus	herb	*mixed*	mixed	growth	herbivory	associational avoidance
	Iris pseudacorus	herb	*mixed*	mixed	fitness	herbivory	associational avoidance
Armas and Pugnaire (2005)	*Cistus clusii*	shrub	*Stipa tenacissima*	graminoid	growth	drought	reduced water loss through shading
Cavieres et al. (2005)	*Azorella monantha*	shrub	*Taraxacum officinale*	herb	survival	drought	reduced water loss through shading
Dickie et al. (2005)	*Quercus ellipsoidalis*	tree	*Quercus macrocarpa*	tree	growth	nutrient deficiency	mycorrhizal networks and natural grafts
Ervin (2005)	*Juncus effuses*	graminoid	*mixed*	herb	species richness	waterlogging	ground elevation
Forrester et al. (2005)	*Acacia mearnsii*	tree	*Eucalyptus. Globulus*	tree	growth	nutrient deficiency	soil nutrient enrichment
Gomez-Aparicio et al. (2005a)	*Acer opalus ssp. granatense*	tree	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading
	mixed	mixed	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading
	mixed	shrub	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading

Gomez-Aparicio et al. (2005b)	*Salvia lavandulifolia ssp. vellerea*	shrub	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading
	Genista versicolor	shrub	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading
	Salvia lavandulifolia ssp. vellerea	shrub	*Quercus pyrenaica*	tree	survival	drought	reduced water loss through shading
	Salvia lavandulifolia ssp. vellerea	shrub	*Quercus ilex*	tree	survival	drought	reduced water loss through shading
	Genista versicolor	shrub	*Quercus ilex*	tree	survival	drought	reduced water loss through shading
Callaway et al. (2005)	*Cirsium obalatum*	herb	*mixed*	mixed	species richness	herbivory	biotic refuge
	Veratrum lobelianum	herb	*mixed*	mixed	species richness	herbivory	biotic refuge
	Cirsium obalatum	herb	*Anthoxanthum odoratum*	graminoid	growth	herbivory	biotic refuge
	Veratrum lobelianum	herb	*Phleum alpinum*	graminoid	growth	herbivory	biotic refuge
Klanderud (2005)	*Dryas octopetala*	shrub	*Thalictrum alpinum*	herb	growth	chill	reduced convective heat loss and low albedo
	Dryas octopetala	shrub	*Carex vaginata*	graminoid	growth	chill	reduced convective heat loss and low albedo
Liancourt et al. (2005)	*mixed*	graminoid	*Brachypodium rupestre*	graminoid	survival	drought	reduced water loss through shading
	mixed	graminoid	*Arrhenatherum elatius*	graminoid	survival	drought	reduced water loss through shading
Molina-Montenegro et al. (2005)	*Macrocystis pyrifera*	nonvascular	*Ulva lactuca*	nonvascular	growth	drought	reduced water loss through shading
Zanini et al. (2006)	*mixed*	mixed	*Inga virescens*	tree	survival	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Inga virescens*	tree	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Araucaria angustifolia*	tree	survival	herbivory	associational avoidance
Aerts et al. (2006)	*Euclea racemose*	shrub	*Olea europaea ssp. Cuspidate*	tree	survival	radiation	shelter from radiation by taller neighbors
Milbrandt and Tinsley (2006)	*Batis maritima*	shrub	*Avicennia germinans*	tree	survival	waterlogging	ground elevation
Akhalkatsi et al.	*Rhododendron*	shrub	*Betula litwinowii*	tree	survival	radiation	shelter from radiation by

(2006)	*caucasicum*						taller neighbors
Baumeister and Callaway (2006)	*Pinus flexilis*	tree	*Pseudotsuga menziesii*	tree	survival	wind	shelter against wind by larger neighbors
	Pinus flexilis	tree	*Ribes cereum*	shrub	survival	wind	shelter against wind by larger neighbors
Cavieres et al. (2006)	*Laretia acaulis*	shrub	*Cerastium arvense*	herb	survival	drought	reduced water loss through shading
	Laretia acaulis	shrub	*Hordeum comosum*	graminoid	survival	drought	reduced water loss through shading
Frerot et al. (2006)	*Anthyllis vulneraria*	herb	mixed	mixed	growth	soil contamination of metal	uptake of heavy metals from soil
Holzapfel et al. (2006)	*mixed*	shrub	*mixed*	herb	species richness	drought	reduced water loss through shading
Kennedy and Sousa (2006)	*Pseudotsuga menziesii*	tree	*Pseudotsuga menziesii*	tree	survival	drought	increased water availability
	Pseudotsuga menziesii	tree	*Lithocarpus densiflora*	tree	survival	drought	increased water availability
Pages and Michalet (2006)	*mixed*	tree	*Galium odoratum*	herb	survival	radiation	shelter from radiation by taller neighbors
Ramirez et al. (2006)	*mixed*	mixed	*Helleborus foetidus*	herb	survival	heat	decreased temperature under canopy
Reisman-Berman (2007)	*Sarcopoterium spinosum*	shrub	*Sarcopoterium spinosum*	shrub	survival	drought	reduced water loss through shading
Groeneveld et al. (2007)	*Polytrichum strictum*	nonvascular	*Sphagnum*	nonvascular	growth	radiation	shelter from radiation by taller neighbors
Bos and van Katwijk (2007)	*Zostera marina*	herb	*Zostera marina*	herb	survival	wave	reduced wave velocity
Graff et al. (2007)	*Stipa speciosa*	graminoid	*Poa ligularis*	graminoid	growth	herbivory	associational avoidance
	Stipa speciosa	graminoid	*Bromus pictus*	graminoid	growth	herbivory	associational avoidance
Karban (2007)	*Artemisia tridentata*	graminoid	*Wyethia mollis*	herb	growth	herbivory	associational avoidance
Smit et al. (2007)	*Rosa rubiginosa*	shrub	*Fagus sylvatica*	tree	survival	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Acer pseudoplatanus*	tree	survival	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Abies alba*	tree	survival	herbivory	biotic refuge

