

Reassessing the role of competition in the evolution and expression of adaptive strategies in plants

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REASSESSING THE ROLE OF COMPETITION IN THE EVOLUTION AND EXPRESSION OF ADAPTIVE STRATEGIES IN PLANTS

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Thesis submitted for the degree of Doctor of Philosophy

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Thesis/Dissertation Sheet

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In this thesis, I utilise the vast amount of competition literature that has accumulated to conduct four literature surveys testing the predictions of traditional strategy theory on the role of competition in the evolution of plant strategies and life histories. Traditional theory predicts that seedlings emerging from large seeds have the advantage over those emerging from small seeds in environments of dense vegetation. Through my synthesis I show that large seed size is associated with high competitive ability but only when plants are competing against other seedlings. My findings offer a new interpretation of seed size strategies suggesting that seedlings have little chance of establishing in dense communities but rather, mainly emerge in open spaces. Next I tested whether shade avoidance plasticity was an adaptive response under competition. Shade avoidance responses have often been thought of as a strategy plants use to outcompete their neighbours for light resources. I found that shade avoidance plasticity was not associated with an increase in competitive performance as has been predicted by theory but that instead the adaptive value of shade avoidance lies in gathering resources to allow earlier reproduction under competition. I tested if these findings extended to plasticity in general which theory predicts gives plants a competitive advantage by allowing them to adjust growth to acquire more of the available resources than their competitors. I found that plasticity was not associated with an increase in competitive ability in either short or longlived species. Instead plasticity was correlated with increased reproductive efficiency in short-lived species whilst this did not occur in long-lived species. Finally, I tested whether functional traits specific leaf area (SLA) and maximum height were good predictors of competitive ability. I found that neither maximum height nor SLA were good predictors of competitive performance. My findings highlighted that the theoretical basis of our understanding of competition needs to be improved before we can effectively use functional traits to predict competitive outcomes. Overall, this thesis challenges some of the key foundational assumptions of strategy theory and illustrates the need for a change in the way we measure competitive ability.

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ABSTRACT

In this thesis, I utilise the vast amount of competition literature that has accumulated to conduct four literature surveys testing the predictions of traditional strategy theory on the role of competition in the evolution of plant strategies and life histories. Traditional theory predicts that seedlings emerging from large seeds have the advantage over those emerging from small seeds in environments of dense vegetation. Through my synthesis I show that large seed size is associated with high competitive ability but only when plants are competing against other seedlings. My findings offer a new interpretation of seed size strategies suggesting that seedlings have little chance of establishing in dense communities but rather, mainly emerge in open spaces. Next I tested whether shade avoidance plasticity was an adaptive response under competition. Shade avoidance responses have often been thought of as a strategy plants use to outcompete their neighbours for light resources. I found that shade avoidance plasticity was not associated with an increase in competitive performance as has been predicted by theory but that instead the adaptive value of shade avoidance lies in gathering resources to allow earlier reproduction under competition. I tested if these findings extended to plasticity in general which theory predicts gives plants a competitive advantage by allowing them to adjust growth to acquire more of the available resources than their competitors. I found that plasticity was not associated with an increase in competitive ability in either short or longlived species. Instead plasticity was correlated with increased reproductive efficiency in short-lived species whilst this did not occur in long-lived species. Finally, I tested whether functional traits specific leaf area (SLA) and maximum height were good predictors of competitive ability. I found that neither maximum height nor SLA were good predictors of competitive performance. My findings highlighted that the theoretical basis of our

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understanding of competition needs to be improved before we can effectively use functional traits to predict competitive outcomes. Overall, this thesis challenges some of the key foundational assumptions of strategy theory and illustrates the need for a change in the way we measure competitive ability.

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CHAPTER ONE

GENERAL INTRODUCTION

Reassessing the role of competition in the evolution and expression of adaptive strategies in plants

Competition for resources for growth, survival and reproduction has been regarded as one of the most important forces in shaping ecological strategies and community composition and dynamics since the early days of ecology (Pianka 1970; Grime 1977; Bonser and Aarssen 1996; Coomes and Grubb 2003). Whilst most organisms experience competition at some stage of their lives, a large body of theory maintains that competition has an especially strong influence on the lives of plants because of the largely overlapping resource needs of plant species coupled with their sessile nature (Silvertown and Law 1987; Wilson et al. 1987). Thus, over the past few decades, considerable effort has been placed into understanding the role competition has played in the evolution of the large range of form, function and life histories expressed by plants. A number of influential conceptual theories have been developed with the aim of explaining the diversity of form and function observed along environmental gradients of different densities, amounts of resource availability, and intensities of competitive interactions (e.g. Pianka 1970; Grime 1973; 1977; 1979; Tilman 1982; 1985; 1988). Many of these theories tended to be strategy theories – theories based on the idea that there are groups of functional traits that recur widely among species which confer similar ecological behaviour (Smith 1982), grouping species into functional types or along functional spectrums.

The r/K selection theory is one of the earliest and most well-known of these strategy theories modelling competition (MacArthur and Wilson 1967; Pianka 1970). This theory was formed to predict the evolution of strategies on gradients varying in the intensity of competition. Under this theory, in unstable environments (e.g. environments with a high

frequency of disturbance) where competition is low, organisms with a strategy which focusses on exploiting resources through reproducing quickly rather than investing in competitive adaptations are favoured (r-strategists). Traits of r-strategists include a short life-span, a short time to first reproduction, producing many small offspring, a small body size, low parental care and a low survival rate. Stable environments where populations have not yet reached the carrying capacity of the environment and where there is therefore higher competition are predicted to favour long-lived organisms which delay reproduction and invest more in traits associated with resource acquisition in order to become better competitors (K-strategists). Traits of K-strategists include a long life-span, a long time to reaching reproductive maturity, producing a few large offspring, providing offspring with high levels of parental care and a high survival rate.

This idea of a fast-slow continuum from the r/K selection theory was expanded on in Grime's C-S-R (competitor-stress tolerator-ruderal) model (Grime 1973; 1977; 1979; Grime and Hodgson 1987). Grime (1973) proposed that plants differed in life history characteristics depending on the degrees of stress and disturbance which they were adapted to. In this theory, plants are presented on a spectrum of 3 principal strategies. Plants with more "competitive" strategies are predicted to have adapted to low levels of disturbance and stress and described as having traits which would allow them to maximise the capture of resources e.g. moderate to long life spans (perennial), relatively low yearly reproductive effort, high potential relative growth rate, high productivity (growth in height, lateral spread and root mass), high dense canopies of leaves, abundant litter as well as high morphological plasticity which would allow them to adjust the allocation of resources to various parts of the plant in response to environmental conditions. Similar to the K-

strategists of the r/K theory, these species are predicted to produce few but large offspring and be long-lived species such as perennial herbs, shrubs or trees. Plants which adapted under higher resource stress are described as having more "stress-tolerant" strategies with an ability to conserve resources under low resource availability. Stress tolerators possess traits of long life span and low reproductive effort but have slow growth rates, little but persistent litter and little morphological plasticity. These species are also predicted to produce few but large offspring and have long lifespans and be lichens or long-lived perennial herbs, shrubs or trees. Those adapted to high disturbance and low stress were predicted to have a "ruderal" strategy with a strategy that ensures the production of seeds. Ruderals have very short life spans and high reproductive rates, tending to produce large numbers of seeds in a similar way to the r-strategists of the r/K theory. Competition is predicted to be most intense in resource-rich environments and less important in stressful unproductive low resource environments where the plants would have low biomass and therefore use fewer resources (Grime 1977).

Tilman's resource ratio model (Tilman 1982, 1988) is another prominent strategy theory developed to describe plant strategies in response to competition. Tilman's model predicts that species which are capable of extracting resources at lower resource concentrations than other species have the highest competitive ability. Species which have low resource requirements are able to continue to grow at low resource levels thus displacing those with higher resource requirements. However, whilst Grime defines competitive ability by resource capture, Tilman defines competitive ability by tolerance to low resource levels leading to some differences in their predictions about what traits confer superior competitive ability as well as the conditions under which competition is intense. For

example, under Grime's C-S-R theory, competition is predicted to increase with increasing productivity. In contrast under Tilman's resource ratio model, competition is predicted to be intense across productivity gradients. These opposing views have led to some long-lived and fierce debates of the nature of competition on environmental gradients as well as led others to forward different models and hypotheses to try and resolve the problems encountered by the two models (Grime 1973; Newman 1973; Grime 1977; 1979; Tilman 1988; Grace 1990; Berendse *et al.* 1992; Goldberg and Novoplansky 1997; Craine 2005; 2007; Grime 2007; Tilman 2007).

I do not provide a full review of the literature on competition and adaptive strategies in plants, rather this highlights how ecologists have struggled to form generalisations on the role of competition in the evolution of plant strategies and life histories. Traditional strategy theories are some of the most longstanding and influential theories predicting competitive ability in plants and have remained the foundation of a lot of the research into how plant-plant competitive interactions affect community assembly even if there has been highly inconsistent evidence found to support them. Issues with how we measure competitive ability and success under competition likely contribute to our lack of a unifying concept of competitive ability.

Traditional ecological strategy theories have predicted an advantage under competition where plants with a longer lifespan and larger maximum size are favoured. In recent years, findings have been emerging that suggest the capacity to reproduce under competition is more important than lifespan and size. For example, 97% of the variation in seed

production between species under competition was due to differences in the number of surviving plants which were still able to reproduce under conditions where growth was suppressed (Neytcheva and Aarssen 2008). Further, being efficient reproducers in the presence of competition was more important than being large as predicted under traditional strategy theories (Bonser and Ladd 2011). Contrary to the predictions that competitive environments favour large long-lived perennial species with delayed reproduction, individuals under competition have been shown to have considerably reduced growth rates and increased mortality (Bonser 2013). Under intense competition, there would be a high probability of the individual dying before it is able to reproduce if it employs a strategy of delayed reproduction. Although it has long been assumed that largesized species have higher lifetime fecundity, there is a trade-off in woody (Thomas 1996; Davies and Ashton 1999) and herbaceous vegetation (Tracey and Aarssen 2011; 2014; Nishizawa and Aarssen 2014) between the maximum potential body size a species can reach and the minimum size of reproduction. Larger species generally have to reach a larger threshold size before they can initiate reproduction. Larger species are good competitors unless competition is strong or prolonged causing them to be unable to reach the large size they are capable of. This suggests that contrary to traditional theory, small plants are not inferior to large plants at passing on their genes when under intense competition.

More generally, these studies indicate that our traditional views on competition may not be correct. Reassessing how plants adapt to competition will be important to improve our understanding of the evolution of plant strategies and the diversity of ecological communities. For example, these new findings have shown that-traditional strategy

theories do not place sufficient importance on the role of reproduction and fecundity under competition. This is problematic as the production of offspring is the key unit of currency in evolution by natural selection, and reproduction under competition should be central in resolving strategy theory and evolutionary theory. Whilst there has been debate about the differences between what Grime (1973; 1977) and Tilman (1982; 1988) defined as competitive success, both Grime and Tilman's theories whether through obtaining more resources or through using less resources tended to place more emphasis on the importance of being able to ensure continued growth/survival under competitive conditions. These issues demonstrate gaps in our current understanding of the conditions underlying the evolution of competitive abilities and suggest that we need to reappraise a number of the influential theories and models in plant ecology regarding the evolution of traits in which competition plays a predominant role in.

The substantial interest in plant competition has meant a plethora of empirical studies has accumulated and large-scale data compilations are now possible. In this thesis, I aim to utilise the large amount of published data available to test the predictions of traditional strategy theory on the role of competition in the evolution of plant life histories to gain a better understanding of the circumstances in which they are applicable and to develop a new predictive framework for understanding the evolution of adaptive strategies in plants under competition. I present four studies where I used data from the extensive plant competition literature to test how aspects of plant strategies are related to performance under competition. These studies challenge traditional assumptions of the traits associated with competitive ability in plants. These studies are outlined below.

Ch 2. What is the value (if any) of large seed size under competition? Is seed size related to competitive ability?

In chapter 2 I tested whether large seed size is important to competitive ability as predicted by the traditional ecological theories and if so, in what way? Seed size represents an important strategy axis for plants (Westoby et al. 2002). The size of the seeds a species produces has been proposed to be an important component of its strategy with the large number of offspring smaller seeded species are able to produce (for a given amount of energy) making them good colonisers and the larger amount of resources large seeds are provided with making large-seeded species good competitors. Previously, one of the reasons large plants were believed to dominate communities was because they tended to produce larger seeds which would be advantageous under competition with more resources to ensure rapid growth allowing them to outgrow smaller-seeded competitors (Geritz 1995; Rees and Westoby 1997; Geritz et al. 1999). The traditional way of thinking has always been that seedlings with a large seed size would have the advantage in environments of dense vegetation. However, the problem with this idea is that seedlings are unlikely to be able to compete against dense adult vegetation no matter how much of a seed size advantage they have. Whilst an individual that emerged from a large seed size may be a better competitor than one that emerged from a smaller one later in life (due to the correlation of seed size with other life history factors such as adult size and growth form), in the early stages, a seed typically requires an open environment to germinate and grow well. Incorporating these ideas and in light of findings that smaller seeded species were more efficient reproducers (Moles et al. 2004; Tracey and Aarssen 2011) and that being able to reproduce under competition has a larger effect on representation in communities (Neytcheva and Aarssen 2008), we reconsider what is the value of a large

seed size. I demonstrate that large seed size is only associated with higher competitive ability in environments where the plant is competing with similarly aged plants and that seed size does not confer higher competitive ability in environments of dense established vegetation.

Ch. 3 Is shade avoidance plasticity an adaptive response under competition?

In crowded and light limited environments, one of the common responses plants show are a group of elongation traits which allow the plants greater access to light collectively known as "shade avoidance responses" (Smith 1982). The ability to obtain resources for growth is central to traditional plant strategies and plant height (especially for resources for which there is asymmetric competition for such as light), is one of the key traits predicted to confer competitive ability (Grime 1973). Traditionally it has been believed that these shade avoidance responses are an attempt by plants to increase their competitive ability by growing taller faster than their neighbours so that their leaves can be placed above those of neighbours, outcompeting the neighbours for light resources (Givnish 1982; Falster and Westoby 2005). However, in an environment of increasing competition, it is unlikely putting energy towards growing tall is a strategy that would allow a plant to achieve competitive dominance especially in the case of short-lived herbaceous plants. Positioning leaves above those of their neighbours to intercept a larger proportion of light resources has been shown to give trees a strong selective advantage (Falster and Westoby 2005). However, whilst it may be important for long-lived species to obtain more resources to reach their higher reproductive threshold size, it does not make sense for a short-lived individual which only has a short time in which to live and reproduce to try and gather resources to outgrow neighbours under increasing levels of

competitive stress. Rather, by putting resources into growth and delaying reproduction under competitive conditions there is a high chance the plant may end up dying before being able to produce any offspring. Thus, shade avoidance plasticity may be adaptive, though as a response to quickly acquire light resources to maximise reproduction prior to competition intensifying for short-lived species rather than as a response to increase competitive ability. In this chapter I surveyed the literature to test if shade avoidance plasticity is associated with an increase in competitive ability in short-lived herbaceous plants and if it is associated with an increase in reproductive efficiency. I show that in line with our predictions, shade avoidance plasticity does not increase competitive performance but is an adaptive response under competition by increasing reproductive efficiency for short-lived plants.

Ch. 4 Is phenotypic plasticity associated with competitive ability?

Following on from the previous project, in chapter 4 I asked if having a plastic phenotype in general is associated with competitive ability. Traditionally phenotypic plasticity is predicted to be an important characteristic for plants with competitive strategies because it allows plants to make adjustments to their growth in response to resource availability throughout their lifespan thus maximising resource acquisition across environments (Grime 1979; Grime *et al.* 1986; Bazzaz 1991; de Kroon and Hutchins 1995; Huber *et al.* 1999). However, plasticity is costly in time, energy and resources to gather information and to make developmental responses and there is a risk inappropriate responses could lead to death without reproduction (DeWitt *et al.* 1998; Givinish 2002). The main problem with the idea that higher plasticity confers greater competitive ability is that competitive ability should evolve under environments of consistently high levels of competition where

specialisation would be favoured whilst plasticity in resource acquisition traits should be advantageous and evolve in environments where competition levels and resource levels are variable. In addition the costs of plasticity would prevent an individual from maximising competitive ability and outcompeting competitive specialists. In this chapter I tested the prediction that plasticity may not actually be associated with greater competitive ability as has been traditionally predicted. I show that for both short and longlived plants, high phenotypic plasticity was linked with lower competitive performance. However, I also show that high phenotypic plasticity is consistent with a strategy of increasing reproductive efficiency in short-lived species under competitive conditions.

Ch. 5 Are functional traits predictive of competitive ability?

In Chapter 5 I investigated if functional traits are predictive of competitive ability. Ecologists are increasingly using easily measured functional traits to predict community responses to environmental conditions. Such trait-based approaches originated from the need for a way to predict the behaviour of plants across environmental gradients. Traits have long been associated with the performance of plants. Traditional strategy theories tended to divide species into functional groups (e.g. Grime 1973's competitor, stress tolerator and ruderal groups) based on the suites of functional traits they possessed. In these strategy theories and newer more recently developed strategy theories such as the leaf-height-seed strategy theory (Westoby 1998; Westoby *et al.* 2002) as well as the leaf economics spectrum (Wright *et al.* 2004), a number of traits have been indicated as having strong impacts on competitive ability and predicted to have globally consistent effects on individual responses to environmental conditions. In this chapter I focus on two of these functional traits (specific leaf area and maximum height) which have both been considered

to be predictors of competitive ability (Grime 1973; 1977; Westoby 1998; Hodgson *et al.* 1999; Weiher *et al.* 1999; Westoby *et al.* 2002; Díaz *et al.* 2004) and utilise the data from the published studies available to test for a relationship between these functional traits and plant performance under competition. I also discuss some of the benefits and limitations of using traits to predict competitive ability. I demonstrate that whilst functional traits such as maximum height can be useful predictors under certain conditions, other functional traits like specific leaf area are too variable and tightly linked with other factors plants encounter to be used as an effective predictor.

Ch. 6 Conclusion

Finally in the last chapter (chapter 6) I summarise the findings of these projects and discuss in detail the implications our findings have on the current understanding of the role of competition in the evolution of plant traits and strategies.

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CHAPTER 2

WHAT IS THE VALUE OF HAVING A LARGE SEED SIZE UNDER COMPETITION?

Clara Pang and Stephen P Bonser

Abstract

Large seed size is predicted to be adaptive under competition. The traditional thinking is that large seeds are able to hold more provisions and resources from the mother plant and this should give the seedlings an advantage in competing against dense vegetation. The problem with this idea is that seedlings probably would not do well against dense adult vegetation no matter how much of a seed size advantage they have. We tested for a relationship between seed size and seedling performance under competition by collating data from experiments in which seedlings were grown in an open environment with other seedlings and experiments in which seedlings were grown in environments with adult neighbours. Our findings showed that in a mature environment where a seedling competes against adult plants, there is no significant reduction in how negatively affected the plants are by competition over several orders of magnitude in seed size variability. The value of a large seed size lies in the open environments where other competitors are also seedlings and competition levels start off low before gradually becoming more intense. Whilst these open environments can and will fill up quite quickly, we found there is a highly significant increase in these open environments in competitive performance as seed size increases. Our findings contradict the traditional prediction that large seed size is an important trait in promoting seedling success in established vegetation. Species with a larger adult body size generally tend to have larger seeds so a larger-seeded plant is likely to be a better competitor than a smaller one later on but in the early stages, a seed regardless of its size still requires an open environment to be able to germinate and grow well in. This study shows that there is no competitive advantage of having a larger seed in those early stages in environments where the competition starts off at high levels.

Introduction

Seed size determines the success of seedling growth and survivorship in communities. Life history decisions on seed size in plants impact the probability of establishment, tolerating stress, competitive ability, and dispersal efficiency (Westoby *et al.* 1996; Leishman *et al.* 2000; Moles *et al.* 2003). Small-seeded species are able to produce more seeds than large-seeded species *for a given amount of energy* and thus have more attempts to achieve successful seedling establishment (Harper *et al.* 1970; Primack 1987; Shipley and Dion 1992; Westoby *et al.* 1992; Jakobsson and Eriksson 2000; Henery and Westoby 2001; Leishman 2001; Moles *et al.* 2004, 2005). On the other hand, larger seeds are better provisioned with more carbohydrates and lipids stored in the seed than smaller-seeded species and are less affected by, and have better chances of surviving, various environmental stresses (Saverimuttu and Westoby 1996; Leishman *et al.* 2000; Walters and Reich 2000). Thus, increasing seed size should be associated with increased seedling success under competition.

Seed size has a long history of being linked to competitive ability. One of the most prevalent explanations of the coexistence of species with different sized seeds is a colonisation and competition trade-off (Rees 1995; Coomes and Grubb 2003). The competition-colonisation hypothesis underlies many of the explanations provided for the maintenance of community diversity (Levins and Culver 1971; Tilman 1994). Seed size represents a key strategy axis of traditional strategy theories and is correlated with a number of life history traits and morphological characteristics including adult size, reproductive lifespan and schedule, dispersal mode, growth form and specific leaf area (Leishman *et al.* 2000). Traditional strategy theory predicts small-seeded, small-sized, short-lived, fast-growing strategies evolved under low competition and that species with these traits are good colonisers but poor competitors (Grime 1973; 1977; 1979; Grime and Hodgson 1987). Species with large-seeded, large-sized, long-lived, slow-growing strategies are predicted to have evolved under high competition and thus are predicted to be good competitors (Grime 1973; 1977; 1979; Grime and Hodgson 1987). Several models incorporating these predictions of traditional strategy theory describe colonisation as a game (Geritz 1995; Rees and Westoby 1997; Geritz *et al.* 1999). In these seed size models, small-seeded species are predicted to be good colonisers of open space as they can produce many seeds, but the seedlings emerging from these seeds are predicted to be poor competitors. In contrast, large-seeded species are predicted to be poor colonisers as they produce fewer seeds, but seedlings from these seeds are well provisioned and are predicted to be good competitors. Larger-seeded species are always able to invade any community because their establishment advantage allows them to outcompete smallerseeded species growing at the same site (Geritz 1995; Rees and Westoby 1997; Geritz *et al.* 1999).

Although seed size is generally believed to be associated with competitive ability, field studies have found little conclusive evidence to support these ideas. Multiple studies have found the seed size game models inapplicable due to issues primarily with the assumptions about the competitive ability of the different seed sizes (Fenner 1978; Reader 1991; Coomes *et al.* 2002; Turnbull *et al.* 2004; Eriksson 2005). One of the major difficulties with finding evidence for the competition-colonisation hypothesis is the extreme asymmetry of competition required for the trade-off mechanism to be able to maintain the diversity of seed size. In order for competition-colonisation models to work,

the plant with a higher competitive ability must win almost every time no matter how slight its advantage (Levine and Rees 2002). Whilst species emerging from larger seeds generally win in experiments in which seeds of different sizes compete against each other (Eriksson 1997; Turnbull et al. 1999; Leishman 2001; Turnbull et al. 2004), the difference between the competitive ability of smaller and larger-seeded species that have been observed under experimental conditions have not been asymmetric enough to explain the observed diversity in seed size (Freckleton and Watkinson 2001; Levine and Rees 2002; Coomes and Grubb 2003; Calcagno et al. 2006). Under the seed size game theories, whether smaller or larger sized seeds are favoured depends on the seed sizes present in the community. However, Eriksson (2005) found recruitment of smaller-seeded species was not affected by larger-seeded species. The competition-colonisation models also have the underlying assumption that seedlings of superior competitors can displace more mature inferior competitors and do not consider that it is difficult for a seedling to colonise a site already occupied by an older, more developed plant, even if the seedling is capable of expressing a high competitive ability (Yu and Wilson 2001; Calcagno et al. 2006). This strongly suggests that the competitive hierarchy is less extreme than has been assumed under the previous theories and that the competitive ability of small-seeded species could be greater than has been thought.

Whilst the seed-size game models have focussed on seedling stress and most of the studies on seed size and competitive ability have only run for the duration of the seedling stage of the life cycle, the effects of seed size may potentially extend into later life. For example, Larios *et al.* (2014) found that seed-size effects under competition can extend beyond the juvenile stage into adulthood where they affect the number of seeds produced

at maturity. The plant's life history strategy such as adult body size, lifespan, and number of reproductive events in life has also been found to be linked with seed size suggesting seed size may have longer-lasting effects on the plant throughout its lifetime (Moles et al. 2004). Falster et al. (2008) took into consideration the newer predictions on the species life history and its seed size and extended on the Smith-Fretwell (1974) model to predict how offspring size is related with its later growth, survival and reproduction to address a number of the issues which have plagued the competitor-colonisation models. This model suggests having a large seed size is beneficial as being large allows rapid growth through the vulnerable juvenile developmental stage *prior* to the onset of competition because they are provided with more resources in the seed (Falster *et al.* 2008). The difficulty with finding evidence for the competitor-coloniser hypothesis has led some ecologists to suggest that perhaps competition is not important in these early establishment stages or that the effects of seed sizes on competitive ability come into play after this initial establishment process (Moles and Westoby 2004 a, b; Larios et al. 2014). Plants may need to reach a certain size before they experience competition for light, nutrients or water from their neighbours because of the size of their depletion zones and nutrient requirements compared to adult plants (Larios et al. 2014). In Falster et al.'s 2008 model, competition is only predicted to affect the individuals when they are larger and resource requirements have increased to the point where additional growth requires a decrease in abundance (self-thinning) and survival depends on the size of other plants in the population where, as the weaker competitors, the relatively smaller individuals are gradually phased out (Falster *et al.* 2008). A key assumption of these newer life history theories is that seedlings are unable to reach the density where competition is at a high enough level to affect their individual fitness and only experience competition from adult plants (Leishman 2001; Moles and Westoby 2004 a, b).

A major insight of this new interpretation of seed size variation in plants is that seedlings emerge predominantly in open spaces. Competition in plants tends to be highly asymmetric, with larger plants acquiring disproportionately more resources than small plants (Weiner 1990) and seedlings have little chance of establishing in the presence of a dense community of established plants. Seedlings of many herbaceous species require open microsites to successfully recruit (Kiviniemi and Eriksson 1999) and seed size strategies likely emerge in response to the early life conditions experienced in the absence of intense competition (at least initially). While in some communities, competition may remain low throughout the early life of plants, in many communities (e.g. old fields, desert herbaceous communities, pastures), plant density following disturbances quickly increases and competition can be intense early in development (Goldberg et al. 2001; Schiffers and Tielbörger 2006). Further, it is during the early establishment stages of life history that plants are most sensitive and vulnerable to competition stress and changes in neighbour density (Grubb 1977; Weiner and Thomas 1986; Foster and Gross 1997, 1998). In communities where competition experienced by juvenile plants can be intense, seed size strategies can evolve due to a correlation between seed size and plant size across species (Thompson and Rabinowitz 1989; Moles et al. 2004; Grubb et al. 2005; Moles and Westoby 2006; Rees and Venable 2007), and a correlation between plant size and size at reproduction across species (Tracey and Aarssen 2011). Thus, large seeds may provide an advantage under competition, but small-seeded species reproduce at smaller sizes (Tracey and Aarssen 2011) and are more fecund (Baker 1972; Moles et al. 2004). Consequently, large-seeded species may have a competitive advantage as the large seeds allow them to take advantage of ephemeral patches which have been opened by disturbances, but in any habitat where the probability of continued disturbances is relatively high, earlyreproducing, small-statured, small-seeded species may be favoured (see Bonser 2013).

The tremendous number of previous competition studies offers an excellent opportunity to test the ecological value of seed size. This study is the first test of alternate mechanisms of large seed size under competition. Neighbour removal experiments are the most common method of assessing the impact of competitors on target plants (Aarssen and Keogh 2002). In neighbour removal experiments, vegetation is removed around a target individual (and not permitted to regrow) and the performance of plants in the neighbour removal treatment is compared to the performance of plants in neighbour-present treatments. However, there are two types of neighbour-present treatment: studies where neighbours are left completely intact; and studies where neighbours were removed at the beginning of the experiment and allowed to regrow or planted as seeds or seedlings with the target plants.

The dichotomy of these neighbour-present treatments establishes the conditions to test for the contrasting predictions on ecological value of seed size variability. The studies where neighbours are left intact around the target seed or seedling allows us to examine whether seed size has any competitive value for seedlings establishing in the presence of a dense community of established plants. The studies where neighbours were removed at the beginning and allowed to regrow allow us to examine whether seed size has any value under competition with other seedlings. We tested the following predictions: 1) Under a traditional ecological strategy prediction, seedlings emerging from large seeds perform better under competition than seedlings emerging from small seeds in both neighbour-
present treatment types; and 2) Under the new life-history prediction, large seed size does not give a seedlings a competitive advantage where neighbour vegetation has been left intact, however seedlings emerging from large seeds will perform better under competition than seedlings emerging from small seeds where neighbours have been removed but allowed to regrow (Fig 1). To test these predictions, we surveyed the literature for competition studies using neighbour removal experiments across a range of species.

Methods

We searched ISI Web of science (Thompson Reuters) in March 2015 using the keywords "plant competition", "plant density", "neighbour removal", "seedling competition", "neighbour interaction*" in order to find plant competition experiments. Studies were included if the study evaluated the effect of neighbours on the performance of a target species, the target plants were placed into the competition treatments as seeds or seedlings, the species names of the target and competitor plants were given, there was a measure of biomass or growth under high and low density conditions and the dates the plants were planted and harvested or the age of the plants at the final harvest. For each study which met all these selection criteria, we extracted the means for the experimental and the control or the high and low density treatment groups and sample sizes.

We compiled trait data on plant growth form, life history, from regional botanical databases which were available online including University and Jepson Herbaria (University of California, Berkeley 2014), E-Flora BC: Electronic Atlas of the Flora of British

Columbia (Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia OR Klinkenberg 2013), Checklist of the Vascular Plants of Washington State (Weinmann *et al.* 2015), Flora of Australia Online (Australian Biological Resource Study 2009), Ecological Flora of the British Isles (Fitter and Peat 1994), Western Australia Flora (Western Australia Herbarium 2009), Flora of Hawaiian Islands (Smithsonian Institution 2009), PLantZAfrica (South African National Biodiversity Institute 2015), Flora of Mozambique (Hyde *et al.* 2015), Flora of Zimbabwe (Hyde *et al.* 2015), Plants of Taiwan (Herbarium of National Taiwan University 2015), The PLANTS Database (USDA NRCS 2015), Flora of Pakistan (Ali and Qaiser 2001), eFloras.org (which includes Flora of North America (Flora of North America Editorial Committee 1993) and Flora of China (Zhengyi *et al.* 2009). Additionally, we collected data on seed mass (Royal botanic gardens of Kew Seed database) (available online at http://data.kew.org/sid/). Data points were removed if seed size could not be obtained for that particular species. Seed sizes were log-transformed prior to analysis.

For studies where multiple levels of nutrient/water/light treatments/origin of plant/soil type were crossed with the competition treatment, we included the data from each different treatment as independent replicates. Some articles reported results for more than one responding species or for more than one experiment. In these cases, results reported for each responding species and experiment was included as separate data points in the analyses. For articles which reported results over the course of the experiment, only the final results at the end of the experiment were used (we recorded the age the plants were at this final harvest). Thus, each single experiment was only represented once in the analyses.

We calculated a log response ratio to estimate the effect of competition on size (see Oksanen *et al.* 2006):

$$\ln RR = \ln (X_r/X_c)$$

(equation 1)

where X_r and X_c are measures of the size of manipulated plants where competitors have been removed and plants whose competitors have been left intact, respectively. Other measures of competition intensity which may be more preferable (Oksanen *et al.* 2006; Weigelt and Jolliffe 2003; Rees *et al.* 2012) require data such as the size of the largest plant or maximum plant performance which were not available in the studies we were able to find for this current study. While there has been some issues raised with using ratios, the log response ratio has been established as the key response variable for meta-analyses and syntheses across disciplines. Newer indices which have been devised in response to criticisms of the mathematical properties of existing competition intensity metrics (e.g. Diaz *et al.* 2017) remain yet to be explored in depth but may prove to be more effective metrics for future studies on competition once they have been independently assessed.

We plotted the log response ratio (InRR) against the logged seed sizes. Linear regression was then used to test for significant relationships between InRR and logged seed size in both the neighbour-present experiment types separately. We also performed regressions separately for the short-lived (annual and biennial) species cases and for the long-lived (perennial) species cases in both the neighbour-present experiment types.

General linear models were used to investigate the relationship between seed size and InRR, the effect of life history on this relationship as well as if the interactions of seed size and life history had any effect in either of the neighbour-present experiment datasets. We also performed additional analyses where we included InRR as the dependent variable, seed size as a main effect and study and species as random effects to test if the overrepresentation of data points from certain studies or species affected our results. All analyses were conducted using SPSS v 25 (SAS Institute, NC, USA).

Results

We found a total of 134 studies where our selection criteria were met. From these studies, we were able to compile data from 845 independent data points or cases from experiments. Of these, 471 cases were open environment with 128 different target species representing 34 families and 374 cases were mature vegetation with 160 different target species representing 54 families. The details of the studies and species utilised in the dataset are included in appendix B and C.

We found no significant relationship between the size of the seed from which seedlings emerged, and the intensity of competition experienced in experiments where seedlings were planted in established vegetation ($R^2 = 0.007$, P = 0.110; Fig 2a). That is, seedlings planted in established vegetation did not show reduced impact of competition with increasing seed size. However, we found a significant negative relationship between competition intensity and the size of seed from which seedlings emerged in experiments where seedlings were planted in cleared plots and competed against regrowing plants or other seedlings ($R^2 = 0.046$, P < 0.001; Fig 2b). Seedlings planted in these cleared plots and competing against regrowing plants showed higher competitive ability (i.e. a lower negative impact on growth with the presence of competition) with increasing seed size.