	Rosa rubiginosa	shrub	*Picea abies*	tree	survival	herbivory	biotic refuge
Espeland and Rice (2007)	*Plantago erecta*	herb	*Plantago erecta*	herb	growth	nutrient deficiency	mycorrhizal networks and natural grafts
Dona and Galen (2007)	*Salix spp.*	shrub	*Chamerion angustifolium*	herb	survival	wind	shelter against wind by larger neighbors
Zhao et al. (2007)	*Caragana microphylla*	shrub	*Pennisetum centrasiaticum*	herb	survival	substrate mobility	soil stabilization through plant structures
	Caragana microphylla	shrub	*Pennisetum centrasiaticum*	herb	growth	substrate mobility	soil stabilization through plant structures
Eränen and Kozlov (2007)	*Betula pubescens ssp. Czerepanovii*	tree	*Betula pubescens ssp. czerepanovii*	tree	survival	wind	shelter against wind by larger neighbors
	Betula pubescens ssp. Czerepanovii	tree	*Betula pubescens ssp. czerepanovii*	tree	growth	wind	shelter against wind by larger neighbors
Sthultz et al. (2007)	*Fallugia paradoxa*	shrub	*Pinus edulis*	tree	survival	drought	reduced water loss through shading
	Fallugia paradoxa	shrub	*Pinus edulis*	tree	growth	drought	reduced water loss through shading
Zvereva and Kozlov (2007)	*Betula pubescens subsp. czerepanovii*	tree	*Vaccinium myrtillus*	shrub	growth	wind	shelter against wind by larger neighbors
Aerts et al. (2007)	*Acacia etbaica*	shrub	*Olea europaea ssp. cuspidate*	tree	survival	drought	reduced water loss through shading
	Euclea racemosa	shrub	*Olea europaea ssp. cuspidate*	tree	survival	drought	reduced water loss through shading
Altieri et al. (2007)	*Spartina alterniflora*	graminoid	*Chondrus crispus*	nonvascular	growth	substrate mobility	soil stabilization through plant structures
Dickie et al. (2007)	*Quercus ellipsoidalis E.J. Hill*	tree	*Quercus ellipsoidalis E.J. Hill*	tree	survival	nutrient deficiency	mycorrhizal networks and natural grafts
	Quercus ellipsoidalis E.J. Hill	tree	*Quercus macrocarpa Michx.*	tree	survival	nutrient deficiency	mycorrhizal networks and natural grafts
	Sesuvium portulacastrum	herb	*Rhizophora mangle*	tree	survival	waterlogging	oxygen leakage through aerenchyma
	Sesuvium portulacastrum	herb	*Rhizophora mangle*	tree	growth	waterlogging	oxygen leakage through aerenchyma
	Distichlis spicata	graminoid	*Rhizophora mangle*	tree	survival	waterlogging	oxygen leakage through aerenchyma
	Distichlis spicata	graminoid	*Rhizophora mangle*	tree	growth	waterlogging	oxygen leakage through aerenchyma

Boulant et al. (2008)	*Juniperus communis*	shrub	*Pinus sylvestris*	tree	survival	herbivory	biotic refuge
	Juniperus communis	shrub	*Pinus sylvestris*	tree	survival	drought	reduced water loss through shading
	Juniperus communis	shrub	*Pinus nigra*	tree	survival	herbivory	biotic refuge
	Juniperus communis	shrub	*Pinus nigra*	tree	survival	drought	reduced water loss through shading
le Roux and McGeoch (2008)	*Azorella selago*	shrub	*Azorella selago*	shrub	growth	burial	protection from the weight of sediment or sand
	Agrostis magellanica	graminoid	*Agrostis magellanica*	graminoid	growth	burial	protection from the weight of sediment or sand
	Blechnum penna-marina	herb	*Blechnum penna-marina*	herb	growth	burial	protection from the weight of sediment or sand
	Acaena magellanica	shrub	*Acaena magellanica*	shrub	growth	burial	protection from the weight of sediment or sand
Eränen and Kozlov (2008)	*Betula pubescens subsp. czerepanovii*	tree	*Betula pubescens subsp. czerepanovii*	tree	survival	wind	shelter against wind by larger neighbors
	Betula pubescens subsp. czerepanovii	tree	*Betula pubescens subsp. czerepanovii*	tree	growth	wind	shelter against wind by larger neighbors
Goldenheim et al. (2008)	*Suaeda linearis*	herb	*Suaeda linearis*	herb	growth	heat	decreased temperature under canopy
Armas et al. (2008)	*Adesmia volckmanni*	shrub	*Stipa speciosa*	graminoid	growth	heat	decreased temperature under canopy
	Adesmia volckmanni	shrub	*Stipa humilis*	graminoid	growth	heat	decreased temperature under canopy
Cavieres et al. (2008)	*Azorella monantha*	shrub	*Taraxacum officinale*	herb	survival	heat	decreased temperature under canopy
	Laretia acaulis	shrub	*Taraxacum officinale*	herb	growth	heat	decreased temperature under canopy
	Azorella monantha	shrub	*Taraxacum officinale*	herb	growth	heat	decreased temperature under canopy
	Azorella monantha	shrub	*Taraxacum officinale*	herb	fitness	heat	decreased temperature under canopy
	Laretia acaulis	shrub	*Taraxacum officinale*	herb	fitness	heat	decreased temperature under canopy
Gomez-Aparicio et al. (2008)	*mixed*	shrub	*Acer opalus ssp. granatense*	tree	survival	drought	reduced water loss through shading

	mixed	shrub	*Quercus ilex*	tree	survival	drought	reduced water loss through shading
Keyes and Maguire (2008)	*Ceanothus velutinus*	shrub	*Pinus ponderosa*	tree	survival	heat	decreased temperature under canopy
Smit et al. (2008)	*Genista hirsute*	shrub	*Quercus ilex*	tree	survival	drought	reduced water loss through shading
Teste and Simard (2008)	*Pseudotsuga menziesii var. glauca*	tree	*Pseudotsuga menziesii var. glauca*	tree	growth	nutrient deficiency	mycorrhizal networks and natural grafts
van Wesenbeeck et al. (2008)	*Spartina anglica*	graminoid	*Spartina anglica*	graminoid	growth	wave	reduced wave velocity
Wang et al. (2008)	*mixed*	mixed	*Halenia corniculata*	herb	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Thermopsis lanceolata*	herb	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Elymus nutans Griseb*	graminoid	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Deschampsia cespitosa*	graminoid	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Scirpus pumilus Vahl*	graminoid	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Kobresia capillifolia*	graminoid	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Kobresia macrantha*	graminoid	growth	chill	reduced convective heat loss and low albedo
Zhang et al. (2008)	*Suaeda salsa*	herb	*Suaeda salsa*	herb	growth	salinity	limited salt accumulation by shading substrate
Armas and Pugnaire (2009)	*mixed*	mixed	*Juniperus phoenicea*	shrub	survival	drought	reduced water loss through shading
	Pistacia lentiscus	shrub	*Juniperus phoenicea*	shrub	survival	drought	reduced water loss through shading
	Juniperus phoenicea	shrub	*Juniperus phoenicea*	shrub	survival	drought	reduced water loss through shading
	Juniperus phoenicea	shrub	*Pistacia lentiscus*	shrub	survival	drought	reduced water loss through shading
Badano et al. (2009)	*Mimosa luisana*	shrub	*Quercus castanea*	tree	survival	radiation	shelter from radiation by taller neighbors
	Senecio sp.	shrub	*Quercus castanea*	tree	survival	radiation	shelter from radiation by

							taller neighbors
Caccia et al. (2009)	*Chusquea culeou*	graminoid	*Nothofagus dombeyi*	tree	survival	drought	reduced water loss through shading
Chu et al. (2009b)	*mixed*	graminoid	*Kobresia macrantha Boeck*	graminoid	growth	chill	reduced convective heat loss and low albedo
	Eryngium horridum	herb	*mixed*	mixed	species richness	herbivory	associational avoidance
Gea-Izquierdo et al. (2009)	*Quercus ilex L.*	tree	*mixed*	mixed	growth	nutrient deficiency	soil nutrient enrichment
Irving and Bertness (2009)	*Spartina alterniflora*	graminoid	*Suaeda linearis*	herb	survival	substrate mobility	soil stabilization through plant structures
Padilla and Pugnaire (2009)	*Retama sphaerocarpa*	shrub	*Olea europaea*	tree	survival	heat	decreased temperature under canopy
	Retama sphaerocarpa	shrub	*Olea europaea*	tree	survival	nutrient deficiency	soil nutrient enrichment
Poulter et al. (2009)	*Cladium jamaicense*	graminoid	*Pinus taeda*	tree	survival	salinity	limited salt accumulation by shading substrate
Riege and Sigurgeirsson (2009)	*Lupinus nootkatensis*	herb	*Picea sitchensis ,*	tree	growth	chill	reduced convective heat loss and low albedo
	Lupinus nootkatensis	herb	*Salix hookeriana*	tree	growth	chill	reduced convective heat loss and low albedo
	Lupinus nootkatensis	herb	*Betula pubescens*	tree	growth	chill	reduced convective heat loss and low albedo
Saccone et al. (2009)	*mixed*	tree	*Abies alba*	tree	survival	heat	decreased temperature under canopy
Teste et al. (2009)	*Pseudotsuga menziesii var.glauca*	tree	*Pseudotsuga menziesii var.glauca*	tree	survival	nutrient deficiency	mycorrhizal networks and natural grafts
Venn et al. (2009)	*mixed*	mixed	*Brachyscome ridigula*	herb	growth	wind	shelter against wind by larger neighbors
Villarreal-Barajas and Martorell (2009)	*mixed*	mixed	*Microchloa kunthii Desv.*	graminoid	growth	drought	increased water storage by neighbors
	mixed	mixed	*Microchloa kunthii Desv.*	graminoid	fitness	drought	increased water storage by neighbors
Vandenberghe et al. (2009)	*Rosa rubiginosa*	shrub	*Abies alba*	tree	survival	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Picea abies*	tree	survival	herbivory	biotic refuge

	Rosa rubiginosa	shrub	*Acer pseudoplatanus*	tree	survival	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Fagus sylvatica*	tree	survival	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Abies alba*	tree	growth	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Picea abies*	tree	growth	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Acer pseudoplatanus*	tree	growth	herbivory	biotic refuge
	Rosa rubiginosa	shrub	*Fagus sylvatica*	tree	growth	herbivory	biotic refuge
Yang et al. (2009)	*Acacia mangium*	tree	*Castanopsis hystrix*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Acacia mangium	tree	*Michelia macclurei*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Acacia mangium	tree	*Manglietia glauca*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Acacia auriculiformis	tree	*Castanopsis hystrix*	tree	growth	nutrient deficiency	soil nutrient enrichment
	Acacia auriculiformis	tree	*Michelia macclurei*	tree	growth	nutrient deficiency	soil nutrient enrichment
Shararn et al. (2009)	*mixed*	shrub	*Acacia polyacantha*	tree	survival	herbivory	biotic refuge
Chaneton et al. (2010)	*mixed*	shrub	*Austrocedrus chilensis*	tree	survival	drought	reduced water loss through shading
Tsai et al. (2010)	*Zostera japonica*	herb	*Zostera japonica*	herb	growth	drought	increased water storage by neighbors
Fajardo and McIntire (2010)	*Nothofagus pumilio*	tree	*Nothofagus pumilio*	tree	survival	drought	mycorrhizal networks and natural grafts
Luo et al. (2010)	*Glyceria spiculosa*	graminoid	*Carex lasiocarpa*	graminoid	growth	waterlogging	oxygen leakage through aerenchyma
	Glyceria spiculosa	graminoid	*Deyeuxia angustifolia*	graminoid	growth	waterlogging	oxygen leakage through aerenchyma
	Glyceria spiculosa	graminoid	*Carex lasiocarpa*	graminoid	growth	waterlogging	oxygen leakage through aerenchyma
	Glyceria spiculosa	graminoid	*Deyeuxia angustifolia*	graminoid	growth	waterlogging	oxygen leakage through aerenchyma
Huxham et al. (2010)	*Rhizophora mucronata*	tree	*Rhizophora mucronata*	tree	survival	salinity	limited salt accumulation by shading substrate
	Avicennia marina	tree	*Avicennia marina*	tree	survival	waterlogging	ground elevation