There was no relationship between seed size and competitive ability in both the shortlived ($R^2 = 0.014$, P = 0.336; Fig 2a) and long-lived plants ($R^2 = 0.006$, P = 0.182; Fig 2a) in the cases where the seeds were competing against established vegetation. However, there was a significant negative relationship between seed size and competition intensity in the short-lived species growing in the open environments ($R^2 = 0.239$, P < 0.001; Fig 2b) whilst seed size did not affect competitive performance in the long-lived species ($R^2 = 0.001$, P =0.638; Fig 2b).

In the general linear models for the mature vegetation environment, we found that there was a significant seed size x life history (SS x LH) effect (P < 0.001; Table 1) on competition intensity. However, both life history (P = 0.991; Table 1) and seed size effects (P = 0.868; Table 1) were not significant (consistent with Figure 2a). When we controlled for study and species effects, there remained no effect of seed size (P = 0.679; Table 2).

In the general linear models for the open vegetation environment, we found that there was no significant seed size x life history (SS x LH) effect (P = 0.812; Table 3) on competition intensity. However, both life history (P < 0.001; Table 3) and seed size effects (P = 0.011; Table 3) were significant. The relationship between seed size and competition intensity differed for the two life history types (Fig 2b). There was a strong relationship

between seed size and competition intensity for short-lived plants and not for long-lived plants. When we controlled for study and species effects for the open vegetation environment, there was also no longer any significant effect of seed size suggesting that the significant effect of seed size we found in the linear regression analysis for the open vegetation environment could be partly explained by study (P < 0.001; Table 4) and or species (P = 0.015; Table 4) effects. When we controlled for study, the seed size effect remained significant for the studies in mature vegetation (see Table A1 in appendix A). In contrast, when we controlled for species, the seed size effect was no longer significant in the mature vegetation studies (see Table A2 in appendix A). However, this remains different from the mature vegetation experiments where seed size and competition were not related (and remained non-significant when study and species effects were considered).

Discussion

Seed size is traditionally predicted to be a key trait affecting plant performance under competition but tests of this prediction have yielded mixed results (Fenner 1978; Reader 1991; Eriksson 1997; Turnbull *et al.* 1999; Leishman 2001; Coomes *et al.* 2002; Turnbull *et al.* 2004; Eriksson 2005). We found that large seeds were associated with higher competitive ability (i.e. a lower loss in performance under competition) only in experiments where neighbour vegetation was cleared and then allowed to regrow with the target plants. This effect was highly influenced by the study and species effects. In other words, the observed seed size effect on competition was particularly great in some studies and some species, and the observed relationship was highly influenced by these effects. Large seed size did not confer greater competitive ability in experiments where neighbour vegetation was not cleared and target plants were planted amongst these established neighbour plants. The significant seed size x life history (SS x LH) effect observed in the general linear model is likely due to the relatively high sample size and the species effect (i.e. a high representation of some species), and should be treated with caution. The lack of relationship between seed size and competitive ability in established vegetation demonstrates that even having a large seed size does not provide adequate resources to allow seedlings to compete against established vegetation. A large seed size only has a competitive advantage when competing against plants at similar stages of establishment. This likely explains why the results of experiments where seeds of contrasting size were grown together have found larger seeds generally win (e.g. Goldberg and Landa 1991; Eriksson 1997; Turnbull et al. 1999; Leishman 2001; Turnbull et al. 2004) whilst field-based seed size/competitive ability experiments have often failed to find a relationship between seed size and competitive ability (e.g. Fenner 1978; Reader 1991; Coomes et al. 2002; Turnbull et al. 2004; Eriksson 2005). In a recent study, Carrington (2014) tested the 2 main predictions of the seed size-seed number trade-off theories that large numbers of seed are advantageous under low levels of competition while large seed size is advantageous under asymmetric competition. In line with the findings of this study, she did not find any advantage of having larger seeds during establishment into existing vegetation. Species with larger numbers of seeds sown were also found to result in higher seedling density suggesting that seed number has a greater impact than seed size on seedling density when establishing in sites of mature vegetation. Other studies (e.g. Tilman 1997; Foster 2001; Foster et al. 2007; Williams et al. 2007) have also found that when seedlings are competing against more established adult competitors, seed number has a greater impact on the resulting seedling density than seed size. Rather than a strategy of trying to outcompete existing mature vegetation by outgrowing it, species which are able

to produce more seeds would have a higher chance of successfully establishing in established vegetation. This suggests that smaller-seeded species which tend to produce a greater number of offspring may be more advantaged in these mature vegetation environments than larger-seeded species.

Our findings showed a competitive advantage of large seed sizes in the open environment experiments where neighbouring vegetation has been cleared and then allowed to regrow and no competitive advantage of seed size in the mature environment experiments where neighbouring vegetation was not cleared. This suggests that the value of large seed size lies within provisioning the offspring with more maternal resources to withstand stress from environmental variables (e.g. drought, mineral nutrient deficiency, clipping, and leaf litter burial) as well as competition (as reviewed by Leishman et al. 2000). Large seeds are also more likely to be eaten by herbivores, so there is a potential balance in the noncompetition costs and benefits of large seeds (Bonser and Reader 1999). However, these resources are only sufficient to aid competition against other seedlings trying to establish at the same time and not in competing with mature competitors. This is likely to be an important competitive advantage as the seeds of many species tend to germinate after the adult plants have been removed (i.e. following a disturbance) where other seedlings would be the most common competitor for a seedling. Controlling for species effects removed the seed size effect suggesting that there were some small-seeded species which experienced a high impact on growth from competitors or alternately there were largeseeded species which experienced a low impact on growth from competitors that were over-represented in the study. This does not mean there was no seed size effect but just

that the results need to be interpreted with caution. Further empirical studies are required to establish the nature of the seed size – competitive ability relationship in annual plants.

The difficulty in finding evidence for seed size advantages under competition has led newer life history theories for example, the Falster et al. (2008) model to suggest that seedlings may not compete and that the value of seed size may lie elsewhere. Falster et al. (2008) predict that large seeds do not provide a competitive advantage early on but instead provision offspring to get them through the vulnerable juvenile stage (i.e. large seeds minimise this time). We believe this is probably not the case for two reasons: first while large seeds can produce large seedlings at the time of emergence from the seed, seed size and seedling growth rate is often negatively correlated – species with small seeds often have faster growth at least for initial growth (Grime and Hunt 1975; Fenner 1978, Fenner and Lee 1989; Shipley and Peters 1990; Jurado and Westoby 1992, Reich et al 1998; however see Turnbull et al. 2008). Small-seeded species have been shown to compensate for their smaller initial size by fast growth which enables them to achieve biomass similar to that of larger-seeded species (Ben-Hur and Kadmon 2015). Gurevitch et al. (1990) have also shown that when seeds are grown together, the inherent differences in growth rate of smaller-seeded seedlings can allow them to overcome initial differences in seed mass. Second, large seeds tend to be produced by large-sized plant species (i.e. species with large maximum body sizes) (Thompson and Rabinowitz 1989; Moles et al. 2004; Grubb et al. 2005; Moles and Westoby 2006; Rees and Venable 2007), and large-sized plant species have a larger size at life history transitions (large size at reproduction, large size at maturity) (Tracey and Aarssen 2011). Thus, even if seedlings from large seeds grew faster through their juvenile period, the juvenile period for large-seeded species is longer than

for seedlings from small-seeded species. We found a stronger negative relationship for short lived species – for these species, small-seeded and small-sized species are more likely to reach the minimum size for reproduction prior to the onset of competition (especially since these species grow more quickly) - large seeded and large sized annual species are more likely to experience competition, and thus would have evolved higher competitive ability. Therefore, the observed results are most likely due to a competitive advantage of large seed size as seedlings experience competition from other seedlings.

These findings have important consequences on the competition-colonisation theory. One of the key assumptions of the traditional competitor-colonisation models was that the competitive hierarchy was absolute and that inferior competitors cannot persist, reproduce or establish in the presence of superior competitors and will be replaced with the appearance of a superior competitor (Coomes and Grubb 2003). The results of this study are consistent with the findings that the difference in competitive ability between smaller and larger-seeded species is not asymmetric enough to explain the coexistence of large and small seed sizes (as Freckleton and Watkinson 2001; Levine and Rees 2002; Coomes and Grubb 2003 have found). Our findings that larger-seeded are only better competitors when the plant and its competitor are at similar stages suggests that the competitive ability of large-seeded species is not as absolute as required by competitioncolonisation theory and the seed-size game theory models and that there is a pre-emptive effect of earlier establishment. Whilst traditional competitor-colonisation theory assumes that the plant with higher competitive ability must win no matter how slight its advantage and regardless of whether they are competing against more mature plants or not (Geritz 1995; Rees and Westoby 1997; Geritz et al. 1999), our findings do not support this. Smallseeded species which establish earlier can have a competitive advantage over largeseeded species which attempt to establish later. Differences in the order of emergence are known to affect the competitive hierarchy in communities. Plants which germinate earlier have been found to have a competitive advantage over those that germinate later (e.g. White and Holt 2005). Earlier emergence has been suggested to allow for the pre-emption of resources more so than a larger seed size (Seiwa 2000). Early-emerging plants are able to have greater access to resources such as light and nutrients than plants that emerge later and later-emerging plants have been shown to be unable to make up for this advantage offered by earlier germination (Weiner 1986, Harper 1977). Our study shows that in a similar way, those that arrive later into environments of dense vegetation are affected by the greater access to resources by the more established plants which cannot be compensated for even by a large seed size. Stochastic effects can open space for colonisation, and these spaces may be occupied by a range of small and large seeds. However, new seedlings are not likely to emerge in already occupied spaces. If new arrivals are able to germinate and grow quickly, then they could pre-empt the arrival of new and superior competitors.

Competitive hierarchies could potentially differ depending on whether competitive ability is measured by competitive effect (the ability to depress growth and reproduction of neighbours) or competitive response (the ability to withstand the negative effects of neighbours) (Goldberg 1990; 1996). In this study we measured competitive ability as performance under competition which was a measure of the combined outcome of competitive effects and competitive responses. We did not find any difference in overall competitive ability between large and small-seeded species. However, large-seeded

species may have a strong competitive response (as they are more resistant to the presence of neighbours) whilst small-seeded species may have a large competitive effect (through fast growth and high resource acquisition rates). Thus, different competitive strategies can evolve across species to result in a given competitive ability.

Another key assumption of the competitor-colonisation models was that good competitors have extremely low colonisation ability. The findings of this study show that seedlings from all species including large-seeded species (at least in the herbaceous communities that dominate this study) are able to colonise newly available habitat. Although studies by Turnbull (1999); Ehrlen and Eriksson (2000); Guo et al. (2000) and Murray et al. (2005) have found smaller-seeded species tend to occupy a greater number of sites than largerseeded species, there has been little evidence to show smaller-seeded species have higher colonisation ability than large-seeded species. Previously it was believed that the abundance of small-seeded species in communities may have been due to smaller-seeded plants having higher dispersal ability (Turnbull et al. 1999). However, little empirical support has been found for there being higher dispersal ability of smaller-seeded plants (Leishman 2001) and it has also been argued higher dispersal ability is not a good measure of colonisation ability (Cadotte et al. 2006; Molina-Montenegro et al. 2012). Furthermore, recent findings have instead shown large-seeded species to have greater dispersal distances than small-seeded species and plant height to be more important than seed size in determining dispersal ability (Thomson *et al.* 2011). This suggests that the value of small-seed size which has led to their abundance in communities does not lie in dispersal ability but elsewhere. Whilst our results show large-seeded species tend to have a competitive advantage in newly opened sites where the main competitors are other

seedlings, this advantage was quite slight and may not be sufficient to allow large-seeded species to uniformly dominate these newly opened sites. The capacity for small-seeded species to produce more seeds (and do so earlier) may be enough of an advantage to overcome the competitive advantages of producing large seeds. Some studies suggest that in competitor colonisation models, including a pre-emptive effect (where a species already occupying a site would be advantaged) would impede coexistence (e.g. Yu and Wilson 2001). However, others (e.g. Calcagno *et al.* 2006) found pre-emption can actually favour coexistence provided: 1) species are not strongly limited in their colonisation ability and 2) if the strict competitive hierarchy of species is relaxed as our findings have suggested.

Our results also suggest that there are differences in the association between seed size and competitive ability for species with differing life histories. There was no competitive advantage of larger seed size in both the short-lived and long-lived species grown with more established competitors. However, in the open environments where the seedlings were grown with other seedling competitors, we found that seed size was associated with competitive performance in the short-lived species but not in the long-lived species. This may have been due to the short-lived species taking advantage of the opportunity the open environments provided to maximise growth rate before competition has closed in and the canopy closes. Shading has been shown to have particularly negative effects on seedling growth (Augspurger 1984). Augspurger (1984) also found no relationship between seed mass and seedling survival under shaded conditions in tropical tree species. Similarly, in an experiment on the effects of different levels of irradiance on *Desmodium paniculatum*, Wulff (1986) found that whilst seedling survival was correlated with irradiance, seed size had no effect on survivorship of seedlings in the highly shaded forest

sites suggesting that in the mature environments of our study, the large seed the seedlings emerged from may not have been sufficient to counter the effects of shading from the larger competitors. However, in the open environments where the canopy has not yet closed, the benefits of a large seed size remained observable in the short-lived species. The reason this effect was only visible in the short-lived species and not the long-lived species may have been because the short-lived species were under higher pressure to grow to a larger size before the closure of the canopy occurs. Rapid growth before competition intensifies and limits growth may be important to short-lived species which tend to have smaller maximum body sizes and are thus likely to suffer from the effects of asymmetric competition if other establishing seedlings outgrow them. The lack of an effect of seed size on competitive performance in long-lived species could also be due to the slower development of perennial species compared to annual species. Rösch et al. (1997) observed in their experiment to find competitive hierarchy amongst 15 pioneer species, that annual species displayed higher competitive ability than perennial species in cases where the plants were grown from seeds sown at the same time such as those in our open environment dataset. In situations where perennials were allowed to establish for a year or more prior to the annual species being sown, this effect did not occur. They suggest that this could be because perennial species have a delay in their phenological development compared with annuals. Annual plants with large seeds have the resources to obtain a large size and initiate reproduction prior to the onset of intense competition. Large seed size may be important within short-lived species because they tend to have smaller seed sizes relative to longer-lived species and tend to have smaller overall body sizes and would not have the capacity to be able to outgrow long-lived, larger-seeded plants after the early stages when the long-lived species are already well-established. Long-lived species have slow life strategies of obtaining resources over a long period of time and so growth rate

may not have been as important to them although they tend to have larger maximum body sizes.

Although competitive ability has traditionally been associated with large body size (e.g. Grime 1977; 1979), recent work has shown that contrary to the predictions of these traditional strategy theories, having the capacity to reproduce under competition is more important than being able to obtain a greater share of resources to grow to a large size (Bonser 2013). Chambers and Aarssen (2009) found by examining the above-ground dry mass for 20 species of herbaceous angiosperms, most of the offspring were produced by some of the smallest of these species suggesting that species coexisting under high competition are not successful because of their large body size but because they produce higher numbers of offspring. These findings suggest that competitive success can also be associated with relatively small size traits including body size. In some cases, small-sized species and those with small seed sizes may be able to outperform larger species due to the smaller minimum body size the small-sized species are required to reach to reproduce and ensure they are represented in the community. Producing offspring which are capable of growing to a large size is important for fitness only when the age of competitors are similar such as under seedling-seedling competition as we found in our open environment dataset. Traditionally, theory predicted that larger seeds would allow the pre-emption of resources by producing a larger seedling which gain better access to resources than smaller neighbouring plants. Instead, in this study we found that early establishment allows the pre-emption of resources and thus even small-seeded plants can have a competitive advantage over later-establishing seeds. A large seed is unable to offer sufficient competitive ability solely on the basis of seed size alone. These findings all

suggest that contrary to widely-accepted assumptions in the literature, small plants may not be inferior to large plants at passing on their genes when under intense competition.

Studies investigating the effects of seed size variability within species would be interesting as the other effects of physiological capacity of individual plants to resources would be controlled. However, studies effectively investigating these effects are rare. A recent study demonstrates that seed size variation does not affect competitive ability within species, and that differences in competitive ability are due to other factors (such as resource acquisition strategies) that may also be correlated with seed size (Bonser et al., unpublished manuscript). The results of this study also lead to the follow-up questions: does small seed size correlate with higher reproductive efficiency (higher conversion of resources from vegetative growth to reproductive output) or greater reproductive success under competition? Does the relationship between seed size and reproductive performance differ when competing against similarly aged plants and more mature plants? Does the relationship between seed size and reproductive lived woody species and short-lived herbaceous species?

We acknowledge that synthesis studies such as this one could potentially be affected by limitations in current data available and that this could have affected our findings. For example, certain species may have been represented more than others in the available literature and this may have affected our ability to observe patterns across species. However, efforts were made to assess this by performing additional analyses to test whether life history, study or species affected our results. Additionally, there were few

studies which examined the reproductive performance of the plants especially when the target species were trees and longer-lived species. This was partly due to the difficulty with measuring these for longer-lived plants and due to the traditional definition of competitive ability where species are evaluated by their ability to take a larger share of resources which is associated with large plant size (Grime 1977). However our findings suggest that producing seeds may be more important than producing large seeds to reach a large size under competition against more mature competitors. This suggests that in order to truly observe whether seed size has any effect on competitive performance across a plant's entire life, it would be important to extend experiments to measure reproductive performance.

CONCLUSION

In this study we tested whether an alternative mechanism of large seed size in competition is to allow seedlings emerging from large seeds to perform better than seedlings emerging from smaller seeds when establishing in environments where the competitors are of a similar age. We found that whilst a large seed size confers higher competitive ability in environments where more mature vegetation has been cleared and the main competitors are of a similar age, a large seed size does not confer higher competitive ability against more mature competitors. This suggests that the effects of having a large offspring size are an increase in survival against early stresses in life including competitive ability but this is only effective when competing against other seedlings. Although seed size is correlated with other traits which will affect the plant's competitive ability later on, seed size itself is only effective at increasing competitive ability in open environments. Its primary function may be to increase performance against other external stresses a seedling faces during establishment.

The current study assessed the relationship between seed size and competitive ability across a large number of species of differing life histories and growth forms. These findings suggest that competition could potentially be important in the evolution of seed sizes in contrast to the predictions of newer life history theories made in response to the lack of evidence for the competition-colonisation theories. These findings also suggest that smallseeded species are not as limited in their competitive ability as predicted by traditional theories. These issues demonstrate gaps in our current understanding of the conditions underlying the evolution of competitive abilities and the coexistence of different seed sizes. The potential importance of competition in the evolution of smaller seed sizes presents a new challenge to explaining observed patterns of abundance and distribution in the environment. This is important since understanding the forces selecting for competitive ability and shaping life-histories is essential in understanding the diversity of plant strategies.



Fig. 1 Prediction figures showing the predictions of traditional strategy theories compared to the predictions of newer life history theories on the effect of seed size on competitive ability of plants. Under the traditional strategy theories, a larger seed size is predicted to confer greater competitive ability when competing against both adult competitors (a) and against other seedlings (b). Newer life history theories, however, predict seed size is not important for competition (a). Instead these theories predict that the advantage of large seed size is that it allows the capacity to grow large prior to the onset of intense competition – such as the conditions experienced in the open environment experiments where neighbours are removed and allowed to grow back with the target plants (b).



Fig. 2 Regression analysis of log seed size (mg) and an index of competition intensity where competitive performance was measured as the effect of competition on size in **a**) A mature environment where seedlings were competing against adult competitors and **b**) An open environment where seedlings were competing against other establishing seedlings. Closed circles represent short-lived plants and the solid lines the regression lines between them (•, solid line) and open circles represent long-lived plants and the dashed lines the regression lines between them (o, dashed line).

Table 1. Two factor general linear model results showing the impact of seed size and life history

 and their interaction on the competition intensity experienced in the mature vegetation

 environment.

	Competition intensity (InRR)				
Source of variation	Df	MS	F	Р	
Life history (LH)	1	0.001	0.000	0.991	
Error	7.895	7.876			
Seed size (SS)	123	5.166	0.622	0.868	
Error	7.679	8.308			
LH x SS	7	10.232	6.117	<0.001	
Error	242	1.673			

Table 2. General linear model results showing the impact of seed size on the competition intensity

 experienced with study and species included as random effects in the mature vegetation

 environment.

	Competition intensity (InRR)				
Source of	Df	MS	F	Р	
variation					
Seed size	2	0.179	0.388	0.679	
Study	22	4.802	10.394	<0.001	
Species	20	1.917	4.150	<0.001	
Error	190	0.462			

Table 3. Two factor general linear model results showing the impact of seed size and life history

 and their interaction on the competition intensity experienced in the open vegetation environment.

	Competition intensity (InRR)			
Source of variation	Df	MS	F	Ρ
Seed size (SS)	111	3.598	19.694	0.011
Error	3.277	0.183		
Life history (LH)	1	42.876	165.539	<0.001
Error	8.865	0.259		
SS x LH	2	0.151	0.208	0.812
Error	355	0.725		

Table 4. General linear model results showing the impact of seed size on the competition intensity

 experienced with study and species included as random effects in the open vegetation

 environment.

	Competi	Competition intensity (InRR)			
Source of variation	Df	MS	F	Р	
Seed size	2	0.125	0.333	0.717	
Study	19	4.135	11.041	<0.001	
Species	7	0.948	2.532	0.015	
Error	321	0.375			
Error	321	0.375			

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Appendix A:

Table A1. General linear model results showing the impact of life history and seed size on the competition intensity experienced with study included as random effects in the open vegetation environment.

	Competition intensity (InRR)			
Source of variation	Df	MS	F	Ρ
Life history (LH)	1	1.256	3.271	0.071
Error	327	0.384		
Seed size (SS)	72	1.497	3.897	<0.001
Error	327	0.384		
Study	30	4.397	11.449	<0.001
Error	327	0.384		

Table A2. General linear model results showing the impact of seed size on the competition

 intensity experienced with species included as a random effect in the open vegetation

 environment.

	Competition intensity (InRR)				
Source of variation	Df	MS	F	Р	
Seed size (SS)	2	0.125	0.214	0.808	
Error	340	0.585			
Species	17	3.455	5.910	<0.001	
Error	340	0.585			

Appendix B: The list of surveyed studies and their details.

Mature environment dataset

			Life		Primary measure of
Reference	Target Species	Family	History	Competitor species	performance
Aguilera and Lauenroth 1993	Bouteloua gracilis	Poaceae	Р	Bouteloua gracilis	Leaf number
Ashton <i>et al.</i> 1998	Caryota urens	Arecaceae	Р	Pinus caribaea	Total biomass
Ashton <i>et al.</i> 1998	Dipterocarpus zeylanicus	Dipterocarpaceae	Р	Pinus caribaea	Total biomass
Ashton <i>et al.</i> 1998	Pericopsis mooniana	Fabaceae	Р	Pinus caribaea	Total biomass
Ashton <i>et al.</i> 1998	Swietenia macrophylla	Meliaceae	Р	Pinus caribaea	Total biomass
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Agropyron cristatum	Relative growth rate
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Bakker and Wilson 2001	Agropyron cristatum	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Bakker and Wilson 2001	Bouteloua gracilis	Poaceae	Р	Bouteloua gracilis	Relative growth rate
Belcher <i>et al.</i> 1995	Trichostema brachiatum	Lamiaceae	А	Sporobolus heterolepis	Aboveground biomass
Bonner <i>et al.</i> 1998	Carduus nutans	Asteraceae	А	Lolium perenne	Aboveground biomass

Bonser and Reader 1995 Cahill 1999 Cahill 1999 Cahill 2002 Cahill and Casper 2000 Cater and Chapin 2000 പ്പ Cater and Chapin 2000

Poa compressa Abutilon theophrasti Abutilon theophrasti Abutilon theophrasti Amaranthus retroflexus Rumex crispus Plantago lanceolata Abutilon theophrasti Amaranthus retroflexus Rumex crispus Plantago lanceolata Amaranthus retroflexus Picea glauca Picea glauca Picea glauca Betula papyrifera Betula papyrifera Betula papyrifera Picea glauca Picea glauca Picea glauca

Poaceae	Р	Po
Poaceae	Р	Po
Poaceae	Р	Hie
Poaceae	Р	Po
Poaceae	Р	Br
Poaceae	Р	Ph
Poaceae	Р	Sol
Poaceae	Р	Syr
Malvaceae	А	Da
Malvaceae	А	Da
Malvaceae	А	Da
Amaranthaceae	А	Da
Polygonaceae	Р	Da
Plantaginaceae	Р	Da
Malvaceae	А	Da
Amaranthaceae	А	Da
Polygonaceae	Р	Da
Plantaginaceae	Р	Da
Amaranthaceae	А	Da
Pinaceae	Р	Ca
Pinaceae	Р	Eq
Pinaceae	Р	Po
Betulaceae	Р	Ca
Betulaceae	Р	Eq
Betulaceae	Р	Po
Pinaceae	Р	Ca
Pinaceae	Р	Equ
Pinaceae	Р	Po

Poa compressa	Above
Poa compressa	Above
Hieracium floribundum	Above
Poa pratensis	Above
Bromus inermis	Above
Phalaris arundinacea	Above
Solidago canadensis	Above
Symphyotrichum puniceum	Above
Dactylis glomerata	Bioma
Calamagrostis canadensis	Above
Equisetum arvense	Above
Populus tremuloides	Above
Calamagrostis canadensis	Above
Equisetum arvense	Above
Populus tremuloides	Above
Calamagrostis canadensis	Total
Equisetum arvense	Total
Populus tremuloides	Total

eground biomass ass eground biomass eground biomass eground biomass eground biomass eground biomass eground biomass biomass biomass biomass

Cater and Chapin 2000 Cater and Chapin 2000 Cater and Chapin 2000 Cramer et al. 2012 Cramer et al. 2012 Cramer et al. 2012 Curt et al. 2005 De Steven 1991 Dillenburg et al. 1993 Dillenburg et al. 1993 Dormann et al 2000 හ Dormann et al 2000

Betula papyrifera Betula papyrifera Betula papyrifera Vachellia karroo Acacia burkei Schotia brachypetala Fagus sylvatica Fraxinus americana Acer rubrum Pinus taeda Liquidambar styraciflua Ulmus alata Fraxinus americana Acer rubrum Pinus taeda Liquidambar styraciflua Ulmus alata Liquidambar styraciflua Liquidambar styraciflua Artemisia maritima Artemisia maritima Artemisia maritima Halimione portulacoides Halimione portulacoides Halimione portulacoides Plantago maritima Plantago maritima Plantago maritima

Betulaceae	Р	Calamagrostis canadensis	Total biomass
Betulaceae	Р	Equisetum arvense	Total biomass
Betulaceae	Р	Populus tremuloides	Total biomass
Fabaceae	Р	Chloris gayana	Total biomass
Fabaceae	Р	Chloris gayana	Total biomass
Fabaceae	Р	Chloris gayana	Total biomass
Fagaceae	Р	Pinus sylvestris	Total biomass
Oleaceae	Р	Festuca elatior	Height
Sapindaceae	Р	Festuca elatior	Height
Pinaceae	Р	Festuca elatior	Height
Altingiaceae	Р	Festuca elatior	Height
Ulmaceae	Р	Festuca elatior	Height
Oleaceae	Р	Festuca elatior	Height
Sapindaceae	Р	Festuca elatior	Height
Pinaceae	Р	Festuca elatior	Height
Altingiaceae	Р	Festuca elatior	Height
Ulmaceae	Р	Festuca elatior	Height
Altingiaceae	Р	Lonicera japonica	Final leaf biom
Altingiaceae	Р	Parthenocissus quinquefolia	Final leaf biom
Asteraceae	Р	Limonium vulgare	Total biomass
Asteraceae	Р	Artemisia maritima	Total biomass
Asteraceae	Р	Artemisia maritima	Total biomass
Amaranthaceae	Р	Limonium vulgare	Total biomass
Amaranthaceae	Р	Artemisia maritima	Total biomass
Amaranthaceae	Р	Artemisia maritima	Total biomass
Plantaginaceae	Р	Limonium vulgare	Total biomass
Plantaginaceae	Р	Artemisia maritima	Total biomass
Plantaginaceae	Р	Artemisia maritima	Total biomass

al biomass al biomass al biomass al biomass al biomass ght al leaf biomass al leaf biomass al biomass

Dyer and Rice 1999 Dyer and Rice 1999 Egerton and Wilson 1993 Eliason and Allen 1997 Elliott and White 1993 Ellison and Farnsworth 1993 Erneburg 1999 Facelli 1994 പ്പ Facelli 1994

Nassella pulchra Nassella pulchra Celmisia longifolia Artemisia californica Pinus resinosa Rhizophora mangle Anthemis cotula Ailanthus altissima Ailanthus altissima

Poaceae	Р	
Poaceae	Р	
Asteraceae	Р	
Asteraceae	Р	
Pinaceae	Р	
Rhizophoraceae	Р	
Asteraceae	А	
Simaroubaceae	Р	
Simaroubaceae	Р	

Nassella pulchra	Basal Diameter
Nassella pulchra	Basal Diameter
Poa costiniana	Relative growth rate
Avena barbata	Aboveground biomass
Acer pensylvanicum	Total biomass
Acer pensylvanicum	Total biomass
Prunus pensylvanica	Total biomass
Prunus pensylvanica	Total biomass
Acer rubrum	Total biomass
Acer rubrum	Total biomass
Acer pensylvanicum	Total biomass
Acer pensylvanicum	Total biomass
Prunus pensylvanica	Total biomass
Prunus pensylvanica	Total biomass
Acer pensylvanicum	Total biomass
Acer pensylvanicum	Total biomass
Prunus pensylvanica	Total biomass
Prunus pensylvanica	Total biomass
Acer rubrum	Total biomass
Acer rubrum	Total biomass
Acer pensylvanicum	Total biomass
Acer pensylvanicum	Total biomass
Prunus pensylvanica	Total biomass
Prunus pensylvanica	Total biomass
Avicennia germinans	Total biomass
Tripleurospermum inodorum	Aboveground biomass
Setaria faberi	Aboveground biomass
Setaria faberi	Aboveground biomass
Gerry and Wilson 1995 Gill and Marks 1991 Going et al. 2009 റ്റ് Going *et al.* 2009

Agropyron cristatum Bouteloua gracilis Elaeagnus commutata Melilotus officinalis Potentilla pensylvanica Cornus racemosa Pinus strobus Rhamnus cathartica Acer rubrum Pinus strobus Rhamnus cathartica Avena barbata Avena barbata Avena barbata Avena barbata Avena barbata Avena barbata Bromus diandrus Bromus diandrus Bromus diandrus Bromus diandrus Bromus diandrus Bromus diandrus Hordeum murinum Hordeum murinum Hordeum murinum Hordeum murinum Hordeum murinum

Poaceae	Р	Bromus inermis
Poaceae	Р	Bromus inermis
Elaeagnaceae	Р	Bromus inermis
Fabaceae	А	Bromus inermis
Rosaceae	Р	Bromus inermis
Cornaceae	Р	Phleum pratense
Pinaceae	Р	Phleum pratense
Rhamnaceae	Р	Phleum pratense
Sapindaceae	Р	Phleum pratense
Pinaceae	Р	Phleum pratense
Rhamnaceae	Р	Phleum pratense
Poaceae	А	Plantago erecta

Total biomass Aboveground biomass

Hordeum murinum Bouteloua gracilis Koeleria cristata Sporobolus cryptandrus Pascopyrum smithii Pseudoroegneria spicata Trifolium pratense Trifolium pratense Trifolium pratense Calophyllum brasiliense Calophyllum brasiliense Purshia tridentata Rumex obtusifolius Rumex obtusifolius *Rumex* obtusifolius Picea glauca Pinus resinosa Quercus rubra Liriodendron tulipifera Quercus rubra Liriodendron tulipifera Elymus athericus Elymus athericus Elymus athericus Elymus athericus Eucalyptus microcarpa Eucalyptus camaldulensis Artemisia frigida

Poaceae	А	Plantago erecta
Poaceae	Р	Elymus repens
Poaceae	Р	Bromus tectorum
Fabaceae	Р	Festuca pratensis
Fabaceae	Р	Dactylis glomerata
Fabaceae	Р	Dactylis glomerata
Calophyllaceae	Р	Axonopus scoparius
Calophyllaceae	Р	Piper arboreum
Rosaceae	Р	Bromus tectorum
Polygonaceae	Р	Lolium perenne
Polygonaceae	Р	Lolium perenne
Polygonaceae	Р	Lolium perenne
Pinaceae	Р	Betula papyrifera
Pinaceae	Р	Pinus banksiana
Fagaceae	Р	Poa pratensis
Magnoliaceae	Р	Poa pratensis
Fagaceae	Р	Poa pratensis
Magnoliaceae	Р	Poa pratensis
Poaceae	Р	Festuca rubra
Myrtaceae	Р	Eucalyptus microcarpa
Myrtaceae	Р	Eucalyptus camaldulensis
Asteraceae	Р	Populus tremuloides

Aboveground biomass Total biomass Height Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Relative growth rate Total biomass Total biomass Total biomass Total biomass Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Leaf number Leaf number Aboveground biomass

Lamb et al. 2007 Leishman 1999 စ္ Leishman 1999

Chenopodium leptophyllum Artemisia frigida Chenopodium leptophyllum Artemisia frigida Chenopodium leptophyllum Artemisia frigida Chenopodium leptophyllum Achillea millefolium Bromus erectus Bromus erectus Campanula rotundifolia Cirsium acaule Crepis capillaris Cynosurus cristatus Cynosurus cristatus Dactylis glomerata Dactylis glomerata Holcus lanatus Holcus lanatus Medicago lupulina Medicago lupulina Myosotis arvensis Plantago lanceolata Plantago lanceolata Prunella vulgaris Prunella vulgaris Sanguisorba minor Sanguisorba minor