Abdallah and Chaieb (2010)	*Acacia tortilis subsp. raddiana*	tree	*mixed*	herb	growth	nutrient deficiency	soil nutrient enrichment
	Acacia tortilis subsp. raddiana	tree	*mixed*	herb	species richness	nutrient deficiency	soil nutrient enrichment
Kumara et al. (2010)	*Rhizophora mucronata*	tree	*Rhizophora mucronata*	tree	survival	waterlogging	ground elevation
Burkart et al. (2010)	*mixed*	graminoid	*Juncus atratus*	herb	survival	waterlogging	oxygen leakage through aerenchyma
Cuesta et al. (2010)	*Retama sphaerocarpa*	shrub	*Quercus ilex*	tree	survival	radiation	shelter from radiation by taller neighbors
DeWine and Cooper (2010)	*Tamarix sp.*	shrub	*Acer negundo*	tree	survival	heat	decreased temperature under canopy
Yang et al. (2010a)	*Rhodomyrtus tomentosa*	shrub	*Schima superba,*	tree	survival	radiation	shelter from radiation by taller neighbors
	Rhodomyrtus tomentosa	shrub	*Michelia macclurei*	tree	survival	radiation	shelter from radiation by taller neighbors
	Rhodomyrtus tomentosa	shrub	*Castanopsis fissa*	tree	survival	radiation	shelter from radiation by taller neighbors
Diwold et al. (2010)	*grasses such as Hordelymus europaeus (L.) Harz*	graminoid	*Fagus sylvatica*	tree	survival	substrate mobility	soil stabilization through plant structures
Griffith (2010)	*Purshia tridentate*	shrub	*Bromus tectorum*	graminoid	survival	nutrient deficiency	soil nutrient enrichment
	Purshia tridentate	shrub	*Bromus tectorum*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
	Artemisia tridentate	shrub	*Bromus tectorum*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
	Artemisia tridentate	shrub	*Bromus tectorum*	graminoid	survival	drought	reduced water loss through shading
Yu et al. (2010)	*Kobresia tibetica*	graminoid	*mixed*	mixed	species richness	herbivory	associational avoidance
Legras et al. (2010)	*Arctostaphylos patula*	shrub	*Pinus lambertiana*	tree	survival	drought	reduced water loss through shading
	Arctostaphylos patula	shrub	*Pinus lambertiana*	tree	survival	drought	reduced water loss through shading
	Purshia tridentata	shrub	*Pinus jeffreyi*	tree	survival	drought	reduced water loss through shading

	Purshia tridentata	shrub	*Pinus jeffreyi*	tree	survival	drought	reduced water loss through shading
le Roux and McGeoch (2010)	*Azorella selago*	shrub	*Agrostis magellanica*	graminoid	growth	wind	shelter against wind by larger neighbors
Montgomery et al. (2010)	*mixed*	shrub	*Pinus strobus*	tree	survival	radiation	shelter from radiation by taller neighbors
	mixed	shrub	*Acer rubrum*	tree	survival	radiation	shelter from radiation by taller neighbors
Yang et al. (2010b)	*Arenaria polytrichoides*	herb	*mixed*	mixed	survival	nutrient deficiency	soil nutrient enrichment
Saccone et al. (2010)	*Salix alba*	tree	*Acer negundo*	tree	survival	wave	reduced wave velocity
Sullivan and Sveinbjoernsson (2010)	*Eriophorum vaginatum*	herb	*Picea glauca*	tree	survival	chill	reduced convective heat loss and low albedo
Xu et al. (2010)	*Potentilla fruticosa*	shrub	*mixed*	mixed	growth	heat	decreased temperature under canopy
Boughton (2011)	*Juncus effusus*	graminoid	*mixed*	mixed	growth	herbivory	associational avoidance
Bingham and Simard (2011)	*Pseudotsuga menziesii*	tree	*Pseudotsuga menziesii*	tree	survival	drought	mycorrhizal networks and natural grafts
Fajardo and McIntire (2011)	*Nothofagus pumilio*	tree	*Nothofagus pumilio*	tree	survival	drought	reduced water loss through shading
Bacilio et al. (2011)	*Pachycereus pringlei*	tree	*Pachycereus pringlei*	tree	growth	drought	reduced water loss through shading
McIntire and Fajardo (2011)	*Nothofagus pumilio*	tree	*Nothofagus pumilio*	tree	survival	drought	mycorrhizal networks and natural grafts
Farrell et al. (2011)	*mixed*	shrub	*mixed*	herb	survival	salinity	limited salt accumulation by shading substrate
Anthelme et al. (2011)	*Setaria sphacelata*	graminoid	*Ceroxylon echinulatum*	tree	survival	drought	reduced water loss through shading
Becerra et al. (2011)	*mixed*	herb	*Colliguaya odorifera*	shrub	survival	drought	reduced water loss through shading
	mixed	herb	*Schinus polygamous*	shrub	survival	drought	reduced water loss through shading
Biaou et al. (2011)	*mixed*	tree	*Afzelia Africana*	tree	survival	drought	reduced water loss through shading
	mixed	tree	*Khaya senegalensis*	tree	survival	drought	reduced water loss through

							shading
Suzuki and Suzuki (2011)	*Urtica thunbergiana*	herb	*Persicaria longiseta*	herb	survival	herbivory	biotic refuge
Butler and Orians (2011)	*Sedum album*	herb	*Agastache rupestris*	herb	growth	drought	reduced water loss through shading
	Sedum album	herb	*Asclepias verticillata*	herb	growth	drought	reduced water loss through shading
	Sedum. rupestre	herb	*Agastache 'Black Adder'*	herb	growth	drought	reduced water loss through shading
	Sedum. Sexangulare	herb	*Agastache 'Black Adder'*	herb	growth	drought	reduced water loss through shading
	Sedum. spurium	herb	*Agastache 'Black Adder'*	herb	growth	drought	reduced water loss through shading
Wheeler et al. (2011)	*Pleurozium schreberi*	nonvascular	*Picea mariana*	tree	survival	herbivory	biotic refuge
	Pleurozium schreberi	nonvascular	*Picea mariana*	tree	growth	herbivory	biotic refuge
He et al. (2011)	*mixed*	graminoid	*Tamarix chinensis*	shrub	growth	salinity	limited salt accumulation by shading substrate
Munoz Valles et al. (2011)	*Retama monosperma*	shrub	*mixed*	herb	growth	heat	decreased temperature under canopy
	Retama monosperma	shrub	*mixed*	herb	species richness	heat	decreased temperature under canopy
Wang et al. (2011a)	*Cerasus trichostoma*	shrub	*mixed*	mixed	species richness	heat	decreased temperature under canopy
	Ribes glaciale	shrub	*mixed*	mixed	species richness	heat	decreased temperature under canopy
	Rosa omeiensis	shrub	*mixed*	mixed	species richness	heat	decreased temperature under canopy
	Salix sphaeronymphe	shrub	*mixed*	mixed	species richness	heat	decreased temperature under canopy
Boughton et al. (2011)	*Juncus effusus*	graminoid	*Alternanthera philoxeroides*	herb	survival	herbivory	associational avoidance
	Juncus effusus	graminoid	*Panicum repens*	graminoid	survival	herbivory	associational avoidance
	Juncus effusus	graminoid	*Panicum hemitomon*	graminoid	survival	herbivory	associational avoidance
	Juncus effusus	graminoid	*Panicum repens*	graminoid	growth	herbivory	associational avoidance
	Juncus effusus	graminoid	*Panicum hemitomon*	graminoid	growth	herbivory	associational avoidance

Pouliot et al. (2011)	*Eriophorum angustifolium*	graminoid	*mixed*	nonvascular	growth	radiation	shelter from radiation by taller neighbors
	Eriophorum vaginatum	graminoid	*mixed*	nonvascular	growth	radiation	shelter from radiation by taller neighbors
Rivest et al. (2011)	*Retama monosperma*	shrub	*mixed*	mixed	growth	nutrient deficiency	soil nutrient enrichment
Rodriguez-Garcia et al. (2011)	*Cistus ladanifer L.*	shrub	*Pinus pinaster*	tree	survival	drought	reduced water loss through shading
Wang et al. (2011b)	*Ischaemum. aristatum var. glaucum*	graminoid	*mixed*	graminoid	species richness	waterlogging	ground elevation
Le Bagousse-Pinguet et al. (2012)	*Potamogeton perfoliatus*	herb	*Potamogeton perfoliatus*	herb	survival	herbivory	associational avoidance
	Potamogeton perfoliatus	herb	*Potamogeton pectinatus*	herb	survival	herbivory	associational avoidance
	Potamogeton perfoliatus	herb	*Myriophyllum spicatum*	herb	survival	herbivory	associational avoidance
	Potamogeton perfoliatus	herb	*Potamogeton perfoliatus*	herb	growth	herbivory	associational avoidance
	Potamogeton perfoliatus	herb	*Potamogeton pectinatus*	herb	growth	herbivory	associational avoidance
	Potamogeton perfoliatus	herb	*Myriophyllum spicatum*	herb	growth	herbivory	associational avoidance
Suzuki and Suzuki (2012)	*Urtica thunbergiana*	herb	*Persicaria longiseta*	herb	survival	herbivory	biotic refuge
	Urtica thunbergiana	herb	*Persicaria longiseta*	herb	growth	herbivory	biotic refuge
	Urtica thunbergiana	herb	*Persicaria longiseta*	herb	fitness	herbivory	biotic refuge
Howard et al. (2012)	*Senna artemesioides*	shrub	*mixed*	mixed	species richness	nutrient deficiency	soil nutrient enrichment
	Eremophila sturtii	shrub	*mixed*	mixed	species richness	nutrient deficiency	soil nutrient enrichment
van Zonneveld et al. (2012)	*Baccharis vernalis*	shrub	*Myrceugenia correifolia*	tree	survival	drought	increased water availability
	Baccharis vernalis	shrub	*Griselinia scandens*	tree	survival	drought	increased water availability
Cavieres and Penaloza	*Kageneckia*	tree	*Kageneckia angustifolia*	tree	survival	snow cover	less snow accumulation

(2012)	*angustifolia*						under canopy
Casanova-Katny and Cavieres (2012)	*mixed*	nonvascular	*Deschampsia antarctica*	graminoid	growth	chill	reduced convective heat loss and low albedo
Anthelme et al. (2012)	*Azorella aretioides*	shrub	*mixed*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
Bingham and Simard (2012)	*Pseudotsuga menziesii (Mirb.) Franco var. glauca (Mayr) (tree)*	tree	*Pseudotsuga menziesii (Mirb.) Franco var. glauca (Mayr) (tree, seedling)*	tree	survival	drought	mycorrhizal networks and natural grafts
Cavieres and Sierra-Almeida (2012)	*Azorella madreporica*	shrub	*Hordeum comosum*	graminoid	survival	chill	reduced convective heat loss and low albedo
	Azorella madreporica	shrub	*Hordeum comosum*	graminoid	growth	nutrient deficiency	soil nutrient enrichment
He et al. (2012)	*Tamarix chinensis*	shrub	*Suaeda. Glauca*	herb	growth	salinity	limited salt accumulation by shading substrate
Goergen and Chambers (2012)	*Lupinus argenteus*	herb	*Elymus multisetus*	graminoid	survival	drought	reduced water loss through shading
	Lupinus argenteus	herb	*Elymus multisetus*	graminoid	growth	drought	reduced water loss through shading
	Lupinus argenteus	herb	*Bromus tectorum*	graminoid	growth	drought	reduced water loss through shading
	Lupinus argenteus	herb	*Bromus tectorum*	graminoid	fitness	drought	reduced water loss through shading
Grau et al. (2012)	*Vaccinium myrtillus*	shrub	*Betula pubescens*	tree	survival	radiation	shelter from radiation by taller neighbors
Wang et al. (2012)	*Ischaemum. aristatum var. glaucum*	graminoid	*mixed*	herb	survival	waterlogging	ground elevation
Urretavizcaya et al. (2012)	*Austrocedrus chilensis*	tree	*Austrocedrus chilensis*	tree	survival	drought	reduced water loss through shading
Walder et al. (2012)	*Sorghum bicolor*	graminoid	*Linum usitatissimum*	herb	growth	nutrient deficiency	mycorrhizal networks and natural grafts
Jian et al. (2013)	*Asplenium antiquum*	herb	*Haplopteris zosterifolia*	herb	growth	drought	increased water storage by neighbors
Hierro and Cock (2013)	*Euphorbia schickendantzii*	herb	*Bromus catharticus var. rupestris*	graminoid	growth	herbivory	associational avoidance