Chenopodiaceae	А	F
Asteraceae	Р	F
Chenopodiaceae	А	F
Asteraceae	Р	F
Chenopodiaceae	А	F
Asteraceae	Р	F
Chenopodiaceae	А	F
Asteraceae	Р	F
Poaceae	Р	L
Poaceae	Р	F
Campanulaceae	Р	F
Asteraceae	Р	F
Asteraceae	А	F
Poaceae	Р	L
Poaceae	Р	F
Poaceae	Р	L
Poaceae	Р	F
Poaceae	Р	L
Poaceae	Р	F
Fabaceae	Р	L
Fabaceae	Р	F
Boraginaceae	А	F
Plantaginaceae	Р	L
Plantaginaceae	Р	F
Lamiaceae	Р	L
Lamiaceae	Р	F
Rosaceae	Р	L
Rosaceae	Р	F

Populus tremuloides Festuca ovina Leontodon hispidus Festuca ovina Festuca ovina Festuca ovina Festuca ovina Leontodon hispidus Festuca ovina Leontodon hispidus Festuca ovina Leontodon hispidus Festuca ovina Leontodon hispidus Festuca ovina Festuca ovina Leontodon hispidus Festuca ovina Leontodon hispidus Festuca ovina Leontodon hispidus Festuca ovina

Aboveground biomass Total biomass

Leishman 1999 Leishman 1999 Leishman 1999 Leishman 1999 Leishman 1999 Lewis and Tanner 2000 Lewis and Tanner 2000 Liu and Han 2007 Liu and Han 2007 Liu and Han 2007 Liu et al. 2008 Liu et al. 2008 Liu et al. 2008 Maron 1997 McGraw and Chapin 1989 McGraw and Chapin 1989 McGraw and Chapin 1989 McGraw and Chapin 1989 McLeod et al. 2001 McLeod et al. 2001 McLeod et al. 2001 Meiners and Handel 2000 Meiners and Handel 2000 Midoko-Iponga et al. 2005 Midoko-Iponga et al. 2005 Midoko-Iponga et al. 2005 പ്പ Midoko-Iponga et al. 2005

Leishman 1999

Scabiosa columbaria Scabiosa columbaria Trifolium pratense Trifolium pratense Trisetum flavescens Trisetum flavescens Dinizia excelsa Dinizia excelsa Leymus chinensis Leymus chinensis Leymus chinensis Bromus inermis Bromus inermis Bromus inermis Lupinus arboreus Eriophorum vaginatum Eriophorum vaginatum Eriophorum vaginatum Eriophorum scheuchzeri Carya aquatica Quercus lyrata Taxodium distichum Acer rubrum Quercus palustris Athanasia trifurcata Crassula glomerata Leucadendron corymbosum Olea europaea subsp. cuspidata

Caprifoliaceae	Р	Leontoc
Caprifoliaceae	Р	Festuca
Fabaceae	Р	Leontoc
Fabaceae	Р	Festuca
Poaceae	Р	Leontod
Poaceae	Р	Festuca
Fabaceae	Р	Micrand
Fabaceae	Р	Micrand
Poaceae	Р	Artemis
Poaceae	Р	Artemis
Poaceae	Р	Artemis
Poaceae	Р	Leymus
Poaceae	Р	Leymus
Poaceae	Р	Leymus
Fabaceae	Р	Bromus
Cyperaceae	Р	Eriopho
Juglandaceae	Р	Salix nig
Fagaceae	Р	Salix nig
Cupressaceae	Р	Salix nig
Sapindaceae	Р	Achillea
Fagaceae	Р	Achillea
Asteraceae	Р	Cynodo
Crassulaceae	А	Cynodo
Proteaceae	Р	Cynodo
Oleaceae	Р	Cynodo

todon hispidus	Total biomass
ıca ovina	Total biomass
todon hispidus	Total biomass
ıca ovina	Total biomass
todon hispidus	Total biomass
ıca ovina	Total biomass
andropsis scleroxylon	Total biomass
andropsis scleroxylon	Total biomass
misia eriopoda	Leaf number
misia eriopoda	Leaf number
misia eriopoda	Leaf number
nus chinensis	Leaf number
nus chinensis	Leaf number
nus chinensis	Leaf number
nus diandrus	Height
ohorum vaginatum	Aboveground biomass
ohorum vaginatum	Aboveground biomass
ohorum scheuchzeri	Aboveground biomass
horum scheuchzeri	Aboveground biomass
nigra	Height
nigra	Height
nigra	Height
llea millefolium	Total biomass
llea millefolium	Total biomass
don dactylon	Height

Midoko-Iponga et al. 2005 Myster and McCarthy 1989 Nilsson 1994 Nilsson 1994 **Olson and Richards 1989** Paul et al. 1998 Paul *et al.* 1998 Paul et al. 1998 Paul et al. 1998 Paul et al. 1998 Paul *et al.* 1998 Paul et al. 1998 ရာ Paul *et al.* 1998

Relhania fruticosa Carya tomentosa Pinus sylvestris Pinus sylvestris Agropyron desertorum Acorus calamus Anemone canadensis Asclepias incarnata Bidens cernua Calamagrostis canadensis Carex crinata Carex rostrata Cladium mariscoides Coreopsis rosea Cyperus bipartitus Dulichium arundinaceum Eleocharis acicularis Eleocharis calva Eleocharis palustris Epilobium ciliatum Eriocaulon aquaticum Eutrochium maculatum Eupatorium perfoliatum Euthamia galetorum Gratiola aurea Hypericum ellipticum Iris versicolor Juncus bufonius

Asteraceae Ρ Ρ Juglandaceae Ρ Pinaceae Ρ Pinaceae Ρ Poaceae Ρ Acoraceae Ranunculaceae Ρ Ρ Asclepiadaceae Asteraceae А Ρ Poaceae Ρ Cyperaceae Ρ Cyperaceae Ρ Cyperaceae Ρ Asteraceae Cyperaceae А Ρ Cyperaceae Ρ Cyperaceae Ρ Cyperaceae Cyperaceae Ρ Ρ Onagraceae Ρ Eriocaulaceae Ρ Asteraceae Ρ Asteraceae Ρ Asteraceae Ρ Scrophulariaceae Ρ Clusiaceae Ρ Iridaceae Juncaceae А

Cynodon dactylon Aster pilosus Empetrum hermaphroditum Empetrum hermaphroditum Agropyron desertorum Acorus calamus Acorus calamus

Height **Total biomass** Total biomass Total biomass Height Aboveground biomass Aboveground biomass

Paul et al. 1998 Paul *et al.* 1998 Paul et al. 1998 Paul et al. 1998 Paul et al. 1998 Paul et al. 1998 Peltzer 2001 Peltzer 2001 Peltzer 2001 Peltzer and Wilson 2001 o Peltzer and Wilson 2001 Juncus effusus Juncus filiformis Lysimachia ciliata Lysimachia thyrsiflora Lythrum salicaria Mimulus ringens Panicum longifolium Penthorum sedoides Phalaris arundinacea Polygonum hydropiperoides Rumex verticillatus Sabatia kennedyana Scirpus cyperinus Scirpus fluviatilis Schoenoplectus tabernaemontani Sparganium eurycarpum Spartina pectinata Triadenum fraseri Verbena hastata Bouteloua gracilis Bouteloua gracilis Elaeagnus commutata Bouteloua gracilis Agropyron cristatum Picea glauca Pinus banksiana Agropyron cristatum Picea glauca

Juncaceae Ρ Ρ Juncaceae Ρ Primulaceae Ρ Primulaceae Ρ Lythraceae Ρ Scrophulariaceae Ρ Poaceae Crassulaceae Ρ Ρ Poaceae Polygonaceae Ρ Ρ Polygonaceae Ρ Gentianaceae Ρ Cyperaceae Ρ Cyperaceae Ρ Cyperaceae Typhaceae Ρ Ρ Poaceae Ρ Clusiaceae Verbenaceae Ρ Ρ Poaceae Ρ Poaceae Ρ Elaeagnaceae Ρ Poaceae Ρ Poaceae Ρ Pinaceae Ρ Pinaceae Ρ Poaceae Ρ Pinaceae

Acorus calamus Populus tremuloides Bouteloua gracilis Bouteloua gracilis Populus tremuloides Populus tremuloides Populus tremuloides Populus tremuloides Bouteloua gracilis Bouteloua gracilis

Aboveground biomass Relative growth rate Relative growth rate

Peltzer and Wilson 2001 Peltzer et al. 1998 Platt et al. 2004 Rai and Tripathi 1985 Scherber et al. 2003 Seager et al. 1992 Seager et al. 1992 Seager et al. 1992 Seager *et al.* 1992 $_{\infty}$ Suwa and Louda 2012

Pinus banksiana Agropyron cristatum *Fuscospora cliffortioides* Galinsoga quadriradiata Galinsoga quadriradiata Galinsoga quadriradiata Galinsoga quadriradiata Galinsoga parviflora Galinsoga parviflora Galinsoga parviflora Galinsoga parviflora Senecio inaequidens Lolium perenne L. cv. Ellettt Stipa aliena Elymus nutans Elymus nutans *Cirsium vulgare*

Pinaceae	Р
Poaceae	Р
Nothofagaceae	Р
Asteraceae	А
Asteraceae	Р
Poaceae	Р
Asteraceae	А

Bouteloua gracilis Agropyron cristatum Fuscospora cliffortioides Galinsoga quadriradiata Galinsoga parviflora Galinsoga guadriradiata Galinsoga parviflora Galinsoga quadriradiata Galinsoga parviflora Galinsoga quadriradiata Galinsoga parviflora Agrostis capillaris Lolium perenne Lolium perenne Lolium perenne Lolium perenne Schizachyrium scoparium

Relative growth rate Relative height growth Leaf number Height Aboveground biomass Total biomass Total biomass Total biomass Aboveground biomass

Suwa and Louda 2012 Suwa and Louda 2012 Suwa and Louda 2012 Treberg and Turkington 2010 van der Wal et al. 2000 van der Wal et al. 2000 van der Wal et al. 2000 Whigham 1984 Whigham 1984 Whigham 1984 Whigham 1984 Whigham 1984 Whigham 1984 G Wilson 1993

Cirsium altissimum Cirsium vulgare Cirsium altissimum Achillea millefolium Chamerion angustifolium Festuca altaica Linnaea borealis Achillea millefolium Anemone parviflora Festuca altaica Solidago multiradiata Achillea millefolium Anemone parviflora Arctostaphylos uva-ursi Festuca altaica Solidago multiradiata Arctostaphylos uva-ursi Festuca altaica Triglochin maritima Triglochin maritima Triglochin maritima Ipomoea hederacea Ipomoea hederacea Ipomoea hederacea Ipomoea hederacea Ipomoea hederacea Ipomoea hederacea Celmisia longifolia

Asteraceae	Р	Schizachyrium scoparium
Asteraceae	А	Schizachyrium scoparium
Asteraceae	Р	Schizachyrium scoparium
Asteraceae	Р	Picea glauca
Onagraceae	Р	Picea glauca
Poaceae	Р	Picea glauca
Caprifoliaceae	Р	Picea glauca
Asteraceae	Р	Picea glauca
Ranunculaceae	Р	Picea glauca
Poaceae	Р	Picea glauca
Asteraceae	Р	Picea glauca
Asteraceae	Р	Picea glauca
Ranunculaceae	Р	Picea glauca
Ericaceae	Р	Picea glauca
Poaceae	Р	Picea glauca
Asteraceae	Р	Picea glauca
Ericaceae	Р	Picea glauca
Poaceae	Р	Picea glauca
Juncaginaceae	Р	Puccinellia maritima
Juncaginaceae	Р	Limonium vulgare
Juncaginaceae	Р	Halimione portulacoides
Convolvulaceae	А	Ipomoea hederacea
Asteraceae	Р	Poa costiniana

Aboveground biomass Total biomass Total biomass Total biomass Total biomass Total biomass Total biomass Relative growth rate

Wilson 1993	Poa costiniana	Poaceae	P	Poa costiniana	Relative growth rate
Wilcon 1002	Colmicia longifolia	Astoração	' D	Phohalium ovatifalium	Relative growth rate
		Asteraceae	r D		Relative growth rate
Wilson 1993		Poaceae	P	Phebalium ovatifolium	Relative growth rate
Wilson 1993	Eucalyptus pauciflora	Myrtaceae	Р	Phebalium ovatifolium	Relative growth rate
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	А	Schizachyrium scoparium	Total biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	Α	Schizachyrium scoparium	Total biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	Α	Schizachyrium scoparium	Total biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	А	Schizachyrium scoparium	Total biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	А	Schizachyrium scoparium	Total biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Total biomass
Wilson 1994	Setaria viridis	Poaceae	А	Schizachyrium scoparium	Total biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Р	Schizachyrium scoparium	Aboveground biomass

Wilson and Tilman 1991 Wilson and Tilman 1993 Wilson and Tilman 1993 Wilson and Tilman 1995 Wilson and Tilman 1995

Elymus repens Schizachyrium scoparium Schizachyrium scoparium Elymus repens Ambrosia artemisiifolia Chenopodium album Lespedeza capitata Panicum capillare Poa pratensis Schizachyrium scoparium Setaria viridis Elymus repens Ambrosia artemisiifolia Chenopodium album Lespedeza capitata Panicum capillare Poa pratensis Schizachyrium scoparium Setaria viridis

Р
Р
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Р
A

Schizachyrium scoparium Schizachyrium scoparium

Aboveground biomass Relative growth rate Relative growth rate

Open environment dataset

	Reference	Target Species	Family	Life History	Competitor species	Primary measure of performance
71	Aerts 1993	Erica tetralix	Ericaceae	Р	Erica tetralix	Aboveground biomass

Aerts 1993 Ang et al. 1995 Ang et al. 1995 Ang et al. 1995 Ang et al. 1995 Barney et al. 2009 Barney et al. 2009 Bartelheimer et al. 2010

Bartelheimer et al. 2010

Bertness and Yeh 1994

Belanger and Pepper 1978

Erica tetralix Erica tetralix Erica tetralix Erica tetralix Erica tetralix Calluna vulgaris Calluna vulgaris Calluna vulgaris Calluna vulgaris Calluna vulgaris Calluna vulgaris Molinia caerulea Molinia caerulea Molinia caerulea Molinia caerulea Molinia caerulea Molinia caerulea Cirsium arvense Tagetes minuta Tagetes minuta Tagetes minuta Artemisia vulgaris - native Artemisia vulgaris - introduced Jacobaea aquatica Jacobaea vulgaris Platanus occidentalis Iva frutescens

Ericaceae Poaceae Poaceae Poaceae Poaceae Poaceae Poaceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Platanaceae Asteraceae

Р	Molinia caerulea
Р	Calluna vulgaris
Р	Erica tetralix
Р	Molinia caerulea
Р	Calluna vulgaris
Р	Calluna vulgaris
Р	Molinia caerulea
Р	Erica tetralix
Р	Calluna vulgaris
Р	Molinia caerulea
Р	Erica tetralix
Р	Molinia caerulea
Р	Erica tetralix
Р	Calluna vulgaris
Р	Molinia caerulea
Р	Erica tetralix
Р	Calluna vulgaris
Р	Festuca arundinacea
A	Bidens menziesii
A	Tetramolopium arenarium
	Tetramolopium
A	consanguineum
Р	Solidago canadensis
Р	Solidago canadensis
Р	Phleum pratense
A	Phleum pratense
Р	Platanus occidentalis
Р	lva frutescens

Aboveground biomass **Total biomass Total biomass Total biomass** Total biomass Total biomass Total biomass Total biomass Aboveground biomass Total biomass

Bertness and Yeh 1994 Bossdorf et al. 2004 Bozsa and Oliver 1990 Bozsa and Oliver 1990 Bush and Van Auken 1989 Callaway and Aschehoug 2000 Callaway et al. 2006 Callaway et al. 2006 Callaway et al. 2006 Callaway et al. 2006 Casper and Castelli 2007 Casper and Castelli 2007 Casper and Castelli 2007 Casper and Castelli 2007

Iva frutescens	Asteraceae
Iva frutescens	Asteraceae
Alliaria petiolata	Brassicaceae
Glycine max	Fabaceae
Xanthium strumarium	Asteraceae
Prosopis glandulosa	Fabaceae
Koeleria luerssenii	Poaceae
Festuca ovina	Poaceae
Pseudoroegneria spicata	Poaceae
Koeleria luerssenii	Poaceae
Festuca ovina	Poaceae
Pseudoroegneria spicata	Poaceae
Centaurea solstitialis	Asteraceae
Sorghastrum nutans	Poaceae
Andropogon gerardii	Poaceae
Schizachyrium scoparium	Poaceae
Sorghastrum nutans	Poaceae

Р	Juncus gerardi	Total biomass
Р	Iva frutescens	Total biomass
Р	Juncus gerardi	Total biomass
Р	lva frutescens	Total biomass
Р	Juncus gerardi	Total biomass
А	Alliaria petiolata	Total biomass
А	Xanthium strumarium	Aboveground biomass
А	Glycine max	Aboveground biomass
Р	Bouteloua curtipendula	Total biomass
Р	Centaurea diffusa	Total biomass
Ρ	Centaurea diffusa	Total biomass
Р	Centaurea diffusa	Total biomass
Р	Centaurea diffusa	Total biomass
Р	Centaurea diffusa	Total biomass
Р	Centaurea diffusa	Total biomass
А	Avena barbata	Total biomass
А	Nassella pulchra	Total biomass
А	Avena barbata	Total biomass
А	Nassella pulchra	Total biomass
Р	Sorghastrum nutans	Aboveground biomass
Р	Andropogon gerardii	Aboveground biomass
Р	Schizachyrium scoparium	Aboveground biomass
Р	Sorghastrum nutans	Aboveground biomass

Casper and Castelli 2007 Casper and Castelli 2007 Coll et al. 2004 Cook et al. 1972 Cook et al. 1972 Cook et al. 1972 Coomes and Grubb 1998 Coomes and Grubb 1998 Coomes and Grubb 1998 Corbin and D'Antonio 2004 Corbin and D'Antonio 2004 Cottam et al. 1986 Donald 1954 Donald 1954 Donald 1958 Duralia and Reader 1993 Duralia and Reader 1993

Andropogon gerardii Schizachyrium scoparium Fagus sylvatica Agrostis capillaris Plantago lanceolata Anthoxanthum odoratum Micrandra siphonioides Micrandra siphonioides Protium crassipetalum Festuca rubra Nassella pulchra Rumex obtusifolius Trifolium subterraneum Lolium rigidum Lolium perenne Phalaris aquatica Andropogon gerardii Sorghastrum nutans

Poaceae Poaceae Fagaceae Gramineae Plantaginaceae Poaceae Euphorbiaceae Euphorbiaceae Burseraceae Poaceae Poaceae Polygonaceae Fabaceae Poaceae Poaceae

Р	Sorghastrum nutans
Р	Sorghastrum nutans
Р	Festuca rubra
Р	Lolium perenne
Р	Lolium perenne
Р	Lolium perenne
Р	Micrandra siphonioides
Р	Micrandra siphonioides
Р	Protium crassipetalum
Р	Avena barbata
Р	Avena barbata
Р	Festuca rubra
A	Trifolium subterraneum
A	Lolium rigidum
Р	Phalaris aquatica
Р	Lolium perenne
Р	Phalaris aquatica
Р	Lolium perenne
Р	Phalaris aquatica
Р	Lolium perenne
Р	Phalaris aquatica
Р	Lolium perenne
Р	Phalaris aquatica
Р	Lolium perenne
Р	Phalaris aquatica
Р	Lolium perenne
Р	Andropogon gerardii
Р	Sorghastrum nutans

Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Height Leaf number Leaf number Aboveground biomass Aboveground biomass

Duralia and Reader 1993 Dyer and Rice 1999 Dyer and Rice 1999 **Evetts and Burnside 1975 Evetts and Burnside 1975** Evetts and Burnside 1975 Evetts and Burnside 1975 Evetts and Burnside 1975 Ferrero-Serrano et al. 2011 Ferrero-Serrano et al. 2011 Ferrero-Serrano et al. 2011 Ferrero-Serrano et al. 2011 Fogarty and Facelli 1999 Fogarty and Facelli 1999

Dichanthelium oligosanthes Nassella pulchra Nassella pulchra Asclepias syriaca Asclepias syriaca Asclepias syriaca Setaria viridis Amaranthus retroflexus Sporobolus airoides Sporobolus airoides Hesperostipa comata Hesperostipa comata Cytisus scoparius Acacia myrtifolia Acacia myrtifolia Acacia myrtifolia Acacia myrtifolia Hakea rostrata Hakea rostrata Hakea rostrata Hakea rostrata

Poaceae Poaceae Poaceae Asclepiadaceae Asclepiadaceae Asclepiadaceae Poaceae Amaranthaceae Poaceae Poaceae Poaceae Poaceae Fabaceae Proteaceae Proteaceae Proteaceae Proteaceae

Dichanthelium oligosanthes
Nassella pulchra
Nassella pulchra
Setaria viridis
Amaranthus retroflexus
Sorghum bicolor
Asclepias syriaca
Asclepias syriaca
Cirsium arvense
Cirsium arvense
Cirsium arvense
Cirsium arvense
Acacia myrtifolia
Acacia myrtifolia
Acacia myrtifolia
Acacia myrtifolia
Hakea rostrata
Hakea rostrata
Hakea rostrata
Hakea rostrata
Cytisus scoparius

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Aboveground biomass **Basal Diameter Basal Diameter** Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass **Total biomass Total biomass Total biomass Total biomass Total biomass** Aboveground biomass Aboveground biomass

Cirsium arvense Quercus robur Fraxinus pennsylvanica Fraxinus pennsylvanica Juglans nigra Juglans nigra Quercus rubra Quercus rubra Ambrosia artemisiifolia Chenopodium album *Lepidium campestre Lepidium campestre Lepidium campestre Lepidium campestre*

Asteraceae Fagaceae Oleaceae Oleaceae Juglandaceae Juglandaceae Fagaceae Fagaceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Asteraceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Chenopodiaceae Brassicaceae Brassicaceae Brassicaceae Brassicaceae

Р	Lolium perenne	
Р	Festuca rubra	
Р	Trifolium repens	
Р	Dactylis glomerata	
Р	Trifolium repens	
Р	Dactylis glomerata	
Р	Trifolium repens	
Р	Dactylis glomerata	
Р	Ambrosia artemisiifolia	
А	Ambrosia artemisiifolia	

Aboveground biomass **Total biomass** Stem caliper Stem caliper Stem caliper Stem caliper Stem caliper Stem caliper **Total biomass Total biomass Total biomass Total biomass Total biomass Total biomass** Total biomass Total biomass **Total biomass Total biomass** Total biomass **Total biomass** Total biomass **Total biomass Total biomass** Total biomass Total biomass **Total biomass Total biomass** Total biomass

Goldberg and Miller 1990 Gordon *et al.* 1989

Guadarrama *et al.* 2004 Guadarrama *et al.* 2004

Guadarrama et al. 2004

Guadarrama *et al.* 2004 Harmer and Robertson 2003 Irons and Burnside 1982

Lepidium campestre Lepidium campestre Lepidium campestre Lepidium campestre Panicum capillare Quercus douglasii Quercus douglasii Heliocarpus appendiculatus Heliocarpus appendiculatus Tabernaemontana donnellsmithii Tabernaemontana donnellsmithii Betula pendula Acer pseudoplatanus Fraxinus excelsior Acer campestre Crataegus monogyna Sorbus aucuparia Helianthus annuus

Brassica Brassic Brassic Brassic Poacea Poacea Poacea Poacea Poacea Poacea Poacea Poacea Fagace Fagace Malva Malva Apocy Apocy Betula Sapind Oleace Sapind Rosace Rosace Asteraceae

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A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
A	Ambrosia artemisiifolia	Total biomass
Р	Bromus diandrus	Aboveground biomass
Р	Erodium botrys	Aboveground biomass
	Tabernaemontana donnell-	
Р	smithii	Total biomass
Р	Heliocarpus appendiculatus	Total biomass
Ρ	Heliocarpus appendiculatus Tabernaemontana donnell-	Total biomass
Р	smithii	Total biomass
Р	Festuca rubra ssp. rubra	Total biomass
Р	Festuca rubra ssp. rubra	Total biomass
Р	<i>Festuca rubra</i> ssp. <i>rubra</i>	Total biomass
Р	<i>Festuca rubra</i> ssp. <i>rubra</i>	Total biomass
Р	Festuca rubra ssp. rubra	Total biomass
Р	Festuca rubra ssp. rubra	Total biomass
A	Glycine max	Total biomass

Irons and Burnside 1982 Johnston and Pickering 2007 Jones and Sharitz 1990 Jones and Sharitz 1990 King 1971 King 1971 Kitamura *et al.* 1981 Kuefer et al. 2007 Ladd and Facelli 2005 Ladd and Facelli 2005 Lambert 1968 Lee and Bazzaz 1980 Li and Wilson 1998 Linhart 1988 Linhart 1988 ∠ Linhart 1988

Glycine max Achillea millefolium Achillea millefolium Achillea millefolium Poa fawcettiae Poa fawcettiae Poa fawcettiae Triadica sebifera Fraxinus pennsylvanica Festuca rubra Lolium perenne Setaria anceps (Nandi) Cinnamomum verum Eucalyptus camaldulensis Eucalyptus camaldulensis Dactylis glomerata Abutilon theophrasti Picea glauca Picea glauca Picea glauca Picea glauca Symphoricarpos occidentalis Symphoricarpos occidentalis Symphoricarpos occidentalis Symphoricarpos occidentalis Veronica peregrina Veronica peregrina Veronica peregrina

Fabaceae Asteraceae Asteraceae Asteraceae Poaceae Poaceae Poaceae Poaceae Oleaceae Poaceae Poaceae Poaceae Lauraceae Myrtaceae Myrtaceae Poaceae Malvaceae Pinaceae Pinaceae Pinaceae Pinaceae Caprifoliaceae Caprifoliaceae Caprifoliaceae Caprifoliaceae Plantaginaceae Plantaginaceae Plantaginaceae

А	Helianthus annuus	Total bio
Р	Poa fawcettiae	Total bio
Р	Achillea millefolium	Total bio
Р	Poa fawcettiae	Total bio
Р	Achillea millefolium	Total bio
Р	Poa fawcettiae	Total bio
Р	Achillea millefolium	Total bio
Р	Quercus laurifolia	Total bio
Р	Quercus laurifolia	Total bio
Р	Lolium perenne	Total bio
Р	Festuca rubra	Total bio
Р	Desmodium intortum	Abovegr
Р	Cinnamomum verum	Rel. leaf
Р	Avena barbata	Total bio
Р	Avena barbata	Total bio
Р	Dactylis glomerata	Total bio
А	Abutilon theophrasti	Abovegr
Р	Picea glauca	Abovegr
Р	Symphoricarpos occidentalis	Abovegr
А	Agrostis capillaris	Total bio
А	Agrostis capillaris	Total bio
А	Veronica peregrina	Total bio

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Linhart 1988 Litav and Wolovitch 1971 Litav et al. 1963 Litav et al. 1963 Litav et al. 1963 Litav et al. 1963 Liu et al. 2014 Liu et al. 2014 Lucero et al. 2000 Lucero et al. 2000 Lucero et al. 2000 Lucero et al. 2000 Mahmoud and Grime 1976 Mahmoud and Grime 1976 Mahmoud and Grime 1976 Mahmoud and Grime 1976

Veronica peregrina Avena sterilis Sarcopoterium spinosum Sarcopoterium spinosum Sarcopoterium spinosum Sarcopoterium spinosum Bromus inermis Leymus chinensis Trifolium repens Trifolium repens Lolium perenne Lolium perenne Arrhenatherum elatius Arrhenatherum elatius Agrostis capillaris Arrhenatherum elatius

Plantaginaceae Poaceae Rosaceae Rosaceae Rosaceae Rosaceae Poaceae Poaceae Fabaceae Fabaceae Poaceae Poaceae Poaceae Poaceae Gramineae Poaceae

А	Veronica peregrina
А	Agrostis capillaris
А	Agrostis capillaris
А	Veronica peregrina
А	Veronica peregrina
А	Agrostis capillaris
А	Agrostis capillaris
А	Veronica peregrina
А	Veronica peregrina
А	Agrostis capillaris
А	Agrostis capillaris
А	Veronica peregrina
А	Veronica peregrina
А	Oryzopsis holciformis
Р	Avena sterilis
Р	Leymus chinensis
Р	Bromus inermis
Р	Lolium perenne
Р	Lolium perenne
Р	Trifolium repens
Р	Trifolium repens
Р	Agrostis capillaris
Р	Festuca ovina
Р	Festuca ovina
Р	Agrostis capillaris

Total biomass **Total biomass Total biomass Total biomass Total biomass** Total biomass **Total biomass Total biomass Total biomass** Total biomass **Total biomass Total biomass Total biomass** Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass Total biomass **Total biomass** Aboveground biomass Aboveground biomass

Arrhenatherum elatius Agrostis capillaris Agrostis capillaris Festuca ovina Festuca ovina Poa secunda Pseudoroegneria spicata Pseudoroegneria spicata

Poaceae Gramineae Gramineae Poaceae Poaceae

C	Festuca ovina	Aboveground biomass
C	Festuca ovina	Aboveground biomass
C	Arrhenatherum elatius	Aboveground biomass
C	Agrostis capillaris	Aboveground biomass
C	Arrhenatherum elatius	Aboveground biomass
C	Poa secunda	Total biomass
C	Poa secunda	Total biomass
C	Poa secunda	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Bromus tectorum	Total biomass
C	Bromus tectorum	Total biomass
C	Bromus tectorum	Total biomass
C	Taeniatherum caput-medusae	Total biomass
C	Taeniatherum caput-medusae	Total biomass
C	Taeniatherum caput-medusae	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Pseudoroegneria spicata	Total biomass
C	Poa secunda	Total biomass
C	Poa secunda	Total biomass
C	Poa secunda	Total biomass
C	Bromus tectorum	Total biomass
C	Bromus tectorum	Total biomass
C	Bromus tectorum	Total biomass
C	Taeniatherum caput-medusae	Total biomass
C	Taeniatherum caput-medusae	Total biomass

What is the value of having a large seed size under competition?