	Euphorbia schickendantzii	herb	*Hordeum euclaston*	graminoid	growth	herbivory	associational avoidance
	Euphorbia schickendantzii	herb	*Gamochaeta calviceps*	herb	growth	herbivory	associational avoidance
	Euphorbia schickendantzii	herb	*Bromus catharticus var. rupestris*	graminoid	fitness	herbivory	associational avoidance
	Euphorbia schickendantzii	herb	*Hordeum euclaston*	graminoid	fitness	herbivory	associational avoidance
Marzano et al. (2013)	*Pinus sylvestris*	tree	*Pinus sylvestris*	tree	growth	radiation	shelter from radiation by taller neighbors
	Pinus sylvestris	tree	*Larix decidua*	tree	growth	radiation	shelter from radiation by taller neighbors
Castro et al. (2013)	*Medicago truncatula*	herb	*Medicago truncatula*	herb	growth	salinity	limited salt accumulation by shading substrate
	Medicago truncatula	herb	*Medicago truncatula*	herb	fitness	salinity	limited salt accumulation by shading substrate
Gomez-Ruiz et al. (2013)	*Lupinus bogotensis*	shrub	*Solanum oblongifolium*	tree	growth	chill	reduced convective heat loss and low albedo
	Lupinus bogotensis	shrub	*Viburnum tinoides*	tree	growth	chill	reduced convective heat loss and low albedo
	Vicia benghalensis	herb	*Viburnum tinoides*	tree	growth	chill	reduced convective heat loss and low albedo
	Vicia benghalensis	herb	*Solanum oblongifolium*	tree	growth	chill	reduced convective heat loss and low albedo
Guo et al. (2013)	*mixed*	mixed	*Avicennia germinans*	tree	survival	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Avicennia germinans*	tree	growth	chill	reduced convective heat loss and low albedo
Liu et al. (2013)	*Rhodomyrtus tomentosa*	shrub	*Schima superba*	tree	survival	drought	reduced water loss through shading
	Rhodomyrtus tomentosa	shrub	*Schima superba*	tree	growth	drought	reduced water loss through shading
Lloret and Granzow-de la Cerda (2013)	*mixed*	mixed	*Juniperus phoenicea L.*	tree	survival	drought	reduced water loss through shading
Becerra and Montenegro (2013)	*mixed*	mixed	*mixed*	herb	species richness	drought	reduced water loss through shading
Molina-Montenegro et	*Usnea antarctica*	nonvascular	*Deschampsia antarctica*	graminoid	survival	chill	reduced convective heat

al. (2013)							loss and low albedo
Schöb et al. (2013)	*Arenaria tetraquetra*	herb	*mixed*	mixed	species richness	nutrient deficiency	soil nutrient enrichment
Grau et al. (2013)	*Rhododendron ferrugineum L.*	shrub	*Pinus uncinata*	tree	growth	wind	shelter against wind by larger neighbors
Knapp et al. (2013)	*Pinus taeda L.*	tree	*Pinus palustris Mill.*	tree	survival	radiation	shelter from radiation by taller neighbors
Redmond and Barger (2013)	*mixed*	mixed	*Pinus edulis*	tree	survival	drought	reduced water loss through shading
Long et al. (2013b)	*Spartina patens*	graminoid	*mixed*	mixed	species richness	wind	shelter against wind by larger neighbors
Madrigal-Gonzalez et al. (2013)	*Eulychnia acida*	shrub	*Mesembryanthemum crystallinum*	herb	growth	drought	increased water availability
Jankju (2013)	*Astragalus gossypinus*	shrub	*Agropyron desertorum*	graminoid	survival	heat	decreased temperature under canopy
Rolo et al. (2013)	*Cistus ladanifer*	shrub	*Quercus ilex*	tree	survival	radiation	shelter from radiation by taller neighbors
	Cistus ladanifer	shrub	*Quercus ilex*	tree	growth	radiation	shelter from radiation by taller neighbors
	Retama sphaerocarpa	shrub	*Quercus ilex*	tree	survival	radiation	shelter from radiation by taller neighbors
	Retama sphaerocarpa	shrub	*Quercus ilex*	tree	growth	radiation	shelter from radiation by taller neighbors
	Quercus ilex	tree	*Quercus ilex*	tree	survival	radiation	shelter from radiation by taller neighbors
	Quercus ilex	tree	*Quercus ilex*	tree	growth	radiation	shelter from radiation by taller neighbors
Cheng et al. (2014)	*Stellera chamaejasme*	herb	*mixed*	herb	species richness	herbivory	associational avoidance
	Stellera chamaejasme	herb	*mixed*	herb	fitness	herbivory	associational avoidance
Louthan et al. (2014)	*mixed*	herb	*Hibiscus meyeri*	herb	growth	herbivory	associational avoidance
Anthelme et al. (2014)	*Setaria sphacelata*	graminoid	*Ceroxylon echinulatum*	tree	survival	drought	reduced water loss through shading
	Setaria sphacelata	graminoid	*Ceroxylon echinulatum*	tree	growth	drought	reduced water loss through shading
Yang et al. (2014)	*Ulmus pumila L.*	tree	*mixed*	graminoid	growth	drought	reduced water loss through

							shading
Spasojevic et al. (2014)	*mixed*	mixed	*Horkelia sericata*	herb	growth	chill	reduced convective heat loss and low albedo
	mixed	mixed	*Phacelia corymbosa*	herb	growth	chill	reduced convective heat loss and low albedo
Schöb et al. (2014)	*Arenaria tetraquetra*	herb	*mixed*	herb	fitness	drought	increased water storage by neighbors
Poulos et al. (2014)	*Artemisia tridentata Nutt.*	shrub	*Penstemon palmeri A. Gray*	herb	survival	drought	reduced water loss through shading
Grant et al. (2014)	*mixed*	mixed	*Arrhenatherum elatius*	graminoid	growth	drought	reduced water loss through shading
Wang et al. (2014)	*mixed*	mixed	*mixed*	mixed	growth	soil contamination of metal	uptake of heavy metals from soil
Muler et al. (2014)	*Banksia attenuate*	shrub	*Scholtzia involucrate*	shrub	growth	nutrient deficiency	soil nutrient enrichment
Mendoza-Hernandez et al. (2014)	*mixed*	mixed	*Salvia mexicana*	herb	survival	heat	decreased temperature under canopy
	mixed	mixed	*Salvia mexicana*	herb	growth	heat	decreased temperature under canopy
Liu et al. (2014)	*Rhodomyrtus tomentosa*	shrub	*Castanopsis fissa*	tree	survival	radiation	shelter from radiation by taller neighbors
	Rhodomyrtus tomentosa	shrub	*Castanopsis fissa*	tree	growth	radiation	shelter from radiation by taller neighbors
	Rhodomyrtus tomentosa	shrub	*Syzygium hancei*	tree	survival	radiation	shelter from radiation by taller neighbors
	Rhodomyrtus tomentosa	shrub	*Syzygium hancei*	tree	growth	radiation	shelter from radiation by taller neighbors
Kleinhesselink et al. (2014)	*Ericameria ericoides*	shrub	*Bromus diandrus*	graminoid	growth	wind	shelter against wind by larger neighbors
Caldeira et al. (2014)	*Quercus spp.*	tree	*Quercus suber*	tree	survival	heat	decreased temperature under canopy
	Quercus spp.	tree	*Quercus ilex*	tree	survival	heat	decreased temperature under canopy
Good et al. (2014)	*mixed*	graminoid	*Eucalyptus coolabah*	tree	survival	heat	decreased temperature under canopy

Figure S1. Schematic representations of the experimental design. There were three salt treatments, no salt, intermediate (50 mM) and high (100 mM). Each salt treatment included the fully-factorial combination of genotypes, with all 6 genotypes grown individually (target genotype - without neighbours, replicated 12 times) and each target genotype grown with the 6 possible neighbor identities (with neighbors, replicated 6 times).

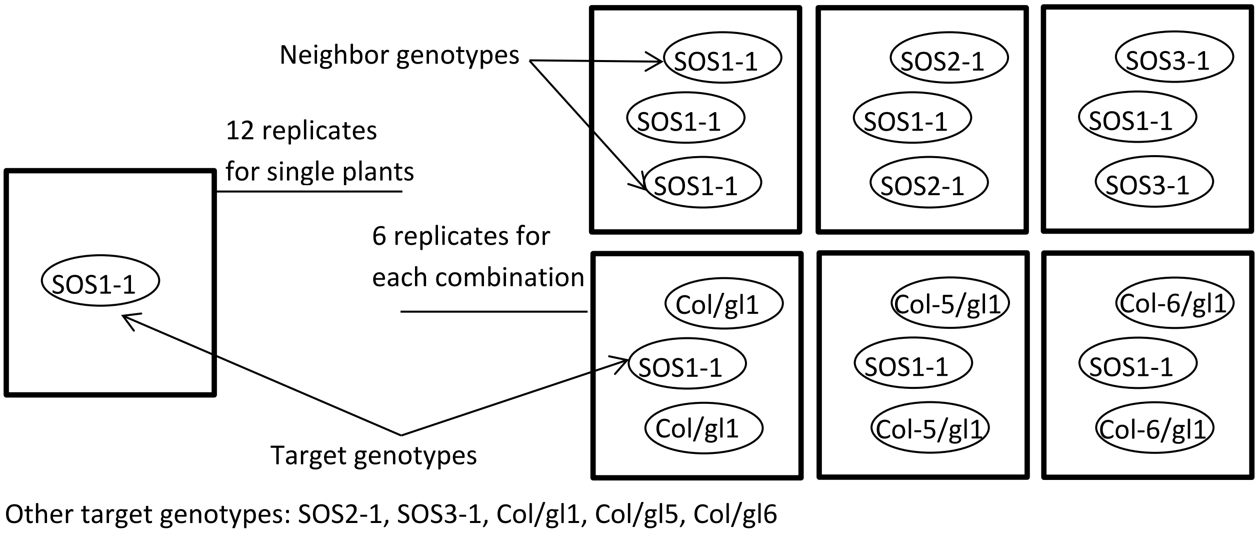


Figure S2. Relationship between sowing density and mean survival rate (± SE) for *Arabidopsis thaliana* populations grown along a salt gradient: no salt (A), low salt stress (50mM, B), intermediate salt stress (100mM, C) and high salt stress (150mM, D). Note that due to large plant size differences among salinity levels, the scales of the y-axes are not the same to facilitate interpretation.