	Mangla <i>et al.</i> 2011
	Mangla <i>et al.</i> 2011
8	Mangla <i>et al.</i> 2011
_	

Pseudoroegneria spicata	Poaceae
Bromus tectorum	Poaceae
Taeniatherum caput-medusae	Poaceae
Poa secunda	Poaceae
Poa secunda	Poaceae
Poa secunda	Poaceae

Р	Taeniatherum caput-medusae	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
Р	Poa secunda	Total biomass
Р	Poa secunda	Total biomass
Р	Poa secunda	Total biomass

Mangla et al. 2011 ∞ Mangla *et al.* 2011

Poa secunda Pseudoroegneria spicata Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum

Poaceae Poaceae

Р	Pseudoroegneria spicata	Total biomass
Р	Pseudoroegneria spicata	Total biomass
Р	Pseudoroegneria spicata	Total biomass
Р	Bromus tectorum	Total biomass
Р	Bromus tectorum	Total biomass
Р	Bromus tectorum	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
Р	Pseudoroegneria spicata	Total biomass
Р	Pseudoroegneria spicata	Total biomass
Р	Pseudoroegneria spicata	Total biomass
Р	Poa secunda	Total biomass
Р	Poa secunda	Total biomass
Р	Poa secunda	Total biomass
Р	Bromus tectorum	Total biomass
Р	Bromus tectorum	Total biomass
Р	Bromus tectorum	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
Р	Taeniatherum caput-medusae	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Pseudoroegneria spicata	Total biomass

Mangla <i>et al.</i> 2011	Bromus tectorum	Poaceae
Mangla <i>et al.</i> 2011	Bromus tectorum	Poaceae
Mangla <i>et al.</i> 2011	Bromus tectorum	Poaceae
Mangla <i>et al.</i> 2011	Bromus tectorum	Poaceae
Mangla <i>et al.</i> 2011	Bromus tectorum	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
Mangla <i>et al.</i> 2011	Taeniatherum caput-medusae	Poaceae
	Lolium perenne (Grasslands	_
Martin and Field 1984	Nui)	Poaceae
Martin and Field 1984	Huia)	Fahaceae
	Lolium perenne (Grasslands	Tabaccac
Martin and Field 1984	Nui)	Poaceae
	Trifolium repens (Grasslands	
Martin and Field 1984	Huia)	Fabaceae
Nortin and Field 1094	Lolium perenne (Grasslands	Decesso
IVIALUIT ATIO FIEIO 1984	ivui) Trifolium renens (Grasslands	ruaceae
Martin and Field 1984	Huia)	Fabaceae
	,	

А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Taeniatherum caput-medusae	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Poa secunda	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Pseudoroegneria spicata	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
А	Bromus tectorum	Total biomass
Р	Trifolium repens	Total biomass
Р	Lolium perenne	Total biomass
Р	Trifolium repens	Total biomass
Р	Lolium perenne	Total biomass
Р	Trifolium repens	Total biomass
Р	Lolium perenne	Total biomass

Martin and Field 1984

Martin and Field 1984

McGraw 1985

McGraw 1985 McGraw and Chapin 1989 McKenney et al. 2007 McKenney et al. 2007 McKenney et al. 2007 McKenney et al. 2007 Meekings and McCarthy 1999 Meekings and McCarthy 1999 Morris et al. 1993 Morris et al. 1993 Morris et al. 1993 Morris et al. 1993 Navas and Moreau-Richard 2005 Navas and Moreau-Richard

Lolium perenne (Grasslands Nui) Trifolium repens (Grasslands Huia) Dryas octopetala - Snowbed ecotype Dryas octopetala - Fellfield ecotype Eriophorum vaginatum Eriophorum scheuchzeri Eriophorum vaginatum Eriophorum scheuchzeri Eriophorum vaginatum Eriophorum scheuchzeri Eriophorum vaginatum Eriophorum scheuchzeri Lepidium draba - native Lepidium draba - native Festuca Ovina Festuca idahoensis Impatiens capensis Acer negundo Pinus taeda Pinus taeda Pinus taeda Pinus taeda Conyza sumatrensis Conyza sumatrensis

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Dograga

Ρ	Trifolium repens	Total biomass
Р	Lolium perenne	Total biomass
Р	Dryas octopetala	Total biomass
Р	Dryas octopetala	Total biomass
Р	Eriophorum vaginatum	Total biomass
Р	Eriophorum scheuchzeri	Total biomass
Р	Eriophorum scheuchzeri	Total biomass
Р	Eriophorum vaginatum	Total biomass
Р	Eriophorum vaginatum	Total biomass
Р	Eriophorum scheuchzeri	Total biomass
Р	Eriophorum scheuchzeri	Total biomass
Р	Eriophorum vaginatum	Total biomass
Р	Festuca Ovina	Total biomass
Р	Festuca idahoensis	Total biomass
Р	Lepidium draba	Total biomass
Р	Lepidium draba	Total biomass
А	Alliaria petiolata	Aboveground biomass
Р	Alliaria petiolata	Aboveground biomass
Р	Liquidambar styraciflua	Height
Р	Andropogon spp.	Height
Р	Sesbania exaltata	Height
Р	Panicum dichotomiflorum	Height
А	Bromus madritensis	Aboveground biomass
А	Dactylis glomerata	Aboveground biomass

2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard

Conyza sumatrensis	Asteraceae
Crepis foetida	Asteraceae
Crepis foetida	Asteraceae
Crepis foetida	Asteraceae
Medicago minima	Fabaceae
Medicago minima	Fabaceae
Medicago minima	Fabaceae
Calamintha nepeta	Lamiaceae
Calamintha nepeta	Lamiaceae
Calamintha nepeta	Lamiaceae
Daucus carota	Apiaceae
Daucus carota	Apiaceae
Daucus carota	Apiaceae
Picris hieracioides	Asteraceae
Picris hieracioides Picris hieracioides	Asteraceae
	<i>i</i> steraceae

А	Brachypodium phoenicoides
Р	Bromus madritensis
Р	Dactylis glomerata
Р	Brachypodium phoenicoides
А	Bromus madritensis
А	Dactylis glomerata
А	Brachypodium phoenicoides
Р	Bromus madritensis
Р	Dactylis glomerata
Ρ	Brachypodium phoenicoides
A	Bromus madritensis
А	Dactylis glomerata
А	Brachypodium phoenicoides
Ρ	Bromus madritensis
Р	Dactylis glomerata
Р	Brachypodium phoenicoides

Aboveground biomass oenicoides Aboveground biomass Aboveground biomass oenicoides Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass oenicoides Aboveground biomass Aboveground biomass oenicoides Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass oenicoides Aboveground biomass Aboveground biomass Aboveground biomass

2005

Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Navas and Moreau-Richard 2005 Nicotra and Rodenhouse 1995 Parkinson et al. 2013 Parkinson et al. 2013 ∞ Parkinson *et al.* 2013

Bromus erectus Poaceae Bromus erectus Poaceae Bromus erectus Poaceae *Centaurea jacea* subsp. qaudinii Asteraceae *Centaurea jacea* subsp. qaudinii Asteraceae Centaurea jacea subsp. gaudinii Asteraceae Inula conyza Asteraceae Inula conyza Asteraceae Inula conyza Asteraceae Chenopodium album Chenopodiacea Chenopodium album Chenopodiacea Chenopodium album Chenopodiacea Chenopodium album Chenopodiacea Chenopodium album Chenopodiace Lomatium macrocarpum Apiaceae Lomatium macrocarpum Apiaceae Lomatium macrocarpum Apiaceae

	Р	Bromus madritensis
	Р	Dactylis glomerata
	Р	Brachypodium phoenicoides
	Р	Bromus madritensis
	Р	Dactylis glomerata
	Р	Brachypodium phoenicoides
	Р	Bromus madritensis
	Р	Dactylis glomerata
	Р	Brachypodium phoenicoides
ae	А	Chenopodium album
	Р	Poa secunda
	Р	Elymus elymoides
	Р	Bromus tectorum

Aboveground biomass Total biomass **Total biomass Total biomass** Total biomass Total biomass Total biomass Total biomass Total biomass

Eriogonum umbellatum Eriogonum umbellatum Eriogonum umbellatum Penstemon speciosus Penstemon speciosus Penstemon speciosus Dieteria canascens Dieteria canascens Dieteria canascens Sphaeralcea munroana Sphaeralcea munroana Sphaeralcea munroana Galinsoga quadriradiata Galinsoga quadriradiata Galinsoga parviflora Galinsoga parviflora Gossypium hirsutum Gossypium hirsutum Pinus taeda Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum Bromus tectorum Poa annua Poa annua Amaranthus retroflexus Lotus corniculatus

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Р	Poa secunda	Tota
Р	Elymus elymoides	Tota
Р	Bromus tectorum	Tota
Р	Poa secunda	Tota
Р	Elymus elymoides	Tota
Р	Bromus tectorum	Tota
Р	Poa secunda	Tota
Р	Elymus elymoides	Tota
Р	Bromus tectorum	Tota
Р	Poa secunda	Tota
Р	Elymus elymoides	Tota
Р	Bromus tectorum	Tota
А	Galinsoga quadriradiata	Leaf
А	Galinsoga parviflora	Leaf
А	Galinsoga quadriradiata	Leaf
А	Galinsoga parviflora	Leaf
Р	Gossypium hirsutum	Tota
Р	Gossypium hirsutum	Tota
Р	Pinus taeda	Abo
А	Bromus tectorum	Abo
А	Poa annua	Abo
А	Arabidopsis thaliana	Abo
А	Lotus corniculatus	Tota
Р	Amaranthus retroflexus	Tota

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Arrhenatherum elatius	Ро
Arrhenatherum elatius	Ро
Holcus lanatus	Ро
Holcus lanatus	Ро
Prunella vulgaris	La
Prunella vulgaris	La
Lotus corniculatus	Fa
Lotus corniculatus	Fa
Arrhenatherum elatius	Ро
Arrhenatherum elatius	Ро
Holcus lanatus	Ро
Holcus lanatus	Ро
Prunella vulgaris	La
Prunella vulgaris	La
Lotus corniculatus	Fa
Lotus corniculatus	Fa

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Lotus corniculatus	Above
Prunella vulgaris	Above
Lotus corniculatus	Above
Prunella vulgaris	Above
Arrhenatherum elatius	Above
Holcus lanatus	Above
Arrhenatherum elatius	Above
Holcus lanatus	Above
Lotus corniculatus	Above
Prunella vulgaris	Above
Lotus corniculatus	Above
Prunella vulgaris	Above
Arrhenatherum elatius	Above
Holcus lanatus	Above
Arrhenatherum elatius	Above
Holcus lanatus	Above

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Arrhenatherum elatius
Arrhenatherum elatius
Holcus lanatus
Holcus lanatus
Prunella vulgaris
Prunella vulgaris
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Lotus corniculatus Prosopis glandulosa var. alandulosa
giunuulosu Buchloe dactyloides
Buchloe dactyloides
Baccharis nealecta
Pseudotsuaa menziesii -
coastal
Pseudotsuga menziesii -
interior
Picea sitchensis
Pinus contorta
Quercus douglasii
Quercus douglasii
Carex stricta
Carex stricta

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Poaceae
Lamiaceae
Lamiaceae
Fabaceae
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Fabaceae
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Pinaceae
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Fagaceae
Fagaceae
Cyperaceae
Cyperaceae

Р	Lotus corniculatus	Aboveground biomass
Р	Prunella vulgaris	Aboveground biomass
Ρ	Lotus corniculatus	Aboveground biomass
Ρ	Prunella vulgaris	Aboveground biomass
Ρ	Arrhenatherum elatius	Aboveground biomass
Ρ	Holcus lanatus	Aboveground biomass
Р	Arrhenatherum elatius	Aboveground biomass
Р	Holcus lanatus	Aboveground biomass
Р	alandulosa	leaf number
P	Buchloe dactyloides	Aboveground biomass
P	Buchloe dactyloides	Aboveground biomass
P	Prosopis glandulosa	Aboveground biomass
Ρ	Pseudotsuga menziesii	Total biomass
Р	Pseudotsuga menziesii	Total biomass
Р	Picea sitchensis	Total biomass
Р	Pinus contorta	Total biomass
Р	Bromus mollis	Aboveground biomass
Р	Stipa pulchra	Aboveground biomass
Р	Phalaris arundinacea	Total biomass
Р	Typha latifolia	Total biomass

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Р	Carex stricta	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Typha latifolia	Total biomass
Р	Carex stricta	Total biomass
Р	Phalaris arundinacea	Total biomass
Р	Phytolacca americana	Height
А	Abutilon theophrasti	Height
Р	Solanum mauritianum	Length of longest leaf
Р	Lycopersicon lycopersicum	Height
Р	Lycopersicon lycopersicum	Height

Appendix C: Reference list of studies used in this data-synthesis.

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CHAPTER 3

REASSESSING THE VALUE OF SHADE AVOIDANCE PLASTICITY UNDER COMPETITION

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Abstract

Under crowded conditions, many species make a suite of developmental adjustments known as "shade avoidance responses" which include an elongation of stems, upward bending of leaves, reduced branching and earlier flowering. Competition for light is asymmetric, and shade avoidance responses are predicted to maximise a plant's ability to overtop its neighbours. Thus shade avoidance responses have been believed to be a strategy for plants to grow larger faster than neighbouring plants in order to increase their competitive ability. However, under intense competition, a strategy allocating resources towards growth and delaying reproduction may result in the plant being unable to reproduce before death. We propose that shade avoidance responses may instead be a strategy for plants to maximise resource acquisition for earlier reproduction under intense competition. A quantitative literature synthesis of studies evaluating the shade avoidance traits and the growth and reproduction under high and low light conditions was performed to evaluate the degree of empirical support for these predictions. We showed that overall there is no relationship between shade avoidance plasticity and competitive ability across species but instead there is a highly significant relationship between shade avoidance plasticity and reproductive efficiency. The demonstration of a potential adaptive value of shade avoidance responses in reproduction rather than in the maintenance of size under competition as has been predicted by theory suggests further exploration of the role of reproduction in plant competitive interactions is needed in order to improve our understanding of the evolution of competitive abilities.

Introduction

Competition for limiting resources is a fundamental interaction in plant communities, limiting individual fitness (Pianka 1981; Grace and Tilman 1990) and driving the evolution of life-histories and adaptive strategies (Pianka 1970; Grime 1977; Bonser and Aarssen 1996). For plants, light is a key limiting resource essential for photosynthesis. Plants grown in close proximity in crowded communities can compete intensely for light by overtopping their neighbours and denying them light (Smith and Whitelam 1997; Pierik and de Wit 2013). Rather than being passive players to the presence of competitors, competition can induce an array of responses from plants. For example, crowding and shading by neighbouring plants can induce a number of changes to their growth and development such as stem and leaf elongation; accelerated elongation of hypocotyl, internodes and petioles; hyponasty – an upward bending of leaves (Morgan and Smith, 1976; 1978; 1981; Whitelam and Johnson 1982) often accompanied by reduced allocation to leaves, branches and roots (Smith 1982; Ballaré et al. 1990; Sultan and Bazzaz 1993; Callaway et al. 2003; Van Kleunen and Fischer 2003). Induced responses in plant architecture and growth are consistent with strategies to increase access to sunlight under competition or the detection of oncoming competition from neighbours. These responses are collectively referred to as "shade avoidance responses" (Smith 1982). In this study, we examine if shade avoidance plasticity is generally associated with an increase in competitive ability in short-lived plants under competition.

Shade avoidance is one of the most well-documented plant responses to competition since the mechanisms of it are relatively well understood. A plant growing in the shade of another plant or near another plant experiences not only a decrease in the quantity of light received (i.e. reduced photosynthetically active radiation - PAR) but also a reduced

ratio of red to far-red wavelengths in the light received compared to daylight (i.e. a lower R:FR ratio) which is characteristic of light filtered through or reflected from the leaves of plants (reviewed in Whitelam and Halliday 2007; Franklin 2008). This change in the spectral quality of light is detected by photoreceptors called Phytochromes and is the main cue plants use to trigger shade avoidance responses (reviewed in Whitelam and Halliday 2007; Franklin 2008). Previous work has demonstrated that shade avoidance plasticity has fitness benefits in habitats with variable light availability when expressed in dense vegetation (Dudley and Schmitt 1996; Leeflang *et al.* 1998; Donohue *et al.* 2000; Weinig 2000; Causin and Wulff 2003) and lowers fitness when grown alone suggesting they are an adaptive response to growing with neighbours (Casal and Smith 1989; Schmitt and Wulff 1993; Smith 1995).

There have been many studies since the early 1990s suggesting shade avoidance plasticity is a mechanism for increasing competitive ability for light when increasing neighbour density threatens a plant's current or future access to light. Due to the perception of light as a uni-directional resource, the traits of those with a strong competitive ability for light have been summed up as "traits leading to overtopping of the neighbours" (Aerts 1999). An intuitive assumption is that those that grow rapidly to reach a large size and shade and suppress the growth of others are the superior competitors. The rapid elongation of stems and leaves associated with shade avoidance responses is hypothesized to be an adaptive developmental response that will allow plants to grow taller than their neighbours, place the photosynthesizing structures of the plant above those of their competitors and in doing so, escape being shaded (Morgan and Smith 1979; Casal and Smith 1989; Schmitt and Wulff 1993; Schmitt *et al.* 1995; Smith 1995; Dudley and Schmitt 1996; Pigliucci and Schmitt 1999). However, the early theoretical work on shade avoidance plasticity has

emphasised the fitness benefits rather than the competitive advantage of shade avoidance plasticity (e.g. Dudley and Schmitt 1996; Donohue *et al.* 2000).

The general consensus has been that plants which grow towards light the fastest and most efficiently became the most successful (see Callahan and Pigliucci 2002). However, we are uncertain if shade avoidance should be a strategy associated with eventual competitive dominance. While shade avoidance plasticity may allow plants to delay the impacts of competitors, the arrival of more and potentially stronger competitors means that it is perhaps unlikely simple shifts in growth form, particularly in short-lived herbaceous plants will confer competitive dominance (see Bonser 2013). Under intense competition, plants may shift to a strategy of early and efficient reproduction to maximise fitness prior to competition preventing future growth or even causing plant death (Bonser 2013; Fazlioglu *et al.* 2016). In an earlier study, shade avoidance plasticity was more strongly associated with reproductive efficiency than the maintenance of size under competition (Fazlioglu *et al.* 2016). Thus, shade avoidance plasticity may be adaptive, though as a response to quickly acquire resources and maximise reproduction prior to the increase in intensity of competition rather than as a response to increase competitive ability.

In this study, we surveyed the literature to assess if shade avoidance plasticity is associated with greater performance under light competition in short-lived herbaceous plants. We tested the following predictions: 1) Increasing shade avoidance plasticity will be associated with decreasing impacts of competition; and 2) Increasing shade avoidance plasticity will be associated with increased allocation to reproduction under competition.

Methods

We searched ISI Web of science (Thompson Reuters) for shade avoidance studies in January 2016 and again in November 2017 using the keywords "shade avoidance", " competition shade avoidance", "light competition", "phenotypic plasticity light competition", "competition light plasticity", "competition AND light AND plasticity", "shade-avoidance respon*", ""canopy shade" plasticity", "foliar shade", and "compet* shade avoidance" and also looked at the reference lists of these papers for related studies. To be included in the analysis, studies must have reported some measure of shade avoidance response traits (e.g. internode length, petiole length, etc.), size or performance data (e.g. total mass, aboveground mass, leaf number, etc.) under a spectral shade treatment and a control treatment. Ideally, studies also included some measure of reproduction (e.g. seed number, fruit number, seed mass, inflorescence mass, etc.). Where more than two spectral treatments were used, we used the highest r:fr as the high shade treatment. Multiple species from the same study were included as replicates. Species included in more than one study were also included as independent replicates, though we assessed the effect of species and study in our analysis (see below). Details of each study used here are included in the Supporting Information (see table S1).

From each study, we recorded shade avoidance traits, plant size and reproduction (where available) under high and low spectral shade treatments, the age the plants were planted and harvested or the age of the plants at the final harvest was extracted. We recorded the percent light reduction by the shading treatment. We also recorded sample sizes for experimental treatments, and (where available) measures of variance on shade avoidance, size, and reproductive traits.

We estimated shade avoidance plasticity for each replicate using an index of phenotypic plasticity (see – Valladares *et al.* 2000):

$$PIv = [Max (X_{hs}, X_{ls}) - Min (X_{hs}, X_{ls})] / Max (X_{hs}, X_{ls})$$
(equation 1)

where X_{hs} and X_{ls} are the means for shade avoidance traits under high shade and low (or no) shade, respectively. We selected a single most relevant shade avoidance trait from each species replicate.

We calculated a relative index of competition intensity to estimate the effect of competition on size:

$$CI = (Size_{ls} - Size_{hs})/(Size_{ls})$$
(equation 2)

where Size_{Is} and Size_{hs} are measures of plant size under low shade and under high shade, respectively. While other measures of competition intensity may be more preferable (Weigelt and Jolliffe 2003; Oksanen *et al.* 2006; Rees *et al.* 2012), these measures require data such as the size of the largest plant or maximum plant performance which were not available in the studies we were able to find. Other potentially improved indices have been suggested in response to criticisms of the mathematical properties of existing competition intensity indices (e.g. Diaz *et al.* 2017). These may prove to be more effective metrics for future competition studies; however, at this time they have not yet been explored in depth or independently assessed. Reproductive efficiency is a measure of the conversion of resources from vegetative growth to reproductive output (i.e. allocation to reproduction relative to vegetative size). The reproductive efficiency in competition (or shade) treatments relative to no competition (or no shade) treatments can be used to assess how plants shift reproductive strategies under competition. We calculated relative reproductive efficiency using the following index (see – Bonser 2013):

$$RRE = \log \left[(R/S)_{hs} / (R/S)_{ls} \right]$$
 (equation 3)

where (R/S)_{hs} and (R/S)_{ls} is the mean reproductive allocation (R) relative to size (S) in high shade (hs) and low shade treatments (ls), respectively. RRE is negative in instances where reproductive efficiency is greater under low simulated competition (i.e. shading) and positive in instances where reproductive efficiency is greater under high simulated competition. We removed all cases where the only values for reproduction and plant size were reproductive mass and total mass (as values of reproduction would be included in both the numerator and the denominator of the index) to prevent autocorrelation.

We used correlation analysis to test for a significant relationship between the expression of the shade avoidance plasticity index (PIv) and competition intensity. This relationship is a measure of the potential for shade avoidance plasticity to alleviate the loss of performance of plants due to shading from neighbours. We also used correlation analysis to test for a significant relationship between PIv and relative reproductive efficiency (RRE). This relationship is a test for the potential for shade avoidance plasticity to be associated with a shift in reproductive strategies in the presence of competitors. We then used partial correlations controlling for the percent light reduction in the shading treatment to assess relationships between shade avoidance PIv and CI, and PIv and RRE. Partial correlations are important in our analysis since shade avoidance plasticity expressed by plants may be due to the intensity of shading and competition intensity (and perhaps also reproductive efficiency) should also be related to the degree of shading. Partial correlation analysis allows us to test for the impact of PIv on CI and RRE for a given degree of shading. We then used weighted General Linear Models to control for differences in sample sizes between studies. Shade-avoidance PIv was included as a main effect, and study was included as a random effect (to control for the contribution of multiple species replicates from any given study). Separate models were conducted with CI and RRE as dependent variables. All analyses were conducted using SPSS v 25 (SAS Institute, NC, USA).

Results

We found 53 instances across 25 studies where the performance of plant species subjected to spectral shading was assessed (see Appendix A). Numerous other studies examined shade avoidance plasticity but did not include spectral shading treatments. We found a significant correlation between the intensity of competition and shade-avoidance plasticity (r=0.44, P=0.001; Fig 1a). There were several cases where the expression of shade avoidance plasticity was associated with reduced impact of competition. However, the expression of high shade avoidance plasticity was associated with poor performance under shade competition. We also found a significant correlation between relative reproductive efficiency and shade-avoidance plasticity (r=0.44, P=0.012; Fig 1b). Correlations between shade avoidance plasticity and competition intensity and relative reproductive efficiency were also significant after controlling for the intensity of shading (partial correlations, Cl versus Plv – df: 47, r=0.39, P=0.006; RRE versus Plv – df: 29, r=0.50, P=0.004). Shade avoidance plasticity explained significant variation in competition intensity but not relative reproductive efficiency in the weighted GLM models (Table 1).

Discussion

We demonstrated that shade avoidance plasticity was associated with poor plant performance under competition (or simulated competition) for light across studies. Shade avoidance plasticity is broadly predicted to be a mechanism for increasing a plant's ability to intercept light in the presence of competitors. Increasing plasticity is associated with an increase in the impact of competition which challenges this presumed adaptive advantage of shade avoidance plasticity. We found a positive (though weaker) relationship between shade avoidance plasticity and the commitment to reproduction under competition. Thus, shade avoidance plasticity is likely to be adaptive, just not in the way that we had assumed it was.

There are two problems with the prediction that shade avoidance plasticity should increase competitive ability – first, there is very little a short-lived species could do to outcompete superior (and longer-lived) competitors. A short-lived herbaceous plant is not likely to be able to outgrow a larger woody plant and usually only has one or two reproductive events in a lifetime. Rather than trying to adjust growth to try and gather resources to live long, energy may be better spent producing offspring earlier especially when it will get harder and harder to produce quality offspring with increasing competition (e.g. Bonser 2013). Second, competitive ability should evolve under consistently high

competition. Costs of plasticity could prevent an individual from maximising competitive ability (and outcompeting competitive specialists) (Pigliucci 2001). Perhaps long-lived plants would be capable of achieving a competitive advantage through shade avoidance plasticity as they have the time to grow and reproduce later. However we were unable to assess that in the current study since experiments tended not to extend until the reproductive maturity of long-lived species. Weinig and Delph (2001) have also shown that internode elongation in response to a low red-far red ratio of light early in life limited further internode elongation in response to the same low red-far red ratio light cue later in life. This suggests that shade-avoidance plasticity would not be a sustainable response for a highly competitive environment where shaded conditions could be prolonged or occur frequently.

Our findings suggest that the functions of shade avoidance responses expressed are likely to be to acquire and allocate more resources towards reproduction so that plants detecting oncoming competition are able to reproduce earlier, prior to the onset of a level of competition that would prevent future reproduction. This may seem contradictive because shade avoidance traits such as reduced branching and reduced leaf and root biomass would reduce the quantity and the quality of the seeds produced overall (Smith 1995; Smith and Whitelam 1997). However, flowering earlier can increase the probability of reproduction under highly limiting conditions associated with early mortality (Schemske 1984; Biere 1995). Donohue *et al.* (2000) found that under high density, *Impatiens capensis* plants suffered from earlier mortality however, plants that flowered earlier were able to produce more fruits and ensure these fruits had sufficient time to mature before the death of the parent plant. In addition, there may be other associated benefits offered

by increased vertical growth such as increased pollination (Lortie and Aarssen 1999) and seed dispersal distance (Thompson *et al.* 2011) especially under crowded conditions. Seeds can remain viable for years with long periods of dormancy and like the plant leaves, use photoreceptors to detect light conditions, often only breaking their dormancy when they sense direct sunlight high in R:FR through phytochromes and in response to blue light through cryptochromes (Chory *et al.* 1996). In comparison to seeds produced by plants growing in the sun, seeds produced by shaded plants have been found to have longer periods of seed dormancy (McCullough and Shropshire 1970; Orozco-Segovia *et al.* 1993). If competition remains persistently high for extended periods, then putting resources into producing seeds which can then disperse and/or remain dormant for long periods of time until they find themselves under less competitive conditions, would increase the probability of successful reproduction.

The results of this study suggest that the adaptive advantage in shade avoidance plasticity is in changing the timing of developmental stages in plants. This has been observed previously in studies demonstrating a change in the timing of reproduction under shaded conditions. For example *Arabidopsis thaliana* (an annual plant that grows as a rosette during its juvenile stages, then bolts and branches to initiate reproduction) has been shown to bolt and shift from juvenile to reproductive adult when placed under spectral shade (e.g. Pigliucci and Schmitt 1999; Bonser and Geber 2005). In addition, seedlings of long-lived trees have also been demonstrated to express plasticity in the timing of developmental shifts under shaded conditions e.g. *Acacia implexa* seedlings delay their shift to phylode leaf production as bipinnate leaves are more adaptive under shade (Forster and Bonser 2009) suggesting that in the cases of both short and long-lived plants, plastic responses which change the developmental stages in plants can be adaptive.

The advantage larger individuals have over smaller individuals has been predicted to be further exacerbated by the asymmetric nature of competition where large individuals can obtain a disproportionate share of the contested resources, growing more than smaller individuals and thus increasing size inequality among plants (Weiner et al. 1990). This is believed to be especially true in competition for light because of its directionality where larger plants shade smaller plants whereas smaller plants have little effect on the light available to the larger plant (Weiner 1990; Schwinning and Weiner 1998). An initial size advantage or overtopping later as a strategy for competition for light has long been used as a classic example of pre-emptive access to a resource (Schwinning and Weiner 1998). Since competition for light is believed to be highly asymmetric, shade avoidance plasticity has been predicted to be a strategy which is able to reduce the degree of size asymmetry in competition by maximising light acquisition to grow larger faster for increased competitive ability (Ballaré et al. 1994, Schwinning and Weiner 1998). Light can change with the depth of the canopy in relation to the number of stems, branches and leaf layers. This can lower light availability below the compensation point for leaves growing beneath the canopy resulting in the death of shaded plants (Givnish 1988; Valladares and Niinemets 2008; Niinemets 2010). In this study, we demonstrated that the height achieved by a plastic response is unlikely to confer much of an advantage especially for short-lived species as plants of more longer-lived and taller species would likely outgrow these species and intercept most of the light. However, a small difference in leaf height may at least temporarily allow a short-lived plant to quickly acquire light to allocate early and intensely to reproduction thus increasing the chances of continued representation in the community. Plant strategies in response to competition may also differ depending on whether their competitors are seedlings or adult plants as competition from seedlings is less intense than

competition from adult plants (refer to chapter 2). Competition against seedling competitors is something that a young plant can overcome. Early allocation to height growth could allow plants to quickly overtop competing seedlings. However, a strategy of high allocation to early height growth is not likely to result in competitive superiority over competing (and tall) adult plants.

Our results suggest size may not be as important in the competitive strategies of shortlived and small-sized plants. Shade avoidance tends to be a particularly common trait in angiosperms (Smith and Whitelam 1997; Morelli and Ruberti 2000; Salter et al. 2003) which reach sexual maturity at a relatively young age and small size and have a relatively small seed size (Aarssen 2008). Larger species usually have a longer life span and hence higher lifetime fecundity; however, they also generally require more time and a larger size before first reproduction (Silvertown et al. 2001). There is a trade-off between the maximum potential body size a species can reach and the minimum size it can reproduce at in both woody (Thomas 1996; Davies and Ashton 1999) and herbaceous vegetation (Tracey and Aarssen 2011; 2014; Nishizawa and Aarssen 2014). These and our findings suggest that contrary to traditional competition theory, small plants are not inferior to large plants in terms of the capacity to produce offspring under intense competition. Under intense or persistent competition where plants of large-sized species are unable to reach their potential size, smaller plants may have the more effective competitive strategy as the ultimate goal should not be attaining a large size but in producing as many offspring which are able to survive until maturity as possible. Our findings show that short-lived species are able to effectively reproduce under competition utilising strategies such as the

shade avoidance responses. These responses are part of the expression of competitive strategies in annual and short-lived perennial plant species (see Bonser 2013)

It should be noted that limitations in current data available may have affected the findings of this study. To date, the number of studies with spectral shade treatments which have also measured reproduction have been limited and those which did take reproductive measurements tended to have used species easily grown in glasshouse experiments (e.g. short-lived, early reproducing, herbs and grasses). Very few have examined reproduction under spectral shade for longer-lived species. As a result, certain species may have been more highly represented in our dataset and this would affect our ability to determine the general patterns across species. However, we made efforts to account for this by assessing the effect of species and study in our analysis. This study highlights the importance of reproduction as part of a plant's effective competitive strategy. Further work which measures reproduction under competition and in more different species will broaden our understanding of adaptive plasticity in mixed communities in natural light environments. Once there is a larger amount of studies which measure reproduction under competition especially for taxa with longer-lived life histories, further quantitative synthesis reviews will shed more light on this surprisingly neglected facet of adaptive strategies under competition in plants.

This study provides the first test of the relationship between shade avoidance and competitive ability and reproduction across studies. We examined whether an alternative benefit of shade avoidance plasticity in competition for light is to allow increased

allocation to reproduction. In summary, the results from the studies published to date support our hypothesis that rather than being valuable for maximising resources towards growing large quickly as the traditional view claims, shade avoidance plasticity can be a mechanism to maximise resource acquisition in order to quickly increase allocation to reproduction. The results demonstrate an alternative strategy employed by short-lived plants to that traditionally predicted to combat the risks of fitness loss imposed by light competition. These findings have interesting implications for the traditional view of the traits which confer a plant competitive ability and strongly suggest that short-lived species could have evolved under competitive environments and developed adaptive responses to competition too. However, many of the ideas about plant competitive ability remain unexplored in the context of earlier reproduction being an effective strategy under competition and this study will hopefully motivate further interest to reconsider a lot of what we currently think we know about plant competitive interactions and the strategies used by short-lived and long-lived species. **Table 1.** General linear model testing the impact of Plv on performance measures competition

 intensity and relative reproductive efficiency with study included as a random effect.

	Competition intensity			Relative reproductive efficiency				
Source of variation	Df	MS	F	Р	Df	MS	F	Р
Intercept	1	27.43	15.40	0.16	1	1.89	4.67	0.54
Plv	24	0.48	2.8x10 ⁴	0.005	19	0.38	0.90	0.70
Study (random)	1	1.833	1.1x10 ⁵	0.002	1	0.41	0.97	0.51
Error	1	<0.0001			1	0.43		



Fig. 1 Correlation for shade avoidance plasticity index and a) Index of competition intensity, and b) Relative reproductive efficiency.

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Reproductive output
Seed no.
Seed no.
Seed no.
No. of flowers
Total seed weight
Total seed weight
Seed no.
Seed no.
Weight of flowers
% of non-dormant
buds
% of non-dormant
No of reprosstructures
No. of flowers + buds
No. of flowers + buds
Total fruit
Total fruit
Fruit no.
Fruit no.

Primary measure

Shade avoidance trait

Flowering scape length

Flowering scape length

Length of leaf sheath

Length of longest leaf

No. of basal branches

No. of basal branches

Height

Height

Height

Height

Height

(mm)

Height

Height

Height

Height

Height

No. of stems

Root weight

of performance

Biomass

Biomass

Biomass

No. of nodes

Longest leaf

Longest leaf

Biomass

Biomass

Biomass

No. of leaves

No. of leaves

No. of leaves

No. of leaves

No. of rosette

No. of rosette

Biomass

leaves

leaves

Biomass

Biomass

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History

Family

Polygonaceae

Asteraceae

Asteraceae

Brassicaceae

Brassicaceae

Convolvulaceae

Balsaminaceae

Balsaminaceae

Balsaminaceae

Malvaceae

Poaceae

Poaceae

Poaceae

Poaceae

Cyperaceae

Ericaceae

Apiaceae

Primulaceae

Appendix A: The list of surveyed studies and their details.