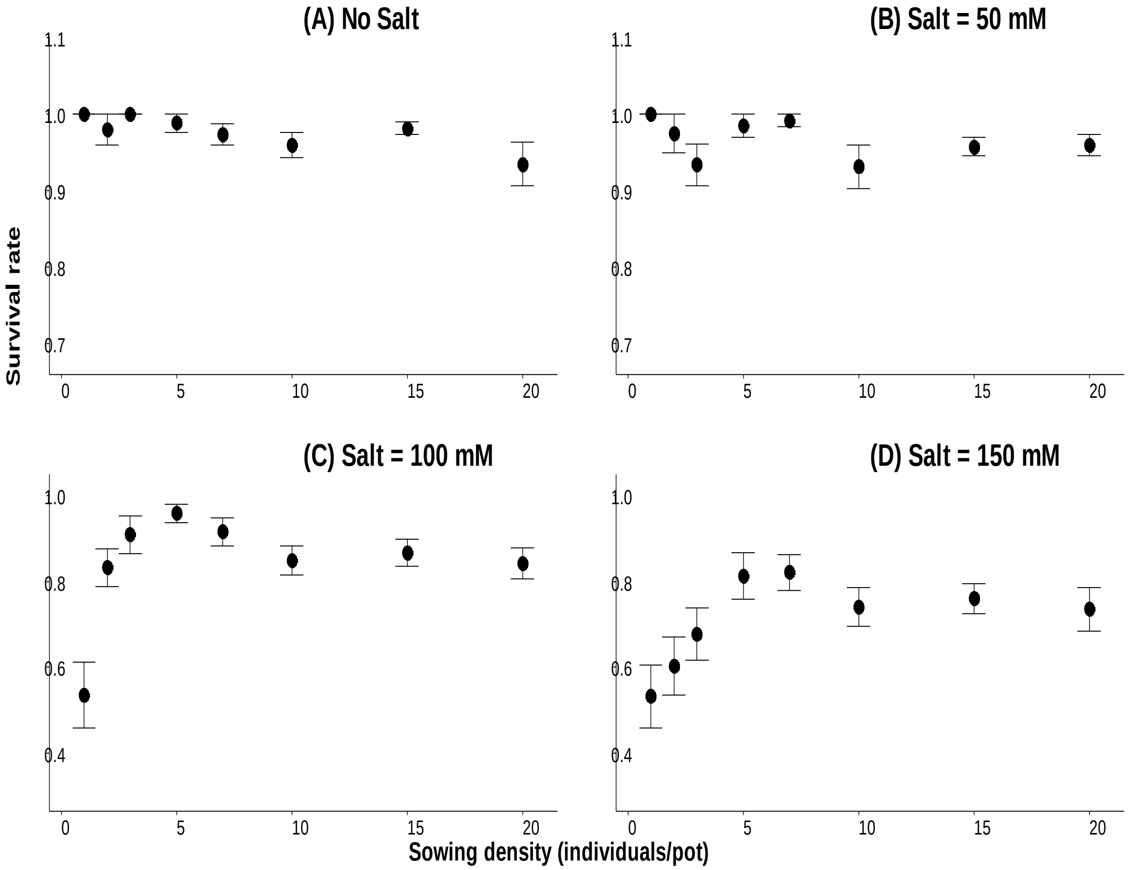
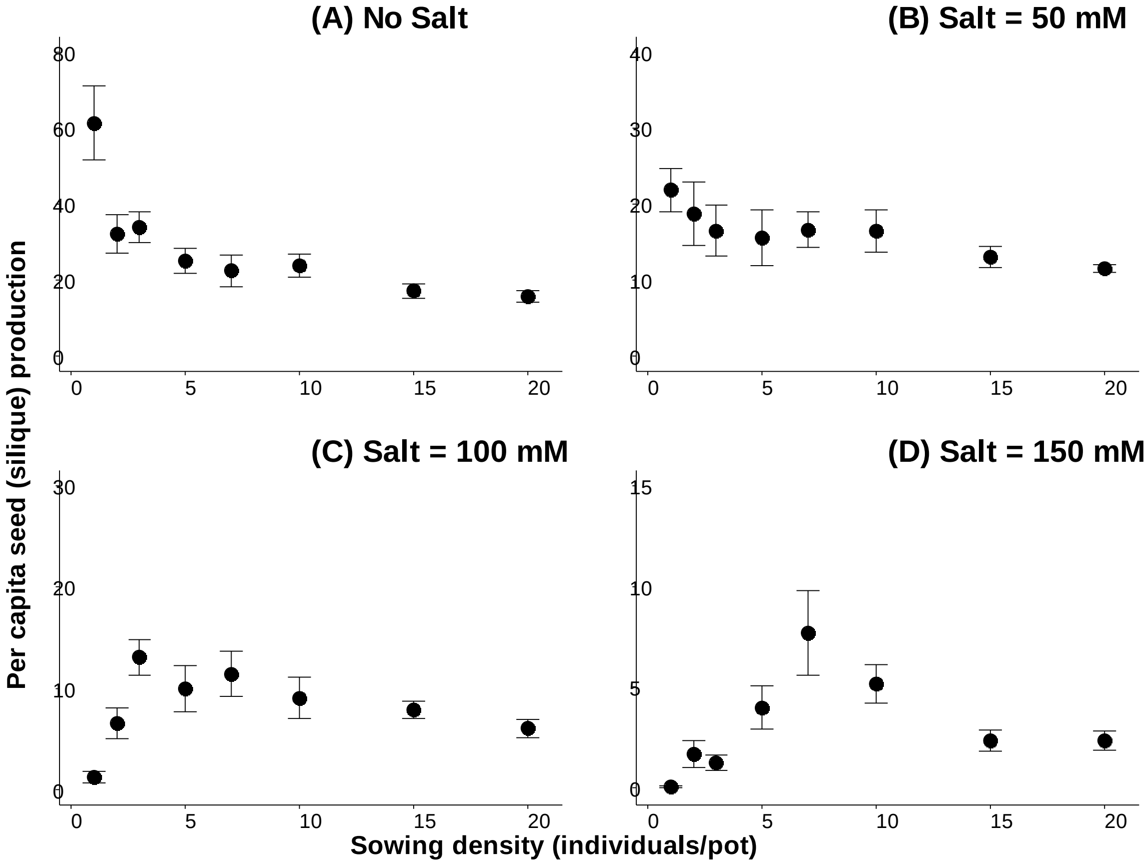


Figure S3. Relationship between sowing density and mean seed production (± SE) for *Arabidopsis thaliana* populations grown along a salt gradient: no salt (A), low salt stress (50mM, B), intermediate salt stress (100mM, C) and high salt stress (150mM, D). Note that due to large plant size differences among salinity levels, the scales of the y-axes are not the same to facilitate interpretation.



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