Target species

Abutilon theophrasti

Datura stramonium

Sorghum halepense

Taraxacum officinale

Echinochloa colona

Taraxacum ceratophorum

Echinochloa glabrescens

Microstegium vimineum

Brachypodium pinnatum

Arabidopsis thaliana

Impatiens capensis

Impatiens capensis

Arabidopsis thaliana

Convolvulus arvensis

Anagallis arvensis

Cyclospermum

leptophyllum

Emex spinosa

Carex flacca

Fazlioglu et al. 2016 130

Study reference

1994

1994

1994

Benvenuti and Stefani

Benvenuti and Stefani

Benvenuti and Stefani

Berjano et al. 2014

Brock et al. 2005

Brock et al. 2005

Chauhan 2013

Chauhan 2013

Dixon et al. 2001

Dorn et al. 2000

Dorn et al. 2000

Fazlioglu et al. 2016

Claridge and Franklin 2002

de Kroon and Knops 1990

de Kroon and Knops 1990

Donohue and Schmitt 1999

Donohue and Schmitt 1999

Fazlioglu <i>et al.</i> 2016
Fazlioglu <i>et al.</i> 2016
Fazlioglu <i>et al.</i> 2016
Fazlioglu <i>et al.</i> 2016

Fazlioglu <i>et al.</i> 2016
Fazlioglu <i>et al.</i> 2016
Gianoli 2004
Gianoli 2004
Godoy <i>et al.</i> 2011
Gruntman <i>et al.</i> 2011
Gruntman <i>et al.</i> 2011

Huber 1995

Huber 1995

Huber 1995 Huber and Hutchings 1997 Huber and Hutchings 1997 Huber and Wiggerman 1997 Kurepin et al. 2012 Kurepin et al. 2012

Leeflang et al. 1998

Cymbalaria muralis Euphorbia peplus Lepidium africanum Oxalis exilis Paronychia brasiliana Stachys arvensis Trifolium dubium Trifolium repens Taraxacum officinale Impatiens capensis Impatiens capensis Prunella vulgaris Medicago truncatula Medicago truncatula Potentilla erecta Potentilla anglica Potentilla reptans

Impatiens capensis

Abutilon theophrasti

Trifolium fragiferum

Stellaria longipes

Stellaria longipes

Hydrocotyle vulgaris

Euphorbiaceae А Brassicaceae Ρ Oxalidaceae Ρ Caryophyllacea Ρ е Lamiaceae А Fabaceae А Ρ Fabaceae Ρ Asteraceae Balsaminaceae А Balsaminaceae А Ρ Rosaceae Ρ Rosaceae Ρ Rosaceae Ρ Fabaceae Caryophyllacea Ρ е Caryophyllacea Ρ е Araliaceae Ρ Brassicaceae А А Poaceae Lamiaceae Ρ Malvaceae А Solanaceae А

Plantaginaceae

А Biomass Bioma Bioma Bioma Bioma Bioma Bioma Bioma Bioma Intern Intern Leaf n Bioma Bioma No. of leaves No. of leaves No. of leaves Bioma Bioma No. of Stem Stem Bioma

ass	Height
ass	Height
node length	Stem length
node length	Stem length
10.	Height
ass	No. of lateral bra
ass	No. of lateral bra
f rosette	
S	Internode length
f rosette	laters de la sette
S f rocotto	Internode length
s	Internode length
3	Branching index
200	Branching index
u35	Dranening maex
f ramets	Apical dominance
length	Leaf area
length	Leaf area
ass	Internode length

dominance

Fruit no. Seed no. Seed no. No. of inflorescences f lateral branches Pod no. f lateral branches Pod no. Inflorescence weight Inflorescence weight Inflorescence weight Weight of flowers Weight of flowers Flower no. Flower no. Flower no. Inflorescence mass ratio

				No. of growth	
Letts <i>et al.</i> 2012	Echinochloaa crus-galli	Poaceae	Р	units	Leaf inclination
				No. of growth	
Letts <i>et al.</i> 2012	Echinochloa glabrescens	Poaceae	А	units	Leaf inclination
Mallik <i>et al.</i> 2012	Kalmia angustifolia	Poaceae	А	Biomass	Height
Novoplansky et al. 1994	Onobrychis squarrosa	Fabaceae	А	No. of leaves	Branch length
Novoplansky et al. 1994	Onobrychis squarrosa	Fabaceae	А	No. of leaves	Branch length
Novoplansky et al. 1994	Onobrychis squarrosa	Asteraceae	А	No. of leaves	Branch length
Paquin and Aarssen 2004	Ambrosia artemisifolia	Poaceae	Р	Biomass	Height
Schmitt 1993	Echinochloa glabrescens	Cyperaceae	Р	No. of leaves	Height
Schmitt 1993	Echinochloa glabrescens	Ericaceae	Р	No. of leaves	Height
Weinig 2000	Carex flacca	Fabaceae	А	No. of internodes	Height
Weinig 2000	Kalmia angustifolia	Fabaceae	А	No. of internodes	Height
Weinig et al. 2006	Arabidopsis thaliana	Fabaceae	А	Rosette diameter	Apical branches

Fruit production Fruit production Flowering shoot no. Fruit no. Fruit no. Fruit no. Seed no. Total reproduction Total reproduction Date of budding Fruit production Appendix B: Reference list of studies used in this data-synthesis.

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CHAPTER 4

PLANT RESPONSES TO THEIR NEIGHBOURS: IS PHENOTYPIC PLASTICITY ASSOCIATED WITH COMPETITIVE ABILITY?

Clara Pang and Stephen P Bonser

Abstract

Competition is widely thought to be an important determinant of the structure and the dynamics of plant communities. Consequently one of the major goals in ecology has been to find what traits are associated with competitive ability. The expression of traits associated with increased competitive ability may allow species to dominate crowded habitats. High phenotypic plasticity has been one of the traits that has been traditionally associated with high competitive ability. Under high competition, phenotypic plasticity is predicted to allow plants to adjust their phenotype to maximise acquisition of resources and take advantage of patches of resources before less plastic neighbours are able to. However, whilst plasticity can offer many potential fitness benefits, its associated costs suggest it should only be favoured under highly variable environments. We suggest that under a persistent competitive environment, a strategy of high plasticity could prevent a plant from maximising competitive ability due to the high costs of expressing phenotypic plasticity. In this study we utilised the data from published empirical studies in order to test this idea across species about whether plants with higher plasticity perform better under high competition. We found that higher plasticity was related with a higher negative impact of competition rather than improved performance under competition across species. We found evidence to suggest the adaptive value of plasticity in short-lived species was instead in higher reproductive efficiency (high plasticity was associated with intense and early reproduction). We found no relationship between reproductive efficiency and plasticity in longer-lived perennial species. These results were in contrast to traditional predictions on traits associated with competitive ability in plants and suggest a revision of theory may be necessary.

Introduction

Competition for resources is a primary selective force in the evolution of adaptive strategies in plants (Grime 1979; Goldberg and Barton 1992; Bonser and Aarssen 1996) and in determining community composition and dynamics (Gurevitch and Unnash 1989; Grace and Tilman 1990). Whether some traits are associated with higher competitive ability than others has been the subject of intense interest (Grime 1979; Tilman 1982). This has led to the accumulation of a large body of work with a focus on seeking the strategies or traits which would allow certain species greater success over other species under competition (reviewed by Goldberg 1996). One of the traits often associated with high competitive ability in plants is high phenotypic plasticity (Grime *et al.* 1986). Phenotypic plasticity is the ability of a genotype to express different phenotypes in response to changes in the environment (Schlichting and Pigliucci 1998; Pigliucci 2005), and the capacity to shift strategies of resource acquisition is commonly believed to be important in the presence of competitors.

Phenotypic plasticity has been perceived to be particularly important to plants as plants are limited in their ability to make changes to their behaviour and in movement which allows other more mobile organisms such as animals to move away from adverse environments (Bradshaw 1965). Most plants rely on these phenotypic adjustments to their growth and allocation to improve their prospects under changing conditions (Sultan 2000). By altering their growth, plants can alter the environment they experience (Donohue 2003). High plasticity in plants can be partially attributed to their modular growth form that allows them to grow organs (e.g. leaves, roots, stems) from development to the end of their lives in response to changing environmental conditions (de Kroon *et al.*

2009). Many studies have shown that plants make such changes for numerous ecologically important morphological and physiological traits, often associated with resource acquisition (Sultan 2000). These changes are predicted to allow plants to maintain stability under highly variable environments, make changes to resource use (by changing growth allocation to be able to obtain more or use less of the various types of resources they require) under periods of low resources as well as allow the plant to take advantage of periods of good conditions (Bradshaw 1965; Schlichting 1986; Sultan 1987; Stearns 1992).

Under competitive conditions, plasticity has been predicted to be mainly morphological and developmental and believed to function as a resource foraging and acquisition strategy (Grime 1979; Grime et al. 1986). Plasticity in these resource foraging and acquisition strategies could maximise resource acquisition across environments, and be associated with competitive ability by redirecting growth away from unfavourable patches of low resource availability towards favourable higher resource patches. Additionally plasticity could allow the plants growing in areas with abundant resources to remain in and maximise their resource capture thus allowing them to more efficiently take advantage of available resources in the environment around them than other plants (Grime 1979; Grime et al. 1986; Bazzaz 1991; de Kroon and Hutchins 1995; Huber et al. 1999). Clonal species have been observed to spread laterally into surrounding patches of habitat with higher levels of resources via structures such as rhizomes and stolons (de Kroon and Knops 1990; Birch and Hutchings 1994; and reviewed by Hutchings and Wijesinghe 1997). Non-clonal species have also been shown to alter their allocation to and placement of roots into patches of higher resource availability as well as alter the placement of photosynthetic structures depending on which resource is manipulated

(reviewed by de Kroon and Hutchings 1995; and Poorter and Nagel 2000). It is generally predicted that plants capable of capturing resources at higher rates than potentially competing plants will be favoured in that environment as these organisms will be able to build more modules with which to capture additional resources as well as form reserves of resources with which to endure periods of low resource availability and to then invest in reproduction (Givnish 2002). Thus, plasticity in resource acquisition traits should allow the maintenance of high fitness under different environments. Plasticity in these traits has been hypothesised to be a mechanism which buffers the negative effects of competition and perhaps can be a mechanism of coexistence in competing species (Callaway *et al.* 2003). Consequently, plasticity been viewed as an important trait to express under competition.

Plasticity in resource allocation traits has been demonstrated to be adaptive in some conditions (e.g. the shade avoidance plasticity responses, Smith 1982; Dudley and Schmitt 1995). Here, we test if plasticity generally confers greater performance under competition. While the traditional interpretation of plasticity is that it confers high competitive ability, there are several reasons why this may not be the case. Plasticity can be costly in the energy and resources required to maintain the sensory and regulatory machinery needed for plasticity; the energy required to produce the trait in a plastic genotype compared to an invariant genotype; the resources needed to acquire information; the exposure to potential competitors, predators or pathogens whilst trying to acquire this information (DeWitt *et al.* 1998). Plasticity can also be costly if any developmental instability occurs due to phenotypically imprecise development leading to a reduction in fitness; as well as genetic costs (Givnish 2002, but see van Kleunen and Fischer 2005). As well as costs, there

are also limitations to plasticity e.g. lag times in their developmental responses and imprecise cues (Tufto 2000) which may make it not as viable a strategy in highly competitive environments where any delayed or inappropriate response can lead to their demise without reproduction (DeWitt *et al.* 1998).

In order for phenotypic plasticity to be adaptive, environmental cues need to be reliable and a plant needs to be able to perceive environmental cues accurately in order to make the appropriate adjustments to their growth and reproduction (Callaway et al. 2003). In the absence of these conditions, local adaptation and specialisation would be favoured (Van Tienderen 1991). With all these costs and limits, a high plasticity strategy would likely only be worth expressing in a highly variable environment. High competition environments are not typically highly variable – competition is generally predicted to worsen until it reaches a high level at which it remains for prolonged periods until some disturbance occurs (Bonser 2013). The main problem with the idea that plasticity increases competitive ability is that competitive ability should evolve under environments of consistently high levels of competition where specialised competitive strategies would be favoured whilst plasticity would be favoured in environments where competition levels and resource levels are variable. The costs of plasticity would prevent an individual from maximising competitive ability and performance of a plastic strategy would not be greater than a competitive strategy under consistently high competition (van Tienderen, 1991, 1997; Moran 1992; Tufto 2000; Pigliucci 2001; Sultan and Spencer 2002). This is especially the case for short-lived species (i.e. annual species) for which it is unlikely their inherently smaller sizes and shorter lifespans would allow them to outcompete longer-lived (perennial) competitors though increased growth through plasticity in resource acquisition traits. This suggests that even if plasticity is adaptive under competition, its adaptive value may not lie in conferring greater competitive ability.

At high levels of competition, plants may be better off placing their efforts into ensuring successful reproduction (Bonser 2013). For example in response to light competition, plants will make a suite of morphological adjustments to their growth to enhance the amount of light they receive which have widely been seen as a strategy to increase their competitive ability for light (Aerts 1999). The plastic changes in the growth of plants in response to differing light conditions has been commonly used as one of the classical examples of adaptive plastic responses of plants to competition. However, in a previous quantitative literature synthesis study (Chapter 3), where we examined the performance of plants under different spectral shading treatment, we found that higher shade avoidance plasticity is connected with poorer plant performance under competition across species. Instead we found a highly significant relationship between shade avoidance plasticity is a strategy to obtain resources to allocate to earlier reproduction rather than to increase competitive ability.

Following our findings from our previous research on shade-avoidance plasticity, we remain uncertain whether high plasticity in general should also be associated with a strategy of competitive ability in plants. Consequently, a follow-up question emerged from that study which forms the basis of this current study: does plasticity in general increase competitive ability as predicted by ecological theory? Many studies have suggested that

highly plastic plants have higher levels of competitive ability, but there have been few empirical tests directly testing this theory (Aerts *et al.* 1991; Li *et al.* 1999), and there have been no syntheses of the findings from previous studies. We predicted that increasing phenotypic plasticity in resource acquisition traits will not be associated with a decrease in competitive effects experienced by plants and that instead it could be associated with an increase in reproductive efficiency. We utilised published studies reporting plant performance and the expression of traits associated with resource acquisition and ecological strategies across competition treatments to test the following predictions: 1) Higher plasticity in resource acquisition or foraging traits will be associated with greater negative impacts of competition; and 2) Higher plasticity in resource acquisition or foraging traits will be associated with increased allocation to reproduction under competition.

Methods

We conducted a literature search on Web of science (Thompson Reuters) and Google Scholar using the keywords "plant competition", "plant density", "neighbour removal", "neighbour interaction*", "plant-plant interaction", "interspecific interaction" in order to find plant competition experiments published up until April 30 2017. We included articles (as well as other articles we found in their reference lists) which evaluated the effect of the presence of neighbours (either conspecific or not) on the competitive performance (measured plant size, biomass, etc.) and other ecologically important physiological traits on a target species. Traits which would provide plasticity measures that related directly to the functional success of plants in their environments were considered as ecologically important (e.g. root to shoot ratio, photosynthetic rate, etc.). The studies we used in our dataset were a bit broader than traditional plasticity experiments where single genotypes were used in different environments. In order to maximise the number of studies included, we included those where seeds from a single stock (single maternal plant or small number of plants from the same population). This selection may have increased variability in the responses, but we do not believe systematically biased our results. We included field, common garden, glasshouse and growth chamber studies but excluded studies using cultivated species e.g. crops and special cultivars of species. We included studies where the same species interaction was simultaneously evaluated for at least two groups we could assign as low and high competition e.g. the target species were grown with high and with no or a low number of neighbours. However, studies that simulated the presence of neighbours rather than using real plants (e.g. by adding branches or artificial shade) were not included in the study.

In order to avoid lack of independence, studies conducted over temporal gradients or with plants differing only in maternal origin were only included in the dataset if they were obtained from different individuals at each sampling date and if the individuals being compared had the same age (to avoid age-dependent effects on plant performance). Studies that manipulated the degree of abiotic stress in a single site (e.g. by watering or by adding nutrients) were also included but both the treatments had to be grown in at least two standardised conditions that differed in competition level only. We included the data from each different treatment as different cases in studies where multiple levels of nutrient/water/light treatments/soil type were crossed with the competition treatment. Where articles reported results for more than one responding species or size/age or origin within a single species) a target species competing against several different competitor

treatments (number per species) or for more than one experiment, each species, size/age class and experiment was included separately in the dataset. For articles which reported results over the course of the experiment, we only included the final results at the end of the experiment. Thus, ensuring species from each single experiment was only represented once.

For each study which met all these selection criteria, we recorded the mean, standard error (SE) and sample size for competitive ability, other physiological trait response variables on target plants growing in the high and low competition treatment groups and reproduction (if available). When the data were reported in a graphical form, the data from these graphs were extracted with the software Data Thief (B. Thumers; http://www.datathief.org). In addition, we compiled information from online botanical databases on plant life history, for each of the target species included in our dataset so that we could examine whether this had an effect.

We estimated an index of phenotypic plasticity for each replicate (see – Valladares *et al.* 2000):

$$Plv = [Max (X_{hc}, X_{lc}) - Min (X_{hc}, X_{lc})] / Max (X_{hc}, X_{lc})$$
(equation 1)

where X_{hc} and X_{lc} are the means for plasticity traits under high competition and low (or no) competition, respectively. We selected a single most relevant physiological trait from each species replicate. The selection of this physiological trait was determined by the treatment

type used in the study (e.g. height to shoot biomass was commonly used in light treatments and allocation to roots in nutrient treatments).

We calculated a relative index of competition intensity to estimate the effect of competition on size:

 $CI = (Size_{lc}-Size_{hc})/(Size_{lc})$

(equation 2)

where Size_{lc} and Size_{hc} are measures of plant size under low competition and under high competition, respectively. Other measures of competition intensity which may be more preferable (Weigelt and Jolliffe 2003; Oksanen *et al.* 2006; Rees *et al.* 2012) require data such as the size of the largest plant or maximum plant performance which were not available in the studies we were able to find for this current study. Some authors have argued that size may not always be a good measure of success under competition (Aarssen and Keogh 2002). However, the best way to measure plant performance under competition remains a controversial topic on which there is currently not yet a common consensus. Our experience in collecting data for the shade avoidance chapter (chapter 3) suggests that far fewer studies publish data on plant reproduction under competition than on size under competition. This limitation made it much more appropriate to use size as the primary measure of performance for this study.

We calculated relative reproductive efficiency (see – Bonser 2013), a measure of the conversion of resources from vegetative growth to reproductive output (i.e. allocation to reproduction relative to vegetative size):

 $RRE = \log \left[(R/S)_{hc} / (R/S)_{lc} \right]$

(equation 3)

where $(R/S)_{hc}$ and $(R/S)_{lc}$ is the mean reproductive allocation (R) relative to size (S) in high competition (hc) and low competition treatments (lc), respectively. The reproductive efficiency in competition treatments relative to no competition treatments can be used to assess how plants shift reproductive strategies under competition. RRE is negative in instances where reproductive efficiency is greater under low competition treatments and positive in instances where reproductive efficiency is greater under high competition treatments. We removed all cases where the only values for reproduction and plant size were reproductive mass and total mass (as values of reproduction would be included in both the numerator and the denominator of the index) to prevent autocorrelation.

We used a linear regression analysis to investigate the relationships between phenotypic plasticity PIv and competition intensity CI and between phenotypic plasticity PIv and relative reproductive efficiency RRE in the plants. We also performed separate regressions for short-lived and long-lived species to test if there were differences in life history groups.

We used a general linear model to investigate the relationship between phenotypic plasticity PIv and competition intensity CI. CI was included as the dependent variable, PIv was included as a main effect, and study was included as a random effect (to control for the contribution of multiple species replicates from any given study). This analysis was then repeated to investigate the relationships between PIv and RRE with RRE included as the dependent variable PIv included as a main effect and species included as a random effect to control for the inclusion of a given species in multiple studies.

We then used partial correlations controlling for the density of neighbours applied to the plants in the high competition treatments to assess relationships between PIv and CI, and PIv and RRE. This is important in our analysis since the level of plasticity PIv expressed and thus the CI and RRE expressed by the plants could be due to the level of competition the plants are subjected to. Unfortunately, not all the results of the studies which matched our other criteria for inclusion in the dataset had comparable measures of density and so we were only able to utilise a subset of the data for which we had a sufficient number of data points to test for effects of density. These were from studies which measured density in terms of plants per m² or for which we were able to obtain a comparable measure of density and convert to plants per m². Partial correlation analysis allows us to test for the impact of PIv on CI and RRE for a given degree of neighbour density. Plant strategies in response to competition may vary depending on whether competitor plants are seedlings or adults (see chapter 2). In this study, tests were done on the relationship between Plv and RRE relative to competition intensity which allowed us to control for the differences between seedling competition and competition with adults (studies on seedling competition will likely have lower competition intensity). All analyses were conducted using SPSS v 25 (SAS Institute, NC, USA).

Results

Our final data set comprised of 202 independent data points or cases across 38 studies where the growth as well as the plasticity of plant species which were grown with competing neighbours was assessed (see supplementary material). Of these, 50 different target species were represented from 24 families. 52 target species were short-lived

(annuals and biennials) and 150 species were long-lived (perennial). Only 82 of the cases from the 202 cases we found examined allocation to reproduction or fecundity which were required to calculate RRE values. Data sources and study species are provided in the supplementary material (Appendix A and B).

We found a significant positive relationship between competition intensity (the degree to which the growth of a plant is reduced by the presence of competition) and plasticity ($r^2 = 0.16$, P<0.001; Fig 1a) across species. Our results demonstrate that those plants with the highest plastic shade-avoidance responses also perform more poorly under competition. We also found a significant positive relationship between reproductive efficiency and plasticity ($r^2 = 0.162$, P<0.001; Fig 1b) showing plants which were more plastic had higher reproductive efficiency.

When we analysed our data by life history, we found a significant positive relationship between competition intensity and plasticity in the short-lived species ($r^2 = 0.402$, P<0.001; Fig 1a). We also found a significant positive relationship between reproductive efficiency and plasticity in the short-lived species ($r^2 = 0.163$, P =0.003; Fig 1b). Whilst there was also a significant positive relationship in the long-lived species between competition intensity and plasticity ($r^2 = 0.058$, P =0.003; Fig 1a), there was no significant relationship between reproductive efficiency and plasticity ($r^2 = 0.085$, P =0.118; Fig 1b) in these long-lived species. When we controlled for study and for species, relationships between competition intensity and PIv and reproductive efficiency and PIv across species were no longer significant (Tables 1, 2). We could not obtain values for study and species effects when running the general linear model to investigate the relationships between PIv and RRE. This was probably due to the small subset of studies and species which provided measures of reproductive performance. However, in both analyses, the inclusion of the random effect removed the significance of the relationship between RRE and PIv.

We found that CI and PIv were still highly positively correlated even when we controlled for density of competing plants (partial correlation CI versus PIv – df: 94, r= 0.559, P<0.001). RRE and PIv also remained highly positively correlated even when we controlled for density of competing plants (partial correlation RRE versus PIv – df: 68, r= 0.443, P<0.001).

Discussion

Plasticity has been predicted to be a highly important part of competitive strategies, allowing plants to acquire more of the available resources than their neighbours and maximise growth (Grime *et al.* 1986). To the best of our knowledge, there are no previous studies that suggest other mechanisms for plasticity. The results of this study demonstrate that in contrast to these predictions, increasing plasticity is instead associated with poorer competitive performance across species. In line with our predictions, the decrease in competitive performance with higher plasticity suggests the high costs associated with plasticity for example of gathering reliable information, redirecting resources and of deviating from the usual developmental trajectory to make these

physiological/morphological changes would prevent plants from maximising competitive ability (especially in comparison to competitive specialists). Highly phenotypically plastic plants can be superior competitors in temporally variable environments (Callaway et al. 2003) but our findings suggest this is only because these environments were variable. When the environment is not variable, such as in the studies which we included in our study (where the effect of competition was consistent), we found that having plasticity in traits which allowed for greater resource acquisition did not reduce the impact of the presence of competitors on growth. This is important as competition levels can remain high for an extensive period of time and often even intensify before easing following a disturbance. In contrast to previous predictions, the findings of this study suggest that in environments where competition is high, high plasticity is not associated with greater competitive ability. Placing resources into changing the growth and architecture to be able to obtain more resources to outgrow neighbouring plants is likely to be a risky strategy when time is limited and high levels of competition could restrict further growth and ultimately lead to failure to reproduce (e.g. Aarssen 2008; Bonser 2013). In an intensely competitive environment, plasticity in growth traits is unlikely to increase the plant's chances of reaching competitive dominance. However, that Plv did not explain significant variation in CI in the GLM models where we controlled for study and for species suggests that the significance observed in the linear regression analyses may be due to some of the studies and/or species expressing high plasticity and the plants in these cases experiencing high competition rather than a true relationship between Cl and Plv. While there was no clear increase in competition intensity (or RRE) with increasing plasticity (as controlling for study and species made this relationship non-significant), there was definitely no evidence for an increase in performance under competition.

In our previous study (Chapter 3, where short-lived species were the target species of most of the experiments), we demonstrated that shade avoidance plasticity was associated with poor plant performance under competition for light across studies. Instead, we found shade avoidance plasticity to be associated with an increase in allocation to reproduction. As such, shade avoidance plasticity was not a mechanism for increasing a plant's competitive ability and for obtaining more resources to accelerate reproduction under competition. The findings of this study were consistent with those earlier findings in that it similarly suggests that plasticity does not confer greater competitive ability. In this study we additionally demonstrate this is also the case in long-lived species. In line with the findings of Chapter 3, we also found that higher plasticity was positively related with higher reproductive efficiency in the short-lived species. However, we did not see this effect in the long-lived species suggesting there are differences in competitive strategies of the life history types.

Short-lived species

One of the reasons why we did not see any increase in the competitive performance in the short-lived species with increasing plasticity is that their inherently smaller sizes and short life spans make it unlikely for them to be able to outgrow a large, long-lived plant just by obtaining more resources for growth. Although it has been thought that small, short-lived plants have higher relative growth rates (Enquist *et al.* 1999), this has been found to only be an initial effect and the initial high growth rates inevitably level off as plants reach their maximum size (see Turnbull *et al.* 2008; 2012). On the other hand, the lower reproductive threshold size of short-lived species gives them more flexibility to reproduce earlier

compared to long-lived species which require long periods of vegetative growth before they can reach a size at which they are able to reproduce (Harper 1977). If competition remains high for extended periods, then placing resources into producing seeds as early as possible which can then disperse or remain dormant until competition levels ease would maximise the persistence of populations of short-lived plant species. The function of plasticity responses under high competition for short-lived species is likely to be to acquire and allocate more resources towards earlier reproduction prior to light and nutrient availability declining to a level which would prevent successful reproduction. For example, it has been shown that under conditions where plants have a high chance of early mortality, plants which flowered earlier were able to successfully reproduce while plants which reproduced at their usual time did not have sufficient time for their fruits to mature before death (Donohue et al. 2000). Whilst delaying reproduction to reach an optimum size could lead to increased reproductive output and increased quality of the offspring produced if conditions improve, the short lifespan of short-lived species makes it unlikely they would be able to survive until conditions improve. These findings show that plasticity is likely to be an adaptive response to competition in short-lived species, however, not by increasing competitive ability through becoming larger than neighbouring plants, but through maximising the capacity to acquire resources to allocate to early reproduction prior to intense crowding and competition from neighbouring plants.

Long-lived species

Long-lived plant species were more likely to achieve a competitive advantage through plasticity as their longer lifespans allow them time to grow and reproduce later. Yet, longer-lived species also did not perform better under competition with increasing plasticity further providing support for the idea that plasticity does not confer competitive ability. Additionally, in contrast to our findings in the short-lived species, we did not observe any significant reproductive efficiency advantage associated with higher plasticity in the long-lived species. The growth of plants with higher plasticity was more affected by competition. Long-lived species may have been limited in their reproductive efficiency by the larger minimum required size for reproduction and thus a longer time to first reproduction (Harper 1977). Growth is often limited under competitive conditions and long-lived plants may be further limited by their higher minimum reproductive threshold size and thus be unable to reproduce earlier without increasing growth first.

Alternatively, the adaptive value of high plasticity in long-lived species could potentially lie in a component of fitness we were unable to assess – survival. Plasticity may be important in long-lived species for obtaining additional resources for survival until reproduction is possible. Besides not being able to reproduce earlier due to physical constraints, there are several factors that would make allocating to survival more beneficial to long-lived species than short-lived species. Reproductive events are usually spread out over the years of a perennial plant's life. The reproductive output of one reproductive event of a longer-lived species (except monocarpic perennial species of which there were few in our dataset) is likely to be a much smaller percentage of their potential lifetime reproductive output than for a short-lived species. Perennial species may not exhibit the same plasticity in the timing and allocation to reproduction as annual species because their longer potential life spans means seed production does not affect their persistence from one year to the next in the environment as much as it does annuals which rely on their offspring to be able to persist in the environment. Subsequently, in long-lived species, plasticity could be more tightly

linked to survival rather than other fitness components of growth and reproduction. However, most studies in our dataset did not assess survival and terminated their experiments before the natural demise of the plants. Nonetheless, in accordance with our predictions, our findings demonstrate that plasticity also does not confer greater competitive ability in long-lived species.

Further implications of the findings

A few questions become imminently apparent in plant competition theory in light of these findings that phenotypic plasticity does not necessarily confer high competitive ability. In particular, (a) What does this mean about the importance of size in competitive interactions? (b) If the importance of size is less important than what was previously believed, what does this mean for the predictions of traditional theory on the competitive abilities of small short-lived species and larger long-lived species?

Traditionally it is predicted that in order to achieve competitive dominance, plants should grow to a large size and take up more space relative to the other plants in their community leaving less resources for them (Grime 1973; Goldberg 1996; Tracey and Aarssen 2014). There has been much debate about how competitive hierarchies could potentially differ depending on whether competitive ability is measured by competitive effect (the ability to depress growth and reproduction of neighbours) or competitive response (the ability to withstand the negative effects of neighbours) (Goldberg 1990; 1996). The focus of this study was on whether plasticity had any effect on plant responses to competition (competitive ability was measured as the effect of competition on size) although we did try

to control for competitive effect of neighbouring plants (by controlling for the density of competing plants). Generally, body size has been seen as a key indication of competitive ability because it is believed to be closely tied to the ability of a plant to acquire resources and deny resources to its neighbours especially when competition for resources is asymmetric – where larger individuals are able to obtain more resources and make them unavailable to smaller individuals (Gurevitch *et al.* 1990; Schwinning and Weiner 1998). Subsequently it was assumed having high plasticity would be an important trait that would help plants to acquire the maximum amount of resources they could in a crowded environment. The findings of this study suggest that gathering resources to increase size as a way of increasing competitive ability may not be as important as previously has been thought. Growing to a large size may be important only in terms of reaching the required minimum size for reproduction to occur. Plasticity could increase chances of reproduction under competition instead (for short-lived species by allowing them to reproduce earlier and for long-lived species by allowing them to survive until they reach their size for reproduction).

The greater importance of reproducing over growing to a large size under competition suggests that under severe levels of competition, the strategy of short-lived species could allow them achieve higher fitness than large-sized species. Whilst long-lived species may be able to produce more offspring in a lifetime, under conditions like severe competition where growth can be limited or where the lives of plants have a high chance of being curtailed early on, shorter-lived species would have greater chances of successfully producing offspring than longer-lived species which do not reproduce earlier. However, if longer-lived species are able to survive until conditions improve, these species could have

potentially greater lifetime reproduction provided they are able to reach their required size for reproduction. These findings suggest that contrary to predictions of traditional strategy theories that competition was only important in the evolution of long-lived largesized species (Grime 1973), the strategies of both short-lived small-sized species and longlived large-sized species evolved under competition.

Plasticity has also long been associated with the success of invasive species in outcompeting newly encountered and already established competitors (Baker 1965; Sultan 2004; Richards *et al.* 2006; Funk 2008). As well as allowing invasive species to cope with an environment that is different from that which they evolved in and to establish under novel conditions (Schlichting and Levin 1986; and reviewed by Richards *et al.* 2006), Baker (1965) proposed that higher plasticity could allow invasive species to produce more seeds under favourable conditions and have relatively less reduction in seed production under stressful conditions. Our findings lend support for this proposed advantage of plasticity in seed production.

This research, however, may be subject to some possible limitations. Species which are more easily grown and measured can often be more favoured than others to use in plasticity experiments especially since our selection criteria also required reproduction to have been measured. Many studies could not be included in our dataset as they did not measure reproduction. We acknowledge such biases in the published literature towards certain species could potentially affect our findings. In this study we made efforts to account for these effects by controlling for study and species. The scarcity of empirical studies in plants which test for reproductive performance in addition to plant growth

under competition for longer-lived species most likely derives from feasibility difficulties with carrying out experiments (e.g. difficulties with carrying out experiments which span for the duration it takes for a long-lived plant's lifetime reproduction and researchers being limited by short funding cycles). However, that there are also very few studies which examine reproductive performance of short-lived species under competition, reflects the overwhelming belief in the importance of size in the competitive performance of a plant and the contrastingly lower importance placed on reproduction as an indication of performance under competition. The findings of this study illustrate the importance of extending research to allow the measurement of lifetime reproductive output in future competitive ability experiments if we are to truly assess the competitive performance of species. Further studies assessing survival until reproduction for a large number of taxa from differing life history backgrounds would also be important in understanding the adaptive value of traits under competition.

This study demonstrates alternative means used by plants with different life histories to mitigate risks of fitness-loss imposed by competition to those predicted by theory. Our quantitative synthesis of current research suggests that higher plasticity is not associated with higher competitive ability in both short-lived and long-lived species and instead is associated with higher and earlier allocation to reproduction in short-lived species and perhaps survival until reproduction in long-lived species. However, these early findings are still limited due to the lack of studies which measure the fitness components of survival and reproduction especially for longer-lived species. This study provided a much-needed test of the role of plasticity in competitive ability, and we conclude there is no competitive advantage of being more plastic in contrast to the predictions of ecological theory.



Fig. 1 Regression analysis of plasticity index PIv and **a**) Relative index of competition intensity where competitive performance was measured as the effect of competition on size, and plasticity index PIv and **b**) Relative reproductive efficiency (i.e. allocation to reproduction relative to vegetative size). Closed circles (•) represent annual plants and the solid lines their regression lines and open circles (•) represent perennial plants and the dashed lines their regression lines.

Table 1. General linear model testing the impact of plasticity Plv on competition intensity with

study included as a random effect.

	Competition intensity					
Source of	Df	MS	F	Р		
variation						
Plv	164	0.054	0.632	0.792		
Study (random)	2	0.126	1.470	0.405		
Error	2	0.086				

Table 2. General linear model testing the impact of plasticity Plv on competition intensity with species included as a random effect.

	Competition intensity						
Source of	Df	MS	F	Р			
variation							
Plv	150	0.048	0.560	0.829			
Species (random)	2	0.126	1.470	0.405			
Error	2	0.086					

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Appendix A: The list of surveyed studies and their details.

Reference	Target species	Family	Life History	Competitor species	Vegetative size	Plasticity trait	Reproduction trait
Agrawal 2004	Asclepias syriaca	Asclepiadaceae	Р	Bromus sp.	Total biomass	Stem height/plant mass	Number of fruits
Ang <i>et al.</i> 1995	Cirsium arvense	Asteraceae	Ρ	Festuca arundinacea	Aboveground biomass	Length of roots	Plants produced/original plant
Berendse and Moller 2009	Plantago Ianceolata	Plantaginaceae	Ρ	Plantago lanceolata	Total biomass	Shoot to root ratio	
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	A	Calamagrostis canadensis	Aboveground biomass	Relative growth rate	
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	Ρ	Equisetum arvense	Aboveground biomass	Relative growth rate	
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	Р	Populus tremuloides	Aboveground biomass	Relative growth rate	
Cater and Stuart Chapin 2000	Betula papyrifera	Betulaceae	Р	Calamagrostis canadensis	Aboveground biomass	Relative growth rate	

Cater and Stuart Chapin 2000	Betula papyrifera	Betulaceae	A/B/P	Equisetum arvense	Aboveground biomass	Relative growth rate
Cater and Stuart Chapin 2000	Betula papyrifera	Betulaceae	Р	Populus tremuloides	Aboveground biomass	Relative growth rate
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	Ρ	Calamagrostis canadensis	Total biomass	Height/biomass
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	Ρ	Equisetum arvense	Total biomass	Height/biomass
Cater and Stuart Chapin 2000	Picea glauca	Pinaceae	Ρ	Populus tremuloides	Total biomass	Height/biomass
Cater and Stuart Chapin 2000	Betula papyrifera	Betulaceae	Ρ	Calamagrostis canadensis	Total biomass	Height/biomass
Cater and Stuart Chapin 2000	Betula papyrifera	Betulaceae	Ρ	Equisetum arvense	Total biomass	Height/biomass
Cater and Stuart Chapin 2000	Betula papyrifera Amphibromus	Betulaceae	Ρ	Populus tremuloides	Total biomass	Height/biomass Allocation to roots
Cheplick 1997	scabrivalvis	Poaceae	Р	Lolium perenne	Total biomass	(%)

Cottam <i>et al.</i> 1986	Rumex obtusifolius	Polygonaceae	Р	Festuca rubra	Aboveground biomass	Root mass/leaf mass	
Cramer <i>et al.</i> 2012	Acacia karroo	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia karroo	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia karroo	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia karroo	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia burkei	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia burkei	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia burkei	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Acacia burkei	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Schotia brachypetala	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Schotia brachypetala	Fabaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Schotia brachypetala	Fabaceae	A	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Schotia brachypetala	Fabaceae	A	Chloris gayana	Total biomass	Shoot to root ratio	
7							
Cramer <i>et al.</i> 2012	Spirostachys africana	Euphorbiaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
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Cramer <i>et al.</i> 2012	Spirostachys africana	Euphorbiaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Spirostachys africana	Euphorbiaceae	Р	Chloris gayana	Total biomass	Shoot to root ratio	
Cramer <i>et al.</i> 2012	Spirostachys africana	Euphorbiaceae	Ρ	Chloris gayana	Total biomass	Shoot to root ratio	
Donohue and Schmitt 1999	Impatiens capensis	Balsaminaceae	Ρ	Impatiens capensis	Number of leaves	Total leaf area	Number of flowers
Donohue and Schmitt 1999	Impatiens capensis	Balsaminaceae	Р	Impatiens capensis	Number of leaves	Total leaf area	Number of flowers
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Acer rubrum	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Р	Acer rubrum	Total biomass	Specific leaf area	
Elliott and White 1993	Pinus resinosa	Pinaceae	Ρ	Acer pensylvanicum	Total biomass	Specific leaf area	

Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	A/B	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	A/B	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	A/B	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Acer rubrum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Acer rubrum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Acer pensylvanicum	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
Elliott a White 2	and 1993	Pinus resinosa	Pinaceae	Р	Prunus pensylvanica	Total biomass	Specific leaf area	
171 Ernebu	ırg 1999	Anthemis cotula	Asteraceae	Ρ	Tripleurospermum inodorum	Aboveground biomass	Root to shoot ratio	Achene production

Fowler and	Aristolochia				Aboveground		
Rausher 1985	reticulata	Aristolochiaceae	Р	Schizachyrium scoparium	biomass	Root to shoot ratio	Reproductive mass
Friedli and	Cincing and an	Astoresses	0	Lolium perenne, Lolium multiflorum, Dactylis	Aboveground		Number of
Bacher 2001	Cirsium arvense	Asteraceae	Р	giomerata	blomass	Root to shoot ratio	flowerneads per pot
Heger <i>et al.</i> 2014	Erodium cicutarium	Geraniaceae	Ρ	Bromus hordeaceus	Aboveground biomass	Specific leaf area	Seed number
Johnson <i>et al.</i> 1998	Pinus resinosa	Pinaceae	Р	Pinus banksiana	Final volume	Relative growth rate	
Johnson <i>et al.</i> 1998	Pinus resinosa	Pinaceae	Р	Pinus banksiana	Final volume	Relative growth rate	
Kawaletz <i>et al.</i> 2014	Quercus robur	Fagaceae	Р	Quercus robur	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 2014	Quercus robur	Fagaceae	Р	Carpinus betulus	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 2014	Quercus robur	Fagaceae	Р	Robinia pseudoacacia	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 2014	Quercus robur	Fagaceae	Р	Prunus serotina	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 2014	Carpinus betulus	Betulaceae	Р	Quercus robur	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 2014	Carpinus betulus	Betulaceae	Р	Carpinus betulus	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et al.</i> 172 2014	Carpinus betulus	Betulaceae	Р	Robinia pseudoacacia	Aboveground biomass	Root to shoot ratio	

Kawaletz <i>et</i> 2014	al. Carpinus betulus	Betulaceae	Р	Prunus serotina	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Robinia pseudoacacia	Fabaceae	Р	Quercus robur	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Robinia pseudoacacia	Fabaceae	Р	Carpinus betulus	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Robinia pseudoacacia	Fabaceae	Ρ	Robinia pseudoacacia	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Robinia pseudoacacia	Fabaceae	Ρ	Prunus serotina	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Prunus serotina	Rosaceae	Ρ	Quercus robur	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Prunus serotina	Rosaceae	Ρ	Carpinus betulus	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Prunus serotina	Rosaceae	Р	Robinia pseudoacacia	Aboveground biomass	Root to shoot ratio	
Kawaletz <i>et</i> 2014	al. Prunus serotina	Rosaceae	Р	Prunus serotina	Aboveground biomass	Root to shoot ratio	
Kok <i>et al.</i> 19	86 Carduus nutans	Asteraceae	Р	Festuca arundinacea	Aboveground biomass	Root to stem ratio	Number of seeds
Kok <i>et al.</i> 19	86 Carduus nutans	Asteraceae	Ρ	Festuca arundinacea	Aboveground biomass	Root to stem ratio	Number of seeds
Kok <i>et al.</i> 19	86 Carduus nutans	Asteraceae	Ρ	Festuca arundinacea	Aboveground biomass	Root to stem ratio	Number of seeds
Kromer and Gross 1987	Oenothera biennis	Onagraceae	Ρ	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kromer and کی Gross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield

Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Ρ	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Kı G	romer and ross 1987	Oenothera biennis	Onagraceae	Р	Oenothera biennis	Total biomass	Height/biomass	Seed yield
Li 19	and Wilson 998	Picea glauca	Pinaceae	Р	Picea glauca	Aboveground biomass	Root to shoot ratio	
Li 19	and Wilson 998	Picea glauca	Pinaceae	Р	Picea glauca	Aboveground biomass	Root to shoot ratio	
Li 19	and Wilson 998	Picea glauca	Pinaceae	Ρ	Picea glauca	Aboveground biomass	Root to shoot ratio	
Li 19	and Wilson 998	Picea glauca	Pinaceae	Ρ	Picea glauca	Aboveground biomass	Root to shoot ratio	
Li 19	and Wilson 998	Symphoricarpos occidentalis	Caprifoliaceae	Р	Symphoricarpos occidentalis	Aboveground biomass	Root to shoot ratio	
Li 174	and Wilson 998	Symphoricarpos occidentalis	Caprifoliaceae	Р	Symphoricarpos occidentalis	Aboveground biomass	Root to shoot ratio	

Li and Wilson 1998	Symphoricarpos occidentalis	Caprifoliaceae	Ρ	Symphoricarpos occidentalis	Aboveground biomass	Root to shoot ratio	
Marcuvitz and Turkington 2000	Trifolium repens	Fabaceae	Ρ	Dactylis glomerata	Aboveground biomass	Specific leaf area	
Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Роасеае	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Martinkova and Honek 2011	Echinochloa crus- galli	Роасеае	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds

Martinkova and Honek 2011	Echinochloa crus- galli	Poaceae	Ρ	Echinochloa crus-galli	Aboveground biomass	Root to shoot ratio	Number of seeds
Meekins and McCarthy 2000	Alliaria petiolata	Brassicaceae	Ρ	Alliaria petiolata	Aboveground biomass	Height/shoot biomass	Number of seeds
Meekins and McCarthy 2000	Alliaria petiolata	Brassicaceae	Ρ	Alliaria petiolata	Aboveground biomass	Height/shoot biomass	Number of seeds
Meekins and McCarthy 2000	Alliaria petiolata	Brassicaceae	Р	Alliaria petiolata	Aboveground biomass	Height/shoot biomass	Number of seeds
Meekins and McCarthy 2002	Alliaria petiolata	Brassicaceae	Ρ	Alliaria petiolata	Aboveground biomass	Root biomass	Fruit biomass
Meekins and McCarthy 2002	Alliaria petiolata	Brassicaceae	Ρ	Alliaria petiolata	Aboveground biomass	Root biomass	Fruit biomass
Pepperkorn <i>et</i> al. 2005	Acacia longifolia	Fabaceae	Р	Acacia longifolia	Total biomass	Root to shoot ratio	
Pepperkorn <i>et</i> <i>al.</i> 2005	Acacia longifolia	Fabaceae	Р	Halimium halimifolium	Total biomass	Root to shoot ratio	
Pepperkorn <i>et</i> al. 2005	Acacia longifolia	Fabaceae	Р	Pinus pinea	Total biomass	Root to shoot ratio	
Pepperkorn <i>et</i> <i>al.</i> 2005	Halimium halimifolium	Cistaceae	Ρ	Halimium halimifolium	Total biomass	Root to shoot ratio	
Pepperkorn <i>et</i> 176 <i>al.</i> 2005	Halimium halimifolium	Cistaceae	Ρ	Acacia longifolia	Total biomass	Root to shoot ratio	

Pepperkorn <i>et</i> al. 2005	Pinus pinea	Pinaceae	Р	Pinus pinea	Total biomass	Root to shoot ratio	
Pepperkorn <i>et</i> al. 2005	Pinus pinea	Pinaceae	Ρ	Acacia longifolia	Total biomass	Root to shoot ratio	
Pitelka <i>et al.</i> 1980	Aster acuminatus	Asteraceae	Ρ	Aster acuminatus	Aboveground biomass	Allocation to roots (%)	Sexual reproductive effort (%)
Pluess and Stocklin 2005	Geum reptans	Rosaceae	Ρ	Poa alpina	Aboveground biomass	Root to shoot ratio	Number of flowers
Pluess and Stocklin 2005	Geum reptans	Rosaceae	Ρ	Poa alpina	Aboveground biomass	Root to shoot ratio	Number of flowers
Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant

	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
178	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant

	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
179	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant

	Ruiz de Clavijo and Jimenez 1998	Catanache lutea	Asteraceae	Ρ	Catanache lutea	Aboveground biomass	Height/shoot biomass	Number of amphicarpic capitula/plant
	Sanderson and Antunes 2013	Vincetoxicum rossicum	Apocynaceae	Ρ	Solidago canadensis	Total biomass	Root to Shoot ratio	Seedpod number
	Sanderson and Antunes 2013	Solidago canadensis	Asteraceae	Р	Vincetoxicum rossicum	Total biomass	Root to Shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa bladhii	Poaceae	Р	Bothriochloa bladhii	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa bladhii	Poaceae	A/B	Bothriochloa ischaemum	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa bladhii	Poaceae	A/B	Andropogon gerardii	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa bladhii	Poaceae	A/B	Schizachyrium scoparium	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa bladhii	Poaceae	В	Bouteloua curtipendula	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa ischaemum	Poaceae	В	Bothriochloa bladhii	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa ischaemum	Poaceae	В	Bothriochloa ischaemum	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bothriochloa ischaemum	Poaceae	В	Andropogon gerardii	Aboveground biomass	Root to shoot ratio	
08T	Schmidt <i>et al.</i> 2008	Bothriochloa ischaemum	Poaceae	В	Schizachyrium scoparium	Aboveground biomass	Root to shoot ratio	

	Schmidt <i>et al.</i> 2008	Bothriochloa ischaemum	Poaceae	В	Bouteloua curtipendula	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Andropogon gerardii	Poaceae	В	Bothriochloa bladhii	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Andropogon gerardii	Poaceae	В	Bothriochloa ischaemum	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Andropogon gerardii	Poaceae	В	Andropogon gerardii	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Andropogon gerardii	Poaceae	В	Schizachyrium scoparium	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Andropogon gerardii	Poaceae	A	Bouteloua curtipendula	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Schizachyrium scoparium	Poaceae	A	Bothriochloa bladhii	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Schizachyrium scoparium	Poaceae	A	Bothriochloa ischaemum	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Schizachyrium scoparium	Poaceae	A	Andropogon gerardii	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Schizachyrium scoparium	Poaceae	A	Schizachyrium scoparium	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Schizachyrium scoparium	Poaceae	A	Bouteloua curtipendula	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Bouteloua curtipendula	Poaceae	A	Bothriochloa bladhii	Aboveground biomass	Root to shoot ratio
	Schmidt <i>et al.</i> 2008	Bouteloua curtipendula	Poaceae	A	Bothriochloa ischaemum	Aboveground biomass	Root to shoot ratio
181	Schmidt <i>et al.</i> 2008	Bouteloua curtipendula	Poaceae	В	Andropogon gerardii	Aboveground biomass	Root to shoot ratio

	Schmidt <i>et al.</i> 2008	Bouteloua curtipendula	Poaceae	В	Schizachyrium scoparium	Aboveground biomass	Root to shoot ratio	
	Schmidt <i>et al.</i> 2008	Bouteloua curtipendula	Poaceae	В	Bouteloua curtipendula	Aboveground biomass	Root to shoot ratio	
	Sheppard <i>et al.</i> 2001	Echium plantagineum	Boraginaceae	В	Vulpia myuros	Aboveground biomass	Root to Shoot ratio	Seed number
	Sheppard <i>et al.</i> 2001	Echium plantagineum	Boraginaceae	В	Vulpia myuros	Aboveground biomass	Root to Shoot ratio	Seed number
	Steinger 1992	Centaurea maculosa ssp. rhenana	Asteraceae	A	Festuca pratensis	Aboveground biomass	Shoot to root ratio	
	Steinger 1992	Centaurea maculosa ssp. rhenana	Asteraceae	А	Festuca pratensis	Aboveground biomass	Shoot to root ratio	
	Stocklin 1997	Epilobium dodonaei	Onagraceae	A	Festuca rubra	Aboveground biomass	Root to shoot ratio	Number of flowering shoots
	Trtikova 2009	Erigeron annuus	Asteraceae	A	Festuca rubra	Number of leaves	Height	Total number of capitula
	Trtikova 2009	Erigeron annuus	Asteraceae	A	Festuca rubra	Number of leaves	Height	Total number of capitula
	Uddin <i>et al.</i> 2014	Melaleuca ericifolia	Myrtaceae	A	Phramites australis	Aboveground biomass	Root to shoot ratio	
	Uddin <i>et al.</i> 2014	Melaleuca ericifolia	Myrtaceae	A	Phramites australis	Aboveground biomass	Root to shoot ratio	
	Uddin <i>et al.</i> 2014	Phragmites australis	Poaceae	A	Melaleuca ericifolia	Aboveground biomass	Root to shoot ratio	
-								

Uddiı 2014	n et al.	Phragmites australis	Poaceae	A	Melaleuca ericifolia	Aboveground biomass	Root to shoot ratio	
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	А	Spergularia marina	Total biomass	Height/biomass	Number of flowers
Unga	r 1992	Spergularia marina	Caryophyllaceae	Ρ	Spergularia marina	Total biomass	Height/biomass	Number of flowers
van K <i>al.</i> 20	(leunen <i>et</i>)00	Ranunculus repens	Ranunculaceae	Ρ	Agrostis stolonifera	Number of rosettes	Length of the first three internodes	Number of flowers
Verm	eulen and ng 2010	Potentilla reptans	Rosaceae	A	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation

Vermeulen and During 2010	Potentilla reptans	Rosaceae	A	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	Ρ	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	Ρ	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation
Vermeulen and During 2010	Potentilla reptans	Rosaceae	A/P	Potentilla reptans	Aboveground biomass	Lamina area of mother ramet	Weight vegetative propagation

Welker <i>et al.</i> 1991	Quercus douglasii	Fagaceae	A/P	Bromus mollis	Aboveground biomass	Specific plant nitrogen content
Welker <i>et al.</i> 1991	Quercus douglasii	Fagaceae	A/P	Stipa pulchra	Aboveground biomass	Specific plant nitrogen content
Zhou <i>et al</i> . 2012	Alternanthera philoxeroides	Amaranthaceae	A/P	Alternanthera philoxeroides	Total biomass	Root to shoot ratio
Zhou <i>et al</i> . 2012	Alternanthera philoxeroides	Amaranthaceae	A/P	Alternanthera philoxeroides	Total biomass	Root to shoot ratio

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CHAPTER 5

ARE FUNCTIONAL TRAITS PREDICTIVE OF COMPETITIVE ABILITY?

Clara Pang and Stephen P Bonser

Abstract

Community ecology is increasingly turning towards trait-based approaches, searching for large-scale patterns in plant performance and their functional traits with the aim of being able to predict the responses of communities to environmental conditions by easily measured functional traits. A number of functional traits have been predicted to have strong impacts on competitive ability and consistently linked to individual responses to competitive interactions. However, it is still unclear how well these traits are able to predict competitive ability across species and environments. Specific leaf area and maximum height are two functional traits related to resource acquisition and use and thus commonly associated with plant competitive ability. In this study we collated the data from studies which measured competitive performance and then collected data from online flora databases with measures of specific leaf area and plant maximum height to perform a quantitative synthesis of studies evaluating the degree of empirical evidence there is to support these predictions of theory. Specifically, we tested the following predictions: 1) performance under competition will be positively correlated with maximum height and 2) performance under competition will be negatively correlated with SLA. We found that neither maximum height which is strongly tied to the life history of species nor specific leaf area which has also been linked with many other external abiotic and biotic environmental factors was significantly correlated with competitive performance. While the current results indicate that some traits could potentially be good predictors of competitive ability, our understanding of the role of functional traits in controlling competitive ability remains insufficient. It will be necessary to improve our understanding of competition before we can effectively test and make appropriate choices as to which traits would be good predictors of competitive ability.

INTRODUCTION

Competitive interactions between plants and their neighbours for resources are thought to have a large influence on patterns of distribution and abundance and community composition, and are predicted to determine which species are able to become dominant and which species risk being displaced from a community (Wilson and Tilman 1995). Thus, understanding competitive ability in plants is an important goal in ecology. Traditionally, much of the work towards understanding the results of environmental and biotic changes in communities mainly utilised a species or taxonomic approach (Lavorel and Garnier 2002; McGill et al. 2006). For example, predictions on the outcome of competitive interactions were based on detailed experimental studies on the interaction between pairs of species or very few species (McGill et al. 2006). However, such an approach involves the immense task of gathering large amounts of species-specific and environment-specific data for the interpretation to not be limited to narrow taxonomic groups or geographical locations (Keddy 1992; Cornelissen et al. 2003). Thus, interest has increasingly shifted towards traitbased approaches which instead aim to determine ecologically important functions (e.g. response to environmental change or competitive ability) on the basis of their functional traits (Adler et al. 2014) – traits that are functionally important and strongly influence or are strongly coordinated with the fitness of the plant across differing environments either in growth, survival or reproduction (Violle *et al.* 2007).

Trait-based approaches involve seeking patterns between morphological and physiological traits and ecological strategies across species (e.g. whether species with certain traits

respond to competition in similar ways or function in similar ways in their communities) to establish general rules which can be applied across different communities. Placing the focus on the traits of species rather than the identity of species allows us to make extensive predictions on competitive ability across many separate species, geographical locations, and environmental gradients and across entire ecosystems without the collection of detailed data across every potentially competing species (Adler et al. 2013; Siefert et al. 2014; Shipley et al. 2016). In contrast to the primarily experiment-based methods of species-based approaches, trait-based approaches are observational and often entail broad surveys of large numbers of species (McGill et al. 2006). In order to be able to be used as an effective predictor, the chosen traits should be easily and quickly measurable so that many species in many sites may be measured (Grime 1979b; Westoby 1998). Traits with these qualities tend to be 'soft traits' which can serve as proxies for harder to measure but more directly related to fitness 'hard traits' (Hodgson et al. 1999). Trait-based approaches are based on the premise that these inherent differences among species are able to reflect the differences in their fitness across differing environments (Grime 1977; McGill et al. 2006; Westoby and Wright 2006; Shipley et al. 2016) and thus could be utilised to predict the ecological performance of species under ecological adversities such as competition. How strongly correlated the chosen trait is with the plant's fitness determines how useful the trait is as a predictor.

Since competitive ability is believed to have a major influence on the assembly and distributions of species, the possibility that the competitive ability and where a species belongs in the spectrum of life history strategies could be discerned by a few key functional traits has generated great interest. Sets of plant functional traits have been

integral in the development of strategy theories which aim to predict how ecological communities respond to environmental processes such as competition (e.g. Grime 1973; Grime 1974; 1977; Tilman 1987; Westoby 1998). Further, the discovery of patterns on a global scale in the occurrence of a number of these traits e.g. through the leaf economics spectrum (Reich *et al.* 1997; Díaz *et al.* 2004; Wright *et al.* 2004), the seed size-seed number trade-offs (Geritz 1995; Rees and Westoby 1997; Geritz et al. 1999) and the wood economics spectrum (Chave *et al.* 2009) has demonstrated how a number of plant traits are interconnected and could potentially have a significant impact on whole plant performance. These findings have shown trait-based approaches as promising for achieving a general understanding of the otherwise highly complex processes behind community and ecosystem assembly and also helped identify plant traits which are likely to have functional importance.

Identifying traits which can predict competitive ability has been difficult due to a number of issues with the theoretical basis of why certain traits are predicted to be linked to competitive ability (e.g. differences in definition of competitive ability authors of the different plant strategy schemes and theoretical frameworks have used (see Goldberg 1996). It is not yet well-understood to what extent these traits influence plant fitness under competitive conditions. Kunstler *et al.'s* (2016) recent study is probably one of the most high-profile attempts at using functional traits to predict competitive ability. Their study investigated the relationship between competitive ability and plant functional traits (specific leaf area, wood density, height) in trees from plots around the world. They demonstrated a significant relationship between functional traits and competitive ability. However, the authors did not experimentally manipulate the plants but examined

the growth of trees in the presence of different densities of neighbours in natural conditions. This is a problem because natural densities may not necessarily be reliable indicators of the competition experienced by a given plant. Competition can also be intense in low density conditions depending on the availability of resources (e.g. Taylor *et al.* 1990). Competition is assessed as the performance of plants in the experimentally established absence of competitors (or a low density of competitors) relative to the performance in the presence of competitors. Using a large number of competition studies where competition has been assessed appropriately, can be a more effective test of functional traits and competitive ability. In this study we will utilise such competition studies and focus on testing whether two of these functional traits, maximum plant height and specific leaf area (SLA) are good predictors of competitive ability.

Maximum plant height

Plant size is an important part of plant strategies (Grime 1977; Westoby *et al.* 2002; Díaz *et al.* 2004; Moles and Leishman 2008; Moles *et al.* 2009). Several important conceptual models have predicted plant height to be an important strategy axis particularly under competitive conditions e.g. Grime's C-S-R triangle (Grime 1973) and the Leaf Height Seed strategy theory (Westoby 1998). Interspecific differences in height are thought to influence whole-plant performance under competition because height positively correlates with greater acquisition for key resources especially those for which there is asymmetric competition for such as light (Gaudet and Keddy 1988; Weiner 1990; Freckleton and Watkinson 2001; Westoby *et al.* 2002). In addition to this, plant height tends to be allometrically related with size traits, and these have also been associated with resource acquisition ability e.g. aboveground biomass, rooting depth, lateral spread and

leaf size, leaf mass fraction, leaf area ratio, leaf nitrogen per area, leaf mass per area and canopy area (Falster and Westoby 2003; Moles *et al.* 2009). Plant height is also correlated with a number of life history traits including life span, seed mass, number of seeds a plant can produce per year, and time to reproductive maturity (Moles and Leishman 2008; Moles *et al.* 2009). Plants which have a larger maximum plant height have been linked to slower life histories growing more slowly, reproducing later and being longer-lived (Moles and Leishman 2008; Moles *et al.* 2009). Thus, plant height is related to the fast-slow life history continuum and is likely associated with the capacity to grow and reproduce under intense competition. As a relatively easily measured plant trait, height is expected to be a particularly convenient trait to be used for predicting plant competitive ability provided it is shown to provide a good approximation of the competitive performance of a plant. Maximum height for species is a consistent value that can be easily garnered from plant floras.

Specific leaf area

Traits relevant to the acquisition and use of resources have been considered to be of key importance for predicting competitive ability (Grime 1977; Tilman 1988). Specific leaf area (SLA) is one of those traits which have been suggested to be able to fulfil this purpose. (Lambers and Poorter 1992; Reich *et al.* 1992; Cornelissen *et al.* 1996; Westoby 1998; Weiher *et al.* 1999). SLA is one of the most frequently reported functional traits of plants. SLA which is the amount of leaf area per unit of dry mass has been considered to have a strong correlation with fitness as it indicates the efficiency for light capture per unit biomass invested relative to its light use efficiency i.e. resource acquisition relative to resource conservation (Poorter *et al.* 2009). SLA has been linked to the ability of species to acquire resources as well as compete with neighbours (Hodgson et al. 1999; Weiher et al. 1999; Westoby et al. 2002; Cornelissen et al. 2003) and leaf longevity (Reich et al. 1997). Species with high SLA have also been associated with higher relative growth rates (RGR) (Garnier 1992; Lambers and Poorter 1992; Reich et al. 1992; Cornelissen et al. 1996; Lavorel and Garnier 2002). SLA plays a central role in the leaf economics spectrum which formalises the trade-off between rapid growth and resource conservation. By studying leaf functional traits that had been measured for a global range of species, Wright et al. (2004) showed that across a large range of species and climates there is a consistent pattern of correlations among leaf traits that demonstrate the trade-offs plants encounter when they produce leaves. On one end of the spectrum are fast-growing, short-lived species which produce short-lived, structurally inexpensive leaves with high SLA and high leaf nitrogen content. These leaves are predicted to be better at capturing light resources with higher photosynthetic rates and favoured in high resource environments. On the other end of the spectrum are slow-growing, long-lived species which tend to put more investment towards constructing well-defended, long-lived leaves with low SLA. Long-lived leaves are favoured in low resource environments where their longer lifespan allows for carbon capture to occur over a longer timeframe to return the investment in producing the leaves. Thus, through the leaf economics spectrum, a range of leaf traits such as long leaf lifespans, low leaf nitrogen content as well as low SLA have all been widely linked to slow, long lifespan, large body-size plant strategies which have traditionally been associated with high competitive ability by classic strategy theories (e.g. Grime 1977). The two different leaf strategies allow plants to maximise their growth under high resource conditions and minimise the loss of tissue under conditions of low resources. SLA is a trait that is potentially able to provide information on many important aspects of a plant's behaviour and performance in different environments including potentially its response to

competitors. However, specific leaf area tends to be a highly variable and plastic trait (Shipley 1995; Garnier *et al.* 1997). Recent studies have also questioned the biological significance of the correlations of the leaf economics spectrum (see Osnas *et al.* 2013, Lloyd *et al.* 2013; Poorter *et al.* 2014). Additionally, its inverse, leaf mass per unit area (LMA) has also been found to not strongly or consistently be related to other plant traits outside of the leaf economics spectrum or to broad environmental gradients (reviewed by Moles 2018) and so this calls into question its effectiveness as a predictor of competitive ability.

Decades of study of competition has yielded a large number of cases of individual species and environments whilst interest in the potential of trait-based methods has yielded a number of general rules that need testing. With the growing interest in the potential of trait-based methods in predicting plant strategies, many ecologists have measured and shared functional trait data including for SLA and maximum height for many species (e.g. the LEDA-Traitbase available online at http://www.leda-traitbase.org). As well as this, a large number of studies which manipulate the density of plants and measure their performance under these differing densities have accumulated over the years. The availability of these data presents an opportunity to evaluate the hypothesized relationships between these two functional traits and competitive ability. Competition experiments (those that experimentally manipulate neighbour density) have never been synthesised to assess the role of plant functional traits in defining competitive ability. In this chapter, we use published data on plant responses to competitive interactions and species average measurements of SLA and maximum height to evaluate whether data currently available supports the predictions of theory that SLA and plant maximum height

are good predictors of competitive ability and whether this remains consistent across species and a wide range of environments. Specifically, we will test the predictions that: 1) performance under competition will be positively correlated with maximum height and 2) performance under competition will be negatively correlated with SLA

METHODS

We assembled studies published up until June 30 2018 which manipulated neighbour density and measured the competitive performance of plants by searching in ISI Web of Science (Thompson Reuters) and Google Scholar databases with the keywords 'neighb* removal' and 'plant compet*'. These searches yielded a large number of articles, however, to ensure competition levels were different between treatment groups, only studies which measured the competitive performance (e.g. the biomass) of target plants under a neighbour removal treatment and a control treatment and reported the density of competitors (e.g. the standing crop or productivity) were included in our quantitative synthesis. In addition, only studies which provided the identity of the target species and their most common competitor species were included. When the data were presented in graphical form, we used DataThief (B. Thumers; http://www.datathief.org) to extract the data from the graphs. For each individual case we recorded the target plant biomasses and productivity measures under the neighbour removal (low competition) and control (high competition) treatments and the species names of the target plants measured and their most common neighbour species.

We then searched published articles, theses, plant databases and floras for measures of the maximum height and the SLA of each of the target species and their most common competitor species. If multiple values were found for these traits for a species, we took the average of the values. Where possible we took the SLA measurements from adult plants of relatively young (but fully expanded and hardened) leaves which were presumably photosynthetically more productive as suggested by Cornelissen *et al.* (2003). Leaf mass per area (LMA) and specific leaf mass which are both equal to 1/SLA were also searched for when no or few values of SLA of species could be found. In cases where there were multiple different species of competitor plants, we obtained maximum height and SLA values of each of these species and then calculated an average value of the height and of the SLAs across these competitor species for each data point. Cases for which this data were not available were not included in the final dataset. The details of each study, species and the data sources used to obtain SLA and maximum height measures are included in appendix A and B.

Following this we calculated a relative index of competition intensity to estimate the effect of competition on size:

 $CI = (Size_{Ic}-Size_{hc})/(Size_{Ic})$

where Size_{lc} and Size_{hc} are measures of plant size under low competition and under high competition, respectively. Size may not always be the best measure of success under competition (Aarssen and Keogh 2002) – however, this remains quite controversial and there is not yet a consensus on the best measures of plant performance under competition. We found in our literature search for this and for previous chapters, that size

was very commonly reported as a measure of performance under competition but reproduction was much more rarely reported. This limitation made it more appropriate to use size as the primary measure of performance for this study. The relative index of competition intensity is a measure of how negatively impacted a plant is by competition and so a larger value corresponds to a lower competitive ability. Other measures of competition intensity which may be more preferable (Oksanen *et al.* 2006; Weigelt and Jolliffe 2003; Rees *et al.* 2012) require data such as the size of the largest plant or maximum plant performance which were not available in the studies that we found.

We used correlation analysis in order to examine whether or not and if so, to what degree a relationship exists between Log maximum plant height and the relative index of competition intensity and between SLA and the relative index of competition intensity. We then used partial correlation analyses controlling for the density of competitors. We also repeated the analysis between Log maximum plant height and the relative index of competition intensity using partial correlation analyses to control for the Log maximum plant height of the competitor species and controlled for SLA of competitor plants by conducting a partial correlation analysis between SLA and the relative index of competition intensity. Partial correlations were important in our analysis to ensure the relationships we found were not due to the intensity of competition or the maximum height or SLA of the competing neighbour species.

We used general linear models to investigate whether the relationship between Log maximum plant height and the relative index of competition intensity, CI were affected by

any study effects as multiple species were often included in a given study. CI was included as the dependent variable, Log maximum plant height was included as a main effect, study was included as a random effect (to control for the contribution of multiple species replicates from any given study). This analysis was then repeated to investigate whether there were any study effects on the relationships between SLA and CI. CI was included as the dependent variable, SLA was included as a main effect, and study was included as random effects. We included a model with growth form for both Log maximum plant height and SLA to test whether growth form affected our results. CI was included as the dependent variable, and growth form with either Log maximum height or SLA were included as independent variables. We also attempted to add a species effect as a given species was sometimes included in multiple studies. However, since there were a large number of unique studies in the analysis, the species effect took a large number of degrees of freedom and we were unable to obtain appropriate p-values for this effect. Plant strategies in response to competition from seedlings may differ to plant strategies in response to competition from adult plants (as shown in chapter 2). In this study, tests were done on the relationship between SLA and Log maximum plant height relative to competition intensity which allowed us to control for the differences between competition with seedlings and competition with adults (studies on seedling competition will likely have lower competition intensity). All the analyses were conducted using SPSS v 25 (SAS Institute, NC, USA).

RESULTS

Maximum height

The literature survey produced a dataset of 193 cases across 24 studies and 68 species which matched all of our selection criteria for maximum height. There were more cases than species as some species were replicated within studies. Of the species included in the dataset, 59 species were perennial and 9 were annuals. We found a negative relationship between the index of competition intensity and Log maximum height, however this was not significant (r= -0.115, P= 0.155; Fig. 1a). Correlations between Log maximum height and competition intensity remained insignificant and negative after controlling for the density of competitors (partial correlation CI versus Log maximum height – df: 150, r= -0.151, P= 0.063; Fig. 1a). Correlations between Log maximum height and competition intensity were also not significant after controlling for the Log maximum height of the competitor species (partial correlation Cl versus Log maximum height – df:150, r= -0.14, P= 0.085). We were unable to obtain values for a species effect when running the general linear model to investigate the relationships between Log target height and competitive intensity. There was also no significant effect of growth form. However, including study, we found a significant study effect (P<0.001) and a significant height effect (P<0.001; Table 1) indicating increased height conferred greater competitive performance.

Specific Leaf Area

We found 151 cases across 20 studies and 50 species for SLA. Of these species, 43 were perennial and 7 were annuals. We did not find any significant relationship between SLA and the index of competition intensity (r= -0.019, P= 0.815; Fig. 1b). We also did not find any significant correlations between SLA and the index of competition intensity after controlling for the density of competitors (partial correlation CI versus SLA – df: 147, r= -

0.014, P= 0.863). There was also no significant correlation between SLA and the index of competition intensity after controlling for the SLA of the competitors (partial correlation CI versus SLA – df: 147, r= -0.087, P= 0.293). Growth form was not significant in the model for SLA. When we controlled for study (which was in effect also controlling for competition experienced in different habitats), the SLA effect was significant (P<0.001; Table 2). Higher SLA confers a slight but significant increase in performance under competition.

DISCUSSION

We did not find significant associations between competitive ability and the functional traits height and SLA. We did find significant effects of species maximum height and SLA when we included study as an effect in the general linear model. Species included in a given study experience the same competitive environment, so the effect of functional traits on performance under competition when the study effect is included could be due the density of competing plants experienced by the target plants within each study. However, controlling for the density or functional traits of competitors did not result in a significant relationship between functional traits and performance under competition (Fig 1). Alternately, our results could be due to non-causal relationships between traits. For example, species examined within a study experience the same environment and similar competitive effects from neighbours. When these environmental effects are held constant, species with the greatest capacity to acquire resources under competition will probably perform the best, and these species may also express common functional traits. However, the relationship between traits and competitive ability may not be causal. For example, long-lived species may be good at acquiring and holding resources, and may also be tall, but it is not height that confers competitive ability. In addition, species with fast root
growth under competition may be good at acquiring resources, and also express high SLA (through a predicted strong relationship between growth rate and SLA – see below), but SLA does not confer competitive ability in these sites. Across studies (and environments), the different impact of competitors and environmental stresses on the target plants can overwhelm these potentially non-biologically relevant correlations between functional traits and competitive ability in plants. We explore these ideas further below.

Maximum height

The idea that maximum height is correlated with competitive ability is consistent with the predictions and findings of previous studies (Grime 1973; 1977; Westoby 1998; Westoby *et al.* 2002; Díaz *et al.* 2004; Moles and Leishman 2008; Moles *et al.* 2009). Gaudet and Keddy (1988) who tested the relationship between a number of plant traits with competitive ability in 44 species also found a strong relationship with plant height and competitive ability. This is not that surprising because taller plants tend to need to live longer and be good at obtaining resources to reach their maximum potential size and so were likely to have been under more pressure to have evolved to deal with competition stresses.

However, the findings of this study have also demonstrated some of the limitations in using maximum height to predict competitive ability. There was only a significant correlation between Log maximum height and competition intensity when we controlled for a study effect. Including a study effect returned a significant study effect as well as a significant height effect indicating that the intensity of competition experienced by target plants is dependent on study and that some experiments were conducted in habitats where competition intensity was higher than in others. We found no significant correlation in our original analysis and when controlled for the density of the competitor plants and when we took into account the heights of competitor plants. This suggests the negative relationship was likely to have been due to the effect of the height (i.e. the competitive effect) of the competitors. A few tall species may have appeared to perform exceptionally well under competition perhaps because their competitors were very short and because resource availability for plants in the competition treatment was high. This suggests that plant height was potentially not driving the negative relationship observed between height and CI competitive ability. Instead the negative relationship was largely driven by a few instances where species which expressed high competitive ability were also tall. The short competitors in these experiments may have provided a benefit in terms of reduced transpiration, or in the accumulation of nutrients, leading to better performance of these individuals in competition treatment relative to the no competition treatment. Thus, maximum height may only be a good predictor of competitive ability (competitive response) when the maximum height of neighbours does not exceed the height of the target plants. While the relationships between height and competition intensity were generally non-significant, there was a suggestion of a negative relationship. It may be a point of potential interest for future studies to examine this further in order to establish the exact nature of this relationship.

Whilst maximum height may often correlate with competitive ability, other studies have demonstrated that height may only be a good predictor in some situations. Rosch *et al.* (1997) tested for a hierarchy in 15 pioneer species in terms of competitive effect as well as whether there was any correlation between certain traits of the species and their

competitive effect. Maximum plant height was not found to be significantly correlated with competitive ability (competitive effect). In their study across forest biomes, Kunstler et al. 2016 found that there was no correlation between maximum height and competitive effect. When they took into account trait dissimilarity between the maximum height of the target and neighbouring species, however, they found a weak but consistent decrease in the competitive suppression of tree growth. The effect of competitors in our study was weak but non-significant. The authors found no competitive effect of plant height, but plant height was a useful predictor of competitive ability when trait dissimilarity was high (i.e. when tall plants competed against short plants). Height is therefore not particularly useful to predict competitive ability in the absence of knowing the traits the plant is competing against. Funk and Wolf (2016) found that height was not a good predictor of competitive outcome with perennial grass species *Festuca perennis* as several shorter native forb species performed relatively well in competition with this species. The authors concluded that their findings were due to the fact that the plants were mainly competing for belowground resources in the top soil layer as the best competitors had shallow roots and high specific root length. This suggests that the correlation of height and competitive ability could be affected by other factors such as what resources were being competed for and the spatial distribution of these resources.

However, there may be differences between findings using height and those using maximum height as maximum height may be more tightly linked to a plant's life history strategy than a measure of height which can be affected by many different factors in the plants' lives. The link between maximum height and a plant's life strategy may mean that competitive species simply happen to be large. Although we found a significant correlation

between height and the competition experienced by plants, caution must be taken when interpreting these results as they were highly limited to perennial species. Plants with relatively long life spans are likely to have effective strategies to acquire resources in the presence of competitors, and tolerate suppression from competitors (Huston and Smith 1987). It is likely that these longer lived species are both better competitors and larger, but large size is not itself related to competitive ability as the mixed findings of studies on height also suggest. Maximum height is potentially a good predictor of competitive ability of the plants in long-lived species, but it remains to be seen whether maximum height is a good predictor of competitive ability in short-lived species.

Specific Leaf Area

Our finding that SLA was not linked (or weakly linked) to competitive performance was in contrast to previous predictions (Hodgson *et al.* 1999; Weiher *et al.* 1999; Westoby *et al.* 2002; Cornelissen *et al.* 2003). Kunstler *et al.* 2016 found that low SLA was correlated with a stronger competitive effect on neighbours but not better tolerance of competition from neighbours. There are a number of reasons why we may not have been able to find evidence of this predicted strong correlation between SLA and performance under competition.

SLA highly plastic and variable

The findings of no consistent correlation between SLA and competitive ability are likely due to SLA being a trait which is connected to a wide range of different factors in a plant's life. Past studies have found SLA to be a relatively poor indicator of life history strategy

due primarily to the plasticity of SLA. For example, in their study of 769 species, Wilson et al. (1999) found that because SLA varied with differences in leaf thickness, it was too variable between replicates to be a good predictor of plant strategy. Abiotic factors can also greatly influence SLA values. For instance, SLA varies strongly with light availability (Poorter et al. 2009; Niinemets et al. 2015) and can even dramatically increase within hours following a reduction in irradiance (Shipley 2000). SLA can also vary in response to precipitation (Schulze et al. 2006; Ordoñez et al. 2009) and altitude (Milla and Reich 2011). The high plasticity means that it is very difficult to get a good single measure of SLA for a species and any relationship between SLA and competitive ability would be highly variable. This is a problem for using SLA as a predictor of competitive ability across communities. Trait-based studies typically rely on mean trait values taken from a small sample of individuals from a species. Siefert et al. (2015) found in a global meta-analysis that intraspecific trait variation was relatively high (25% or more of the total community trait variation) for a range of chemical and morphological traits related to the leaf economics spectrum including for SLA. Functional traits like SLA can vary at the individual level and this variation can influence the interactions among organisms and between organisms and their environment. This suggests that mean trait values which trait-based approaches use may not be able to capture the full extent of SLA variation within and among most plant communities worldwide. Thus, one of the potential reasons why we did not find a correlation between SLA and the competitive performance displayed by the plants in the experiment was because SLA is so plastic and able to be changed by so many different environmental factors independent of competition levels that it is not a reliable indicator of competitive ability unless we take individual measurements of each plant at the site. This value would also be likely to continue to change throughout the life of the plant in response to environmental changes the plant experiences making it difficult to obtain a

meaningful value. Bonser *et al.* (2010) demonstrated that SLA variability in a short-lived annual plant (*Arabidopsis*) is not directly related to fitness. Rather SLA impacts other traits like size at reproduction which does relate to fitness. This suggests that functional traits are not independent measures of performance (e.g. competitive ability); but instead function within individuals to determine performance.

Inconsistent relationships between traits in the leaf economics spectrum

Low SLA was originally linked to high competitive ability through the leaf economics spectrum which suggested it was linked to slow, long lifespan, large maximum body-size plant strategies. However, the leaf economics spectrum has also been challenged in recent years. As well as high plasticity and variability in SLA, there has also been found to be high plasticity in the relationships between the traits of the leaf economics spectrum. For example, the leaf economics spectrum relationships including for SLA/LMA have been found to vary depending on the growth forms of plants in communities (Wright et al. 2004; Funk and Cornwell 2013). There is evidence that the correlations between traits predicted by the leaf economics spectrum exist between closely related species (e.g. Dunbar-Co et al. 2009; Milla and Reich 2011). However, little other evidence has been found to support the existence of the leaf economics spectrum across broad environmental gradients and larger scales (reviewed by Moles 2018). Wright and Sutton-Grier (2012) conducted greenhouse experiments to test the effects of varying water table depth and nitrogen availability on leaf-level trait values and found apart from a significant relationship between SLA and photosynthetic rate under some of the treatments, there was little support for the other relationships predicted by the leaf economics spectrum.

Relative growth rate (RGR) is a key variable in influential conceptual models on plant strategies (Grime 1979a; Tilman 1988; Westoby 1998) and SLA was thought to be useful to infer potential growth rates (Westoby 1998; Wright et al. 2004). Whilst some experimental studies have found strong correlations between RGR and SLA (Garnier 1992; Lambers and Poorter 1992; Reich et al. 1992; Lavorel and Garnier 2002), other studies have reported weak correlations. In their large meta-analysis across 614 species about whether SLA and a few other traits influence the relative growth rate (RGR) of a species, Shipley (2006) found that the importance of SLA in determining the RGR increased with decreasing daily quantum input in experiments using herbaceous species but that this did not occur in the experiments using woody species. Although SLA has been connected to RGR by the models proposed by Tilman (1988) and Westoby (1998) and also the leaf economics spectrum (Wright et al. 2004), Shipley (2006) found there was no relationship between SLA and RGR when comparing across species and across environments and concludes SLA is not a very good general indicator of interspecific variation in RGR across environments. RGR is an important component of the reasoning behind the predicted links between SLA and competitive ability. These varied findings suggest a weaker relationship in how well SLA can be used to predict competitive ability between species of different growth forms and life histories and that the correlation between SLA and other plant traits is highly dependent on environmental factors. This suggests the predictive ability of SLA of competitive ability may be highly limited to certain growth forms and environments.

Predicting competitive ability

Criticism of traditional species-focussed methods used in community ecology have included that their findings cannot be scaled up to community or ecosystem levels and that they neglect the fact that communities occur on different gradients because they focus on narrow groups of species and environments (McGill *et al.* 2006). However, there are a number of issues that need to be resolved in competition theory before we are able to scale up to these levels across communities and before we can effectively test the rules we establish for predicting competitive ability.

Firstly there still remains much debate over whether competitive hierarchies remain consistent across environmental gradients or not. Whether or not competitive ability is consistent among environments or whether they change with environments has remained a contentious issue in competition theory. Grime (1977) predicts that competitive hierarchies remain consistent between environments. However, Tilman (1988) has argued that trade-offs in competitive ability for different resources underlies the patterns of plant distribution. This is a controversial point in competition theory which has not yet been resolved sometimes resulting in different opinions on what particular plant traits confer a competitive advantage to species (Grime 1973; Newman 1973; Grime 1977; 1979a; 1979b; Tilman 1988; Grace 1990; Berendse et al. 1992; Grace 1995; Goldberg and Novoplansky 1997; Craine 2005; 2007; Grime 2007; Tilman 2007). The differing theories also predict differing consequences of low competitive ability of death or no reproduction or reduced growth (Goldberg 1996).

Connected with this issue, there has been discussion about whether competitive hierarchies differ depending on which of the two components of competitive ability of

competitive effect (the ability to depress growth and reproduction of neighbours) and competitive response (the ability to withstand the negative effects of neighbours) are measured (Goldberg 1990; 1996). This study was limited to the effects of traits on competitive response (how the traits impacted the performance of plants under competition) though we did try to control for competitive effect of neighbouring plants (by controlling for size of neighbours). Goldberg (1996) found through a literature synthesis that both competitive response and competitive effect are generally consistent regardless of the identity of competing species suggesting there is potential for finding relationships with traits at least within environments. Among environments, however, the relationship between competitive effect and competitive response are much more variable with the two components only being consistent in half of the cases studied. This suggests that competitive hierarchies are not likely to remain the same under different conditions (even though trait hierarchies may remain the same e.g. as Garnier et al. 2001 has shown in SLA). It is probably for this reason that it has been difficult to find evidence for the general rules predicted by the traditional strategy theories and other trait-based methods across species, environments and ecosystems. It is possible there may be different findings to those found in this study if we were able to examine competitive effects of the plants too. However, studies have rarely measured both competitive effect and competitive response and so currently existing theory and empirical work are not sufficient to determine what conditions competitive hierarchies are likely to be consistent or not under.

Competitive performance can vary depending on what is measured as fitness: growth, survival or reproduction. Functional traits which have been associated with competitive ability have mainly been those which influence growth or acquisition of resources for

growth (e.g. Grime 1977). Whilst the majority of existing literature has focussed on measures of size or other proxy measures of the ability to acquire resources as well as deny resources to other plants, some studies are finding reproduction to be a better indicator of the performance under competition (Neytcheva and Aarssen 2008; Bonser and Ladd 2011) and abundances in communities much better approximated by the ability to reproduce under competition rather than the ability to obtain resources over other plants (Tracey and Aarssen 2011; Tracey and Aarssen, in press). Obtaining more resources is predicted to allow greater competitive ability and thus traits which have been associated with greater competitive ability have mostly been those which are thought to influence the acquisition of resources or be reflective of the potential acquisition of resources of the species. Abundances should be a good indication of those which are able to perform well. However, evidence is increasingly indicating that species which are able to produce more offspring (which are often smaller species which have lower minimum sizes before reproduction can occur) rather than those with traits which would lead to greater resource acquisition are more abundant in environments (Tracey and Aarssen 2011). This suggests that resource acquisition may not be the only important strategy under competition and one of reproduction and high fecundity under competition may be more effective. Species with faster life-histories which have traditionally been associated with poorer ability to acquire resources and thus low competitive ability may have higher competitive performance than those with slower life-histories if measured by reproduction due to their ability to reproduce earlier in their lives (Thomas 1996; Davies and Ashton 1999; Tracey and Aarssen 2011; Nishizawa and Aarssen 2014; Tracey and Aarssen 2014). Competitive ability may differ under different conditions e.g. successional stage of the environment (Huston and Smith 1987) as well as with the timing of establishment of the plant and its competitors (Gioria et al. 2018) and the intensity of competition. There is no trait that

would be able to confer competitive ability under all conditions which is a problem for using functional traits to define competitive ability. This may also help to explain the observed relationship between functional traits and competitive ability within studies (in common environments) but not across studies and environments.

One of the fundamental goals of ecology and the central reason behind the interest in understanding links between plant traits and competitive ability is to be able to predict species abundances (Shipley et al. 2016; Lavorel and Garnier 2002). A study examining the variation in 11 functional traits including SLA and height amongst others found that on large scales there was no relationship between these two traits and relative abundance, however, on smaller more local scales a number of the functional traits including SLA and height were good predictors of relative abundance (Cornwell and Ackerly 2010). Such findings highlight that whilst functional traits can help determine the performance of plants under competitive conditions, they are not measures of competitive ability itself and so may not be good predictors of competitive ability across environments where the plants are affected by differing environmental forces. Both large scale surveys and smaller detailed experiments can reveal important information. At this stage where it is not possible to gather enough actual competitive measurements on every species and species interaction which occurs in natural communities, trait-based ecology approaches can be important to make predictions across community and ecosystem levels. However, smaller detailed experiments will still be required to understand the relationships on more local scales.

Conclusion

This study is the first to assemble data from competition studies to test whether functional traits can define competitive ability in plants. We found neither maximum height nor SLA were particularly good predictors of performance under competition. Our findings illustrated how some functional traits (such as SLA) may be poor predictors of competitive performance across a range of environments/systems due to their high variability and stronger affiliation with other environmental factors than with the life history strategies of the plants. On the other hand, functional traits (such as maximum height) which are tightly linked to the life history strategy of plants can strongly influence the ecological performance of species although they may not be good predictors of competitive performance across all environmental conditions. Trait-based approaches can have the potential to reveal general predictive relationships that are difficult to identify through species-based approaches. However, it is becoming apparent that the trait-based approach will not be able to bring us closer to the goal of being able to predict species abundances in relation to competition unless changes are made to the ecological theory that underlies current work. A major problem with testing the rules predicted by theory of whether certain functional traits are related to competitive ability is that there is currently little consensus about the definition of competitive ability and what we need to measure and how we should be measuring it. The findings from this thesis suggest a potential way forward in research on competition should utilise the evolutionary competitive ability approach suggested by Tracey and Aarssen (Tracey and Aarssen 2014; Tracey and Aarssen, in press) where the most important aspect of competitive ability is the capacity to reproduce under competition rather than focussing on measurements of size as

measurements of performance under competition. In order to achieve this, future studies on competitive ability will need to take into consideration reproductive performance in addition to size and growth performance under competition. We will need to improve the foundational theoretical basis of our understanding of competition if we want to be able to make guided predictions as well as effectively test these predictions to determine under what specific conditions specific traits confer competitive ability.



Fig. 1 Correlation analysis between relative index of competition intensity where competitive performance was measured as the effect of competition on size and **a**) Log maximum height and **b**) Specific leaf area (mm²/mg).

Table 1. General linear model testing the impact of Log maximum height on competition

intensity with study included as a random effect.

	Competition intensity						
Source of variation	Df	MS	F	Р			
Study	15	0.688	7.199	<0.001			
Log max. height	17	0.81	8.474	<0.001			
Error	116	0.096					

Table 2. General linear model testing the impact of SLA on competition intensity with study

included as a random effect.

	Competition intensity					
Source of variation	Df	MS	F	Ρ		
Study	5	0.138	1.989	0.087		
Error	95	0.07				
SLA	35	0.521	7.488	<0.001		
Error	95	0.07				

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Appendix A: The list of surveyed studies and their details.

Maximum Height

			_		Primary
			Life		measure of
Reference	Target Species	Family	History	Competitor species	performance
Bonser and				Poa compressa, Lotus corniculatus, Daucus carota,	Aboveground
Reader 1995	Poa compressa	Poaceae	Р	Panicum capillare	biomass
Bonser and				Poa compressa, Echium vulgare, Medicago lupulina,	Aboveground
Reader 1995	Poa compressa	Poaceae	Р	Potentilla recta	biomass
Bonser and				Hieracium floribundum, Poa compressa, Medicago	Aboveground
Reader 1995	Poa compressa	Poaceae	Р	lupulina, Poa pratensis	biomass
Bonser and	_	_	_	Poa pratensis, Hieracium pratense, Satureja	Aboveground
Reader 1995	Poa compressa	Poaceae	Р	vulgaris, Solidago canadensis	biomass
Bonser and					Aboveground
Reader 1995	Poa compressa	Poaceae	Р	Bromus inermis, Poa pratensis	biomass
Denserand				Dhalania anuadina ang Fauinatum any ang Ciraium	A have are used
Bonser and		D		Phalaris arunainacea, Equisetum arvense, Cirsium	Aboveground
Reader 1995	Poa compressa	Роасеае	Р	arvense, Solanum aulcamara	biomass
Bonser and				Solidago canadensis. Pog pratensis	Aboveground
Reader 1995	Pog compressa	Poaceae	P	Symphyotrichum novae-analiae Tinaria vulaaris	hiomass
	i ou compressu			Symphysemenum novae angliae, Emana Valgaris	510111035
Bonser and				Symphyotrichum puniceum, Glyceria striata,	Aboveground
Reader 1995	Poa compressa	Poaceae	Р	Eupatorium maculatum, Clematis virginiana	biomass
	-			-	

Wilson 1993 Wilson 1993 Wilson 1993 Wilson 1993	Bouteloua gracilis Bouteloua gracilis Populus deltoides Populus deltoides	Poaceae Poaceae Salicaceae Salicaceae	P P P P	Stipa comata, Bouteloua gracilis Stipa comata, Bouteloua gracilis Stipa comata, Bouteloua gracilis Populus tremuloides	Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass
1986	Stipa neomexicana	Poaceae	Р	Stipa neomexicana	Total growth
Gurevitch 1986	Stipa neomexicana	Poaceae	Ρ	Bouteloua gracilis, Bouteloua curtipendula, Bouteloua chondrosioides, Bouteloua eriopoda, Hilaria belangeri, Aristida glauca	Total growth
Gurevitch 1986 Gurevitch 1986	Stipa neomexicana Aristida glauca	Poaceae Poaceae	P P	Bouteloua gracilis, Bouteloua curtipendula, Bouteloua chondrosioides, Bouteloua eriopoda, Hilaria belangeri, Aristida glauca Stipa neomexicana	Total growth Total growth
Gurevitch 1986	Aristida glauca	Роасеае	Ρ	Bouteloua gracilis, Bouteloua curtipendula, Bouteloua chondrosioides, Bouteloua eriopoda, Hilaria belangeri, Aristida glauca	Total growth

Total growth

Aboveground biomass

Aboveground biomass

Aboveground biomass

Aboveground

Aboveground biomass

Aboveground biomass

Aboveground biomass

Aboveground biomass

Aboveground biomass Aboveground biomass Aboveground

biomass

biomass

Gurevitch 1986	Aristida glauca	Poaceae	Р	Bouteloua chondrosioides, Bouteloua eriopoda, Hilaria belangeri, Aristida glauca
Belcher <i>et al.</i> 1995	Trichostema brachiatum	Lamiaceae	A	Danthonia spicata, Senecio pauperculus, Carex crawei, Hieracium piloselloides
Gurevitch and Unnasch 1989	Achillea millefolium	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Cirsium discolor	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Chrysanthemum leucanthemum	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Hieracium pratense	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Linaria vulgaris	Plantaginaceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Oxalis europaea	Oxalidaceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Poa annua	Poaceae	А	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Solidago altissima	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Solidago rugosa	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa
Gurevitch and Unnasch 1989	Taraxacum officinale	Asteraceae	Р	– Dactylis glomerata, Solidago altissima, Solidago rugosa

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Bouteloua gracilis, Bouteloua curtipendula,

Gurevitch and Unnasch 1989	Trifolium agrarium	Fabaceae	A	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Vicia cracca	Fabaceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Whigham 1984	Ipomoea hederacea	Convolvulaceae	A	Erigeron canadensis, Solanum carolinense	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Роасеае	Р	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass
Wilson and Tilman 1991	Agropyron repens	Poaceae	Р	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass

Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Agropyron repens	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Agropyron repens	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Anemone speciosa	Ranunculaceae	Ρ	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass

Onipchenko <i>et</i> al. 2009	Campanula tridentata	Campanulaceae	Р	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Antennaria dioica	Asteraceae	Р	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Trifolium polyphyllum	Fabaceae	Ρ	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Carex ssp.	Cyperaceae	Ρ	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Festuca ovina	Poaceae	Ρ	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Scorzonera cana	Asteraceae	Ρ	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Festuca varia	Poaceae	Р	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Nardus stricta	Poaceae	Р	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Leontodon hispidus	Asteraceae	Р	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass

Onipchenko <i>et</i> al. 2009	Geranium gymnocaulon	Geraniaceae	Ρ	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Hedysarum caucasicum	Fabaceae	Ρ	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Matricaria caucasica	Asteraceae	Ρ	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Phleum alpinum	Poaceae	Ρ	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Minuartia aizoides	Caryophyllaceae	Ρ	Minuartia aizoides, Taraxacum stevenii, Sibbaldia procumbens, Gnaphalium supinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Sibbaldia procumbens	Rosaceae	Ρ	Minuartia aizoides, Taraxacum stevenii, Sibbaldia procumbens, Gnaphalium supinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Gnaphalium supinum	Asteraceae	Р	Minuartia aizoides, Taraxacum stevenii, Sibbaldia procumbens, Gnaphalium supinum	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus	Aboveground biomass

Foster 1999	Andropogon gerardii	Poaceae	Р	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Agropyron repens, Achillea millefolium, Bromus inermis, Melilotus alba	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Bromus inermis, Poa pratensis, Achillea millefolium, Achillea millefolium, Agropyron repens	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Bromus inermis, Agropyron repens, Poa pratensis, Daucus carota	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Agropyron repens, Arrhenatherum elatius, Silene alba, Polygonum scandens	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Bromus inermis, Poa pratensis, Solidago canadensis, Agropyron repens	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Bromus inermis, Poa pratensis, Agropyron repens, Barbarea vulgaris	Aboveground biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Ρ	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis	Aboveground biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Р	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus	Aboveground biomass

	Foster 1999	Schizachyrium scoparium	Poaceae	Р	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Р	Agropyron repens, Achillea millefolium, Bromus inermis, Melilotus alba	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Ρ	Bromus inermis, Poa pratensis, Achillea millefolium, Achillea millefolium, Agropyron repens	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Р	Bromus inermis, Agropyron repens, Poa pratensis, Daucus carota	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Ρ	Agropyron repens, Arrhenatherum elatius, Silene alba, Polygonum scandens	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Р	Bromus inermis, Poa pratensis, Solidago canadensis, Agropyron repens	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Ρ	Bromus inermis, Poa pratensis, Agropyron repens, Barbarea vulgaris	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis, Hieracium aurantiacum	Aboveground biomass
239	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus, Hieracium aurantiacum	Aboveground biomass

	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium, Centaurea maculosa	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Elytrigia repens, Achillea millefolium, Bromus inermis, Melilotus alba, Oxalis stricta	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Р	Bromus inermis, Elytrigia repens, Poa pratensis, Daucus carota, Dactylis glomerata	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Р	Elytrigia repens, Arrhenatherum elatius, Silene alba, Polygonum scandens, Poa pratensis	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Р	Elytrigia repens, Arrhenatherum elatius, Silene alba, Polygonum scandens, Poa pratensis	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
240	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass

	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Роасеае	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
	Wilson 2007	Bouteloua gracilis	Poaceae	Ρ	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
241	Wilson 2007	Bouteloua gracilis	Poaceae	Р	Stipa comata, Carex spp., Bouteloua gracilis, Agropyron spp., Koeleria macrantha, Poa spp., Selaginella densa	Aboveground biomass
Wilson 1994	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Mosses and lichens, Poa pratensis, Polygonum convolvulus	Total biomass	
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Wilson 1994	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Poa pratensis, Setaria viridis, Polygonum convolvulus, Elytrigia repens	Total biomass	
Wilson 1994	Setaria viridis	Poaceae	A	Schizachyrium scoparium, Mosses and lichens, Poa pratensis, Polygonum convolvulus	Total biomass	
Wilson 1994	Setaria viridis	Poaceae	A	Schizachyrium scoparium, Poa pratensis, Setaria viridis, Polygonum convolvulus, Elytrigia repens	Total biomass	
Ladd and Facelli 2007	Eucalyptus microcarpa	Myrtaceae	Ρ	Avena barbata, Pennisetum clandestinum, Briza maxima, Vulpia myuros, Olea europa	Leaf number	
Ladd and Facelli 2007	Eucalyptus camaldulensis	Myrtaceae	Р	Avena barbata, Pennisetum clandestinum, Briza maxima, Vulpia myuros, Olea europa	Leaf number	
Kuijper <i>et al.</i> 2004	Elymus athericus	Poaceae	Р	Festuca rubra, Limonium vulgare, Salicornia europaea	Aboveground biomass	
Kuijper <i>et al.</i> 2004	Elymus athericus	Poaceae	Р	Festuca rubra, Limonium vulgare, Armeria maritima	Aboveground biomass	
Kuijper <i>et al.</i> 2004	Elymus athericus	Роасеае	Р	Festuca rubra, Limonium vulgare, Plantago maritima	Aboveground biomass	
Kuijper <i>et al.</i> 2004	Elymus athericus	Poaceae	Р	Festuca rubra, Limonium vulgare, Armeria maritima	Aboveground biomass	

Treberg and Turkington 2010	Anemone parviflora	Ranunculaceae	Ρ	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass
Treberg and Turkington 2010	Festuca altaica	Poaceae	Ρ	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass
Treberg and Turkington 2010	Mertensia paniculata	Boraginaceae	Ρ	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass

				parviflora, Epilobium angustifolium, Festuca altaica, Luninus arcticus, Mertensia paniculata var	
Treberg and				paniculata, Senecio lugens, Solidago multiradiata,	
Turkington				Arctostaphylos uva-ursi, Linnaea borealis ssp.	Aboveground
2010	Senecio lugens	Asteraceae	Р	americana	biomass
Gerdol <i>et al.</i>					Aboveground
2000	Vaccinium myrtillus	Ericaceae	Р	Vaccinium myrtillus	biomass
Gerdol <i>et al.</i>					Aboveground
2000	Vaccinium uliginosum	Ericaceae	Р	Vaccinium myrtillus	biomass
Gerdol <i>et al.</i>			_		Aboveground
2000	Empetrum hermaphroditum	Ericaceae	Р	Empetrum hermaphroditum	biomass
Gerdol <i>et al.</i>		F		E a carta da la carta da carta da carta	Aboveground
2000	vaccinium uliginosum	Ericaceae	Р	Empetrum nermaphroaitum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Alchemilla pentaphyllea	Rosaceae	Р	Gnaphalium supinum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Poa alpina	Poaceae	Р	Gnaphalium supinum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Ligusticum mutellina	Apiaceae	Р	Gnaphalium supinum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Polygonum viviparum	Polygonaceae	Р	Gnaphalium supinum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Cardamine bellidifolia subsp. alpina	Brassicaceae	Р	Gnaphalium supinum	biomass
Schob <i>et al.</i>				Alchemilla pentaphyllea, Salix herbacea,	Aboveground
2010	Veronica alpina	Plantaginaceae	Р	Gnaphalium supinum	biomass

Achillea millefolium ssp. Borealis, Anemone

Wilson and Tilman 1993	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium, Cyperus spp.	Growth rate
Wilson and	<i>,</i> , , ,			Mollugo verticillata, Panicum capillare, Setaria	
Tilman 1993	Schizachyrium scoparium	Poaceae	Р	viridis	Growth rate
Wilson and					
Tilman 1993	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium, Agropyron repens	Growth rate
Wilson and Tilman 1993	Schizachvrium scoparium	Poaceae	P	Panicum capillare. Setaria viridis	Growth rate
1111011 1999	Schizachynan scopanan	rouccuc	·		Growthrate
Foster and				Centaurea maculosa, Poa compressa, Achillea	Aboveground
Gross 1997	Andropogon gerardii	Poaceae	Р	millefolium, Aster pilosus, Rubus allegheniensis	biomass
Foster and				Agropyron repens, Achillea millefolium, Bromus	Aboveground
Gross 1997	Andropogon gerardii	Poaceae	Р	inermis	biomass
Festered					A la a
FUCTOR 200				μ	<u>N N N N N N N N N N N N N N N N N N N </u>
Gross 1997	Andronogon gerardii	Poaceae	р	Aaronvron renens	hiomass
Gross 1997 Foster and	Andropogon gerardii	Poaceae	Ρ	Agropyron repens	biomass Aboveground
Gross 1997 Foster and Gross 1997	Andropogon gerardii Andropogon gerardii	Poaceae Poaceae	P P	Agropyron repens Bromus inermis, Poa pratensis	Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and	Andropogon gerardii Andropogon gerardii	Poaceae Poaceae	P P	Agropyron repens Bromus inermis, Poa pratensis	Aboveground biomass Aboveground biomass Aboveground
Gross 1997 Foster and Gross 1997 Foster and Gross 1997	Andropogon gerardii Andropogon gerardii Andropogon gerardii	Poaceae Poaceae Poaceae	P P P	Agropyron repens, Arrhenatherum elatius	Aboveground biomass Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and Gross 1997	Andropogon gerardii Andropogon gerardii Andropogon gerardii	Poaceae Poaceae Poaceae	P P P	Agropyron repens Agropyron repens Agropyron repens, Arrhenatherum elatius	Aboveground biomass Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and Gross 1997	Andropogon gerardii Andropogon gerardii Andropogon gerardii	Poaceae Poaceae Poaceae	P P P	Agropyron repens Bromus inermis, Poa pratensis Bromus inermis, Poa pratensis Agropyron repens, Arrhenatherum elatius Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithonoda, Carex	Aboveground biomass Aboveground biomass Aboveground
Gross 1997 Foster and Gross 1997 Foster and Gross 1997 Sammul <i>et al.</i> 2000	Andropogon gerardii Andropogon gerardii Andropogon gerardii Anthoxanthum odoratum	Poaceae Poaceae Poaceae Poaceae	P P P	Agropyron repens Bromus inermis, Poa pratensis, Achinea minejolium, Agropyron repens Agropyron repens, Arrhenatherum elatius Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, Carex flacca. Convallaria maialis	Aboveground biomass Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and Gross 1997 Sammul <i>et al.</i> 2000	Andropogon gerardii Andropogon gerardii Andropogon gerardii Anthoxanthum odoratum	Poaceae Poaceae Poaceae	P P P	Agropyron repens Bromus inermis, Poa pratensis, Achinea minejolium, Agropyron repens Agropyron repens, Arrhenatherum elatius Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, Carex flacca, Convallaria majalis	Aboveground biomass Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and Gross 1997 Sammul <i>et al.</i> 2000	Andropogon gerardii Andropogon gerardii Andropogon gerardii Anthoxanthum odoratum	Poaceae Poaceae Poaceae	P P P	Agropyron repens Bromus inermis, Poa pratensis, Achinea minejolium, Agropyron repens Agropyron repens, Arrhenatherum elatius Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, Carex flacca, Convallaria majalis Hepatica nobilis, Brachypodium pinnatum,	Aboveground biomass Aboveground biomass Aboveground biomass
Gross 1997 Foster and Gross 1997 Foster and Gross 1997 Sammul <i>et al.</i> 2000	Andropogon gerardii Andropogon gerardii Andropogon gerardii Anthoxanthum odoratum	Poaceae Poaceae Poaceae	P P P	 Bromus mermis, Pou pratensis, Achinea minejolium, Agropyron repens Bromus inermis, Poa pratensis Agropyron repens, Arrhenatherum elatius Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, Carex flacca, Convallaria majalis Hepatica nobilis, Brachypodium pinnatum, Convallaria majalis, Plantago lanceolata, Primula 	Aboveground biomass Aboveground biomass Aboveground biomass Aboveground biomass

Sammul <i>et al</i> . 2000	Anthoxanthum odoratum	Poaceae	Р	Dactylis glomerata, Festuca rubra, Helictotrichon pratense, Brachypodium pinnatum, Primula veris, Carlina vulgaris, Carex tomentosa	Aboveground biomass
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Ρ	Salix herbacea, Salix polaris, Vaccinium myrtillus	Aboveground biomass
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Ρ	Festuca rubra, Vaccinium myrtillus, Juniperus communis, Betula nana, Empetrum nigrum	Aboveground biomass
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Р	Vaccinium myrtillus, Trollius europaeus, Festuca rubra, Trientalis europaea	Aboveground biomass
Sammul <i>et al</i> . 2000	Anthoxanthum odoratum	Poaceae	Ρ	Trollius europaeus, Vaccinium vitis-idea, Cirsium heterophyllum, Epilobium angustifolium	Aboveground biomass
Sammul <i>et al</i> . 2000	Anthoxanthum odoratum	Poaceae	Р	Cornus suecica, Solidago virgaurea, Trientalis europaea, Deschampsia flexuosa	Aboveground biomass
Dormann <i>et</i> <i>al.</i> 2000 Dormann <i>et</i>	Artemisia maritima	Asteraceae	Ρ	Limonium vulgare, Puccinellia maritima, Festuca rubra	Total biomass
al. 2000	Artemisia maritima	Asteraceae	Р	Artemisia maritima, Festuca rubra	Total biomass
Dormann <i>et</i> <i>al.</i> 2000	Artemisia maritima	Asteraceae	Р	Artemisia maritima, Festuca rubra, Limonium vulgare	Total biomass
Dormann <i>et</i> <i>al.</i> 2000	Atriplex portulacoides	Chenopodiaceae	Р	Limonium vulgare, Puccinellia maritima, Festuca rubra	Total biomass
Dormann et	Atriplex portulacoides	Chenopodiaceae	Р	Artemisia maritima, Festuca rubra	Total biomass

al. 2000

Dormann et al. 2000	Atriplex portulacoides	Chenopodiaceae	Р	Artemisia maritima, Festuca rubra, Limonium vulgare	Total biomass
Dormann <i>et</i> <i>al.</i> 2000 Dormann <i>et</i>	Plantago maritima	Plantaginaceae	Ρ	Limonium vulgare, Puccinellia maritima, Festuca rubra	Total biomass
al. 2000	Plantago maritima	Plantaginaceae	Р	Artemisia maritima, Festuca rubra	Total biomass
Dormann <i>et</i> al. 2000	Plantago maritima	Plantaginaceae	Ρ	Artemisia maritima, Festuca rubra, Limonium vulgare	Total biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Are functional traits predictive of competitive ability?

Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Panicum capillare	Роасеае	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	А	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Knoop and Walker 1985	Burkea africana	Fabaceae	Р	Burkea africana, Ochna pulchra, Terminalia sericea, Agrostis pallens, Digitaria eriantha	Shoot growth

Knoop and				Burkea africana, Ochna pulchra, Terminalia sericea,	
Walker 1985	Ochna pulchra	Ochnaceae	Р	Agrostis pallens, Digitaria eriantha	Shoot growth
Knoop and Walker 1985	Burkea africana	Fabaceae	Ρ	Burkea africana, Ochna pulchra, Terminalia sericea, Agrostis pallens, Digitaria eriantha	Shoot growth
Knoop and Walker 1985	Ochna pulchra	Ochnaceae	Ρ	Burkea africana, Ochna pulchra, Terminalia sericea, Agrostis pallens, Digitaria eriantha	Shoot growth
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Total biomass
Van der Wal <i>et al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Total biomass

Specific Leaf Area

Reference	Target Species	Family	Life History	Competitor species	Primary measure of performance
Bonser and Reader 1995	Poa compressa	Poaceae	P	Poa compressa, Lotus corniculatus, Daucus carota, Panicum capillare	Aboveground biomass
Bonser and Reader 1995	Poa compressa	Poaceae	Р	Poa compressa, Echium vulgare, Medicago lupulina, Potentilla recta	Aboveground biomass
Bonser and Reader 1995	Poa compressa	Poaceae	Р	Hieracium floribundum, Poa compressa, Medicago lupulina, Poa pratensis	Aboveground biomass
Bonser and Reader 1995 Bonser and	Poa compressa	Poaceae	Ρ	Poa pratensis, Hieracium pratense, Satureja vulgaris, Solidago canadensis	Aboveground biomass Aboveground
Reader 1995	Poa compressa	Poaceae	Р	Bromus inermis, Poa pratensis	biomass
Bonser and Reader 1995	Poa compressa	Poaceae	Ρ	Phalaris arundinacea, Equisetum arvense, Cirsium arvense, Solanum dulcamara	Aboveground biomass
Bonser and Reader 1995	Poa compressa	Poaceae	Ρ	Solidago canadensis, Poa pratensis, Symphyotrichum novae- angliae, Linaria vulgaris	Aboveground biomass Aboveground
Wilson 1993	Populus deltoides	Salicaceae	Р	Stipa comata, Bouteloua gracilis	biomass Aboveground
Wilson 1993	Populus deltoides	Salicaceae	Р	Populus tremuloides	biomass
Gurevitch 1986	Stipa neomexicana	Poaceae	Р	Stipa neomexicana	Total biomass
Gurevitch and Unnasch 1989	Achillea millefolium	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass

Gurevitch and Unnasch 1989	Chrysanthemum Ieucanthemum	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Hieracium pratense	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Linaria vulgaris	Plantaginaceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Oxalis europaea	Oxalidaceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Poa annua	Poaceae	A	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Solidago altissima	Asteraceae	Ρ	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Solidago rugosa	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Taraxacum officinale	Asteraceae	Р	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Trifolium agrarium	Fabaceae	A	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Gurevitch and Unnasch 1989	Vicia cracca	Fabaceae	Ρ	Dactylis glomerata, Solidago altissima, Solidago rugosa	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Р	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass

Wilson and Tilman 1991	Agropyron repens	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp.	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Agropyron repens	Poaceae	Р	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Poa pratensis	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Wilson and Tilman 1991	Agropyron repens	Poaceae	Ρ	Schizachyrium scoparium, Solidago rigida, Ambrosia artemisiifolia, Poa pratensis, Carex sp., Agropyron repens	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Antennaria dioica	Asteraceae	Ρ	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Carex ssp.	Cyperaceae	Р	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass

Onipchenko <i>et</i> <i>al.</i> 2009	Festuca ovina	Poaceae	Р	Anemone speciosa, Campanula tridentata, Antennaria dioica, Trifolium polyphyllum, Carex spp., Festuca ovina	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Nardus stricta	Poaceae	Р	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Leontodon hispidus	Asteraceae	Ρ	Scorzonera cana, Festuca varia, Nardus stricta, Leontodon hispidus	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Geranium gymnocaulon	Geraniaceae	Ρ	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> al. 2009	Phleum alpinum	Poaceae	Р	Geranium gymnocaulon, Hedysarum caucasicum, Matricaria caucasica, Phleum alpinum	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Sibbaldia procumbens	Rosaceae	Р	Minuartia aizoides, Taraxacum stevenii, Sibbaldia procumbens, Gnaphalium supinum	Aboveground biomass
Onipchenko <i>et</i> <i>al.</i> 2009	Gnaphalium supinum	Asteraceae	Р	Minuartia aizoides, Taraxacum stevenii, Sibbaldia procumbens, Gnaphalium supinum	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Ρ	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus	Aboveground biomass
Foster 1999	Andropogon gerardii	Роасеае	Р	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Agropyron repens, Achillea millefolium, Bromus inermis, Melilotus alba	Aboveground biomass

Foster 1999	Andropogon gerardii	Poaceae	Р	Bromus inermis, Poa pratensis, Achillea millefolium, Achillea millefolium, Aaropyron repens	Aboveground biomass
	Andronogon	l'ouccue	•		Aboveground
Foster 1999	gerardii	Poaceae	Р	Bromus inermis, Agropyron repens, Poa pratensis, Daucus carota	biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Agropyron repens, Arrhenatherum elatius, Silene alba, Polygonum scandens	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Bromus inermis, Poa pratensis, Solidago canadensis, Agropyron repens	Aboveground biomass
Foster 1999	Andropogon gerardii	Poaceae	Р	Bromus inermis, Poa pratensis, Agropyron repens, Barbarea vulgaris	Aboveground biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Р	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis	Aboveground biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Р	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus	Aboveground biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Р	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium	Aboveground biomass
	Schizachvrium	1 ouccue	·	Aaronyron renens. Achillea millefolium. Bromus inermis. Melilotus	Aboveground
Foster 1999	scoparium	Poaceae	Ρ	alba	biomass
	Schizachyrium			Bromus inermis, Poa pratensis, Achillea millefolium, Achillea	Aboveground
Foster 1999	scoparium	Poaceae	Р	millefolium, Agropyron repens	biomass
	Schizachyrium	_	-		Aboveground
Foster 1999	scoparium	Роасеае	Ч	Bromus inermis, Agropyron repens, Poa pratensis, Daucus carota	biomass
Foster 1999	Schizachyrium scoparium	Poaceae	Р	Agropyron repens, Arrhenatherum elatius, Silene alba, Polygonum scandens	Aboveground biomass

	Foster 1999	Schizachyrium scoparium	Роасеае	Р	Bromus inermis, Poa pratensis, Solidago canadensis, Agropyron repens	Aboveground biomass
	Foster 1999	Schizachyrium scoparium	Poaceae	Ρ	Bromus inermis, Poa pratensis, Agropyron repens, Barbarea vulgaris	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Andropogon virginicus, Rubus allegheniensis, Danthonia spicata, Solidago nemoralis, Hieracium aurantiacum	Aboveground biomass
	Foster 2000	Andropogon gerardii	Роасеае	Ρ	Rubus allegheniensis, Danthonia spicata, Centaurea maculosa, Andropogon virginicus, Hieracium aurantiacum	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Р	Andropogon virginicus, Danthonia spicata, Rubus allegheniensis, Desmodium rotundifolium, Centaurea maculosa	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Elytrigia repens, Achillea millefolium, Bromus inermis, Melilotus alba, Oxalis stricta	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Bromus inermis, Elytrigia repens, Poa pratensis, Daucus carota, Dactylis glomerata	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Elytrigia repens, Arrhenatherum elatius, Silene alba, Polygonum scandens, Poa pratensis	Aboveground biomass
	Foster 2000	Andropogon gerardii	Poaceae	Ρ	Elytrigia repens, Arrhenatherum elatius, Silene alba, Polygonum scandens, Poa pratensis	Aboveground biomass
	Wilson 1994	Schizachyrium scoparium	Poaceae	Р	Schizachyrium scoparium, Mosses and lichens, Poa pratensis, Polygonum convolvulus	Total biomass
	Wilson 1994	Schizachyrium scoparium	Poaceae	P	Schizachyrium scoparium, Poa pratensis, Setaria viridis, Polygonum convolvulus, Elytrigia repens	Total biomass
1	Wilson 1994	Setaria viridis	Poaceae	A	Schizachyrium scoparium, Mosses and lichens, Poa pratensis, Polygonum convolvulus	Total biomass

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Wilson 1994	Setaria viridis	Poaceae	A	Schizachyrium scoparium, Poa pratensis, Setaria viridis, Polygonum convolvulus, Elytrigia repens	Total biomass
Ladd and Facelli 2007	Eucalyptus camaldulensis	Myrtaceae	Ρ	Avena barbata, Pennisetum clandestinum, Briza maxima, Vulpia myuros, Olea europa	Leaf number
Treberg and Turkington 2010	Anemone parviflora	Ranunculaceae	Ρ	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass
Treberg and Turkington 2010	Festuca altaica	Poaceae	Ρ	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass
Treberg and Turkington 2010 Gerdol <i>et al.</i>	Mertensia paniculata	Boraginaceae	Р	Achillea millefolium ssp. Borealis, Anemone parviflora, Epilobium angustifolium, Festuca altaica, Lupinus arcticus, Mertensia paniculata var. paniculata, Senecio lugens, Solidago multiradiata, Arctostaphylos uva-ursi, Linnaea borealis ssp. americana	Aboveground biomass Aboveground
2000 Cordol et al	Vaccinium myrtillus	Ericaceae	Р	Vaccinium myrtillus	biomass
2000	uliginosum	Ericaceae	Р	Vaccinium myrtillus	biomass
Gerdol <i>et al.</i>	Empetrum	Ericaceae	Р	Empetrum hermaphroditum	Aboveground

2000	hermaphroditum				biomass
Gerdol <i>et al.</i>	Vaccinium				Aboveground
2000	uliginosum	Ericaceae	Р	Empetrum hermaphroditum	biomass
Schob <i>et al.</i>	Alchemilla				Aboveground
2010	pentaphyllea	Rosaceae	Р	Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum	biomass
Schob <i>et al.</i>					Aboveground
2010	Poa alpina	Poaceae	Р	Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum	biomass
Schob <i>et al.</i>	Ligusticum				Aboveground
2010	mutellina	Apiaceae	Р	Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum	biomass
Schob <i>et al.</i>	Polygonum				Aboveground
2010	viviparum	Polygonaceae	Р	Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum	biomass
Schob <i>et al.</i>					Aboveground
2010	Veronica alpina	Plantaginaceae	Р	Alchemilla pentaphyllea, Salix herbacea, Gnaphalium supinum	biomass
Wilson and	Schizachyrium				
Tilman 1993	scoparium	Poaceae	Р	Schizachyrium scoparium, Cyperus spp.	Growth rate
Wilson and	Schizachyrium				
Tilman 1993	scoparium	Poaceae	Р	Mollugo verticillata, Panicum capillare, Setaria viridis	Growth rate
Wilson and	Schizachyrium	_	_		
Tilman 1993	scoparium	Poaceae	Р	Schizachyrium scoparium, Agropyron repens	Growth rate
Wilson and	Schizachyrium	Descess	D	Danieum canillara Cotaria viridia	Crowth rate
11man 1993	scoparium	Poaceae	Р	Panicum capillare, Setaria viriais	Growin rate
Eastar and	Andronagan			Cantauraa maculasa, Raa comprossa, Achillaa millafalium, Actor	Abovoground
Gross 1997	aerardii	Poaceae	D	nilosus Ruhus alleabeniensis	hiomass
	gerurun Andreas and	FUALEAE	F	pilosus, Rubus dilegrieriterisis	
Foster and Gross 1007	Anaropogon aorardii	Boacoao	D	Agropuron ronons, Ashillog millofolium, Promus inarmis	hiomass
	yerurun Andreae an	FUALEAE	٢	Agropyron repens, Achined Innejonum, Bronus inernins	
Foster and	Andropogon	Descase	D	Bromus inermis, Poa pratensis, Achiliea miliefolium, Agropyron	Aboveground
1922 1931	geraran	ruaceae	٢	repens	010111922

Foster and Gross 1997	Andropogon	Doacoao	D	Promus inormis Dog protonsis	Aboveground
Foster and	Andropoaon	POaceae	٢	Biomus mermis, Pou prutensis	Aboveground
Gross 1997	gerardii	Poaceae	Ρ	Agropyron repens, Arrhenatherum elatius	biomass
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Р	Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, Carex flacca, Convallaria majalis	Aboveground biomass
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Ρ	Hepatica nobilis, Brachypodium pinnatum, Convallaria majalis, Plantago lanceolata, Primula veris, Serratula tinctoria, Briza media	Aboveground biomass
				Dactylis glomerata, Festuca rubra, Helictotrichon pratense,	
Sammul <i>et al.</i> 2000	Anthoxanthum odoratum	Poaceae	Р	Brachypodium pinnatum, Primula veris, Carlina vulgaris, Carex tomentosa	Aboveground biomass
Sammul <i>et al.</i>	Anthoxanthum				Aboveground
2000	odoratum	Poaceae	Р	Salix herbacea, Salix polaris, Vaccinium myrtillus	biomass
Sammul <i>et al.</i>	Anthoxanthum			Festuca rubra, Vaccinium myrtillus, Juniperus communis, Betula	Aboveground
2000 Sammul <i>et al.</i>	odoratum	Poaceae	Р	nana, Empetrum nigrum	biomass
2000	Anthoxanthum			Vaccinium myrtillus, Trollius europaeus, Festuca rubra, Trientalis	Aboveground
	odoratum	Poaceae	Р	europaea	biomass
Sammul <i>et al.</i>					
2000	Anthoxanthum			Trollius europaeus, Vaccinium vitis-idea, Cirsium heterophyllum,	Aboveground
	odoratum	Poaceae	Р	Epilobium angustifolium	biomass
Sammul <i>et al.</i>					
2000	Anthoxanthum	Deserves	D	Cornus suecica, Solidago virgaurea, Trientalis europaea,	Aboveground
	odoratum	Роасеае	Р	Deschampsia flexuosa	biomass
Dormann <i>et al.</i>	A	A - I			T 1 h *
2000	Artemisia maritima	Asteraceae	Р	Limonium vuigare, Puccinellia maritima, Festuca rubra	lotal biomass

	2000	Artemisia maritima	Asteraceae	Р	Artemisia maritima. Festuca rubra	Total biomass
	Dormann <i>et al.</i>			-	· · · · · · · · · · · · · · · · · · ·	
	2000					
		Artemisia maritima	Asteraceae	Р	Artemisia maritima, Festuca rubra, Limonium vulgare	Total biomass
	Dormann <i>et al.</i>					
	2000	Atriplex portulacoides	Amaranthaceae	Р	Limonium vulgare, Puccinellia maritima, Festuca rubra	Total biomass
	Dormann <i>et al.</i>					
	2000	Atriplex portulacoides	Amaranthaceae	Р	Artemisia maritima, Festuca rubra	Total biomass
	Dormann <i>et al.</i>					
	2000	Atriplex	Amaranthacaaa	D	Astomicia maritima, Factura subra Limonium vulgara	Total biomass
	Dormann <i>et al</i>	portulacolaes	Amaranthaceae	Р	Artemisia mantima, Festaca Tabra, Limonium valgare	TOTAL DIOLUSS
	2000					
	2000	Plantago maritima	Plantaginaceae	Р	Limonium vulgare, Puccinellia maritima, Festuca rubra	Total biomass
	Dormann <i>et al.</i>					
	2000					
		Plantago maritima	Plantaginaceae	Р	Artemisia maritima, Festuca rubra	Total biomass
	Dormann <i>et al.</i>					
	2000	o				
		Plantago maritima	Plantaginaceae	Р	Artemisia maritima, Festuca rubra, Limonium vulgare	lotal biomass
					Ambrosia artemisiifolia, Chenonodium album, Erigeron strigosus	
					Lenidium campestre. Panicum canillare. Lenidium campestre.	
	Goldberg and	Ambrosia			Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota.	Aboveground
26	Miller 1990	artemisiifolia	Asteraceae	А	Plantago lanceolata, Trifolium repens, Agropyron repens	biomass
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Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	Α	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Ambrosia artemisiifolia	Asteraceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Chenopodium album	Amaranthaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Lepidium campestre	Brassicaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass

Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Poaceae	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Goldberg and Miller 1990	Panicum capillare	Роасеае	A	Ambrosia artemisiifolia, Chenopodium album, Erigeron strigosus, Lepidium campestre, Panicum capillare, Lepidium campestre, Barbarea vulgaris, Potentilla recta, Silene alba, Daucus carota, Plantago lanceolata, Trifolium repens, Agropyron repens	Aboveground biomass
Knoop and Walker 1985	Burkea africana	Fabaceae	Ρ	Burkea africana, Ochna pulchra, Terminalia sericea, Agrostis pallens, Digitaria eriantha	Shoot growth
Knoop and Walker 1985	Burkea africana	Fabaceae	Р	Burkea africana, Ochna pulchra, Terminalia sericea, Agrostis pallens, Digitaria eriantha	Shoot growth
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Ρ	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Ρ	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Ρ	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Aboveground biomass

Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Ρ	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Puccinellia maritima, Limonium vulgare, Suaeda maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Limonium vulgare, Puccinellia maritima, Triglochin maritima	Aboveground biomass
Van der Wal <i>et</i> <i>al.</i> 2000	Triglochin maritima	Juncaginaceae	Р	Atriplex portulacoides, Limonium vulgare, Artemisia maritima	Aboveground biomass
Appendix B: Reference list of studies used in the data-synthesis.

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Species	Data source 1	Data source 2	Data Source 3
Achillea millefolium	Craine et al. 2001	Siefert <i>et al.</i> 2014	Tjoelker <i>et al.</i> 2005
Achillea millefolium			
ssp. <i>Borealis</i>	Craine <i>et al.</i> 2001	Siefert <i>et al.</i> 2014	Tjoelker <i>et al.</i> 2005
Agropyron repens	Craine <i>et al.</i> 2001	Tjoelker <i>et al.</i> 2005	
Alchemilla			
pentaphyllea	Ordonez <i>et al.</i> 2010		
Ambrosia			
artemisiifolia	Craine <i>et al.</i> 2001	Siefert <i>et al.</i> 2014	Tjoelker <i>et al.</i> 2005
Andropogon	0	T	0
gerardii	Craine <i>et al.</i> 2001	I Joelker <i>et al.</i> 2005	Ordonez <i>et al.</i> 2010
Andropogon	Baruch and Goldstein	Ciefert et al 2014	Ciefant et al 2014
Virginicus	1999	Sietert et al. 2014	Siefert <i>et al.</i> 2014
Anemone parvifiora	Laurin 2012 Misc	Drive et al 2014	Ordenez et al 2010
Antennaria dioica	Austrheim <i>et al.</i> 2005	Price <i>et al.</i> 2014	Urdonez et al. 2010
			Poorter.
			Hendrik(1999): A
			comparison of specific
			leaf area, chemical
			composition and leaf
Anthoxanthum	Poorter and De jong	Poorter and De jong	construction costs of
odoratum	1999	1999 Leda Database -	
		Source data from	Leda Database - Villar.
		Niinemets,	Rafael(2001):
		Ülo(2003): Leaf	Comparison of leaf
		structure vs. nutrient	construction costs in
		relationship vary with	woody species with
Arctostanhylos uva-		soli conditions in	in contrasting
ursi	Reich <i>et al.</i> 1998	and trees	ecosystems[151]
	Leda Database -	Leda Database -	
	Source data from	Source data from	Leda Database -
	University of	University of	Source data from
	Sheffield, Dept. of	Sheffield, Dept. of	University of Sheffield,
	Animal and Plant	Animal and Plant	Dept. of Animal and
Armeria maritima	(Thompson)	(Thompson)	(Thompson)
	וווסנקוווסווו	Leda Database -	
		Source data from	Leda Database -
		University of	Source data from
		Sheffield, Dept. of	University of Sheffield,
		Animal and Plant	Dept. of Animal and
Arrhenatherum	Poorter and De jong	Sciences, UK	Plant Sciences, UK
erutius	1222	(mompson)	(mompson)

Appendix C: Sources used for specific leaf area for each species.

		Leda Database -	
	Leda Database -	Source data from Carl	
	Source data from	VOIT OSSIELZKY	
	Groningen	Oldenburg	
	Community and	Landscane Ecology	
	Conservation Ecology	Group DF	
∆rtemisia maritima	Group NI (Steendam)	(Kunzmann)	
	Leda Database -	(Ranzinanny	
	Source data from		
	University of		
	, Sheffield, Dept. of		
	Animal and Plant		
Atriplex	Sciences, UK		
portulacoides	(Thompson)		
	Leda Database -	Leda Database -	
	Lavergne,	Garnier, E. (1997):	
	Sébastian(2003): Do	Specific leaf area and	
	rock endemic and	nitrogen	Leda Database -
	widespread plant	concentration in	Garnier, E.(2001):
	species differ under	annual and perennial	Consistency of species
A	the Leaf-Height-	grass species growing	ranking based on
Avena barbata	Seed	IN	functional leaf traits
	Leua Dalabase -	Leua Dalabase -	
	Liniversity of	University of	
	Sheffield Dent of	Sheffield Dent of	
	Animal and Plant	Animal and Plant	
	Sciences, UK	Sciences, UK	
Barbarea vulgaris	(Thompson)	(Thompson)	
5		Leda Database -	
	Leda Database -	Source data from Carl	Leda Database -
	Bruun, Hans	von Ossietzky	Source data from Carl
	Henrik(2005): Distinct	University of	von Ossietzky
	patterns in alpine	Oldenburg,	University of
	vegetation around	Landscape Ecology	Oldenburg, Landscape
	dens of the Arctic fox	Group, DE	Ecology Group, DE
Betula nana	[28]	(Kunzmann)	(Kunzmann)
Bouteloua			
curtipendula	Craine <i>et al.</i> 2001	Tjoelker <i>et al.</i> 2005	
		Leda Database -	
		Arrendondo, J.	Leda Database -
		Tulio(2003):	Source data from
		Components of leaf	University of Sheffield,
		elongation rate and	Dept. of Animal and
Brachypodium	Poorter and De jong	their relationship to	Plant Sciences, UK
pinnatum	1999	specific leaf area in	(Thompson)
Briza maxima	Ordonez <i>et al.</i> 2010	Ordonez <i>et al.</i> 2010	

Briza media	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Leda Database - Source data from University of Regensburg, Chair of Botany, DE (Kahmen)	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)
		Leda Database - Shipley, B.(2002): Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with	Leda Database - Meziane, Driss(2001): Direct and Indirect Relationships Between Specific Leaf Area, Leaf Nitrogen and Leaf Gas Exchange. Effects of Irradiance and
Bromus inermis	Siefert <i>et al.</i> 2014	daily irradiance[16]	Nutrient Supply [88]
Burkea africana	Matilo <i>et al.</i> 2013	Matilo <i>et al.</i> 2013	Whitecross Phd (2017)
Carex crawei	Ordonez <i>et al.</i> 2010 Poorter and De iong	Leda Database - Volk, Matthias(2001): Genotype x elevated CO2 interaction and allocation in calcereous grassland	Leda Database - Volk, Matthias(2001): Genotype x elevated CO2 interaction and allocation in calcereous grassland
Carex flacca	1999 Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape	species[151]	species[151]
Carex ornithopoda	Ecology Group		
Carex sp.	Siefert <i>et al.</i> 2014 Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape	Ordonez <i>et al.</i> 2010	
Carex tomentosa	Ecology Group Leda Database - Source data from University of Groningen, Community and Conservation Ecology		
Carlina vulgaris	Group, NL (Steendam)	Ordonez <i>et al.</i> 2010	

		Leda Database -	
		Poorter,	Leda Database -
		Hendrik(1999): A	Source data from Carl
		comparison of	von Ossietzky
		specific leaf area,	University of
		chemical composition	Oldenburg, Landscape
Chenopodium		and leaf construction	Ecology Group, DE
album	Craine <i>et al.</i> 2001	costs of field	(Kunzmann)
			Leda Database -
		Leda Database -	Poorter
		Eriksson $Ove(2003)$	Hendrik(1999)· A
		Pecruitment and life-	comparison of specific
		history traits of	leaf area, chemical
		sparse plant species	composition and leaf
Chryconthomum		in subalaiaa	construction costs of
Cinysunthemum	Chiploy 100F	m subaipine	field
leucuntnemum	Suible 1992	grassianus [81]	lielu
			Leda Dalabase -
			Poorter,
			Hendrik(1999): A
			comparison of specific
			leaf area, chemical
			composition and leaf
C	Poorter and De Jong	0.1	Construction costs of
Cirsium arvense	1999	Ordonez et al. 2010	TIEID
	Leda Database -	Leda Database -	
	Source data from Carl	Source data from	Leda Database -
	von Ossietzky	University of	Source data from
	University of	Sheffield, Dept. of	University of Sheffield,
	Oldenburg, Landscape	Animal and Plant	Dept. of Animal and
	Ecology Group, DE	Sciences, UK	Plant Sciences, UK
Convallaria majalis	(Kunzmann)	(Thompson)	(Thompson)
	Leda Database -		Leda Database -
	Source data from Carl	Leda Database -	Source data from
	von Ossietzky	Source data from	University of
	University of	Norwegian Institute	Groningen,
	Oldenburg, Landscape	for Nature Resaerch,	Community and
	Ecology Group, DE	NINA-Trondheim, NO	Conservation Ecology
Cornus suecica	(Kunzmann)	(Aarnes)	Group, NL (Steendam)
Cyperus spp.	Ordonez <i>et al.</i> 2010		
	Poorter and De jong		
Dactylis glomerata	1999	Shipley 1995	Siefert <i>et al.</i> 2014
Danthonia spicata	Siefert <i>et al.</i> 2014	. ,	
		Leda Database -	
		Lavergne	
		Sébastian(2003): Do	
		rock endemic and	Leda Database -
		widespread plant	Garnier, F.(2001):
		species differ under	Consistency of species
		the Leaf-Height-	ranking based on
Daucus carota	Siefert <i>et al</i> 2014	Seed	functional leaf traits
	5.C.C.L.C. UI. 2017		

Deschampsia flexuosa	Poorter and De jong 1999	Poorter and De jong 1999	Poorter and De jong 1999
Digitaria eriantha	Mantlana <i>et al.</i> 2008 Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK	
Echium vulgare	(Thompson) Poorter and De iong	(Thompson)	
Elytrigia repens	1999		
	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from University of Sheffield, Dept. of Animal and
Empetrum nigrum	(Kunzmann)	(Kunzmann) Leda Database -	Plant Sciences
	Leda Database - Bruun, Hans Henrik(2005): Distinct patterns in alpine vegetation around	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape
Epilobium angustifolium	dens of the Arctic fox [28]	Group, DE (Kunzmann) Leda Database -	Ecology Group, DE (Kunzmann)
	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE
Equisetum arvense	(Kunzmann)	(Kunzmann)	(Kunzmann)
Erigeron canadensis	Craine <i>et al.</i> 2001	Ordonez <i>et al.</i> 2010	
Eucalyptus camaldulensis	Ordonez <i>et al.</i> 2010		
Festuca altaica	Grainger and Turkington 2013	HuffMastersThesis	Poorter and De jong
Festuca ovina	Craine <i>et al.</i> 2001	1999	1999
Festuca rubra Geranium	Craine <i>et al.</i> 2001	Poorter and De Jong 1999	Siefert <i>et al.</i> 2014
gymnocaulon Gnanhalium	Ordonez <i>et al.</i> 2010		
supinum	Caccianiga <i>et al.</i> 2006		

Helictotrichon			
pratense	Ordonez <i>et al.</i> 2010	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE
Hepatica nobilis	Jagodziński <i>et al.</i> 2016 Leda Database - Meziane, Driss(2001): Direct and Indirect Relationships Between Specific Leaf Area, Leaf Nitrogen	(Kunzmann) Leda Database - Meziane, D.(1999): Interacting determinats of specific leaf area in 22 herbaceous	(Kunzmann) Leda Database - Source data from
	and Leaf Gas	species: effects of	University of Sheffield,
Hieracium aurantiacum	Exchange. Effects of Irradiance and Nutrient Supply [88]	irradiance and nutrient availability [22] Leda Database -	Dept. of Animal and Plant Sciences, UK (Thompson)
	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology	
Hieracium piloselloides	Ecology Group, DE (Kunzmann) Leda Database - Source data from University of Groningen, Community and Conservation Ecology	Group, DE (Kunzmann)	
Hieracium pratense	Group, NL (Steendam)		
Juniperus communis	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Leda Database - Villar, Rafael(2001): Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems[151]
	(Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK
Koeleria macrantha	Craine et al. 2001	(Thompson)	(Thompson)

		Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology	Leda Database - Source data from Carl von Ossietzky University of
Leontodon hispidus	Poorter and De jong 1999 Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape	Group, DE (Kunzmann) Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant	Ecology Group, DE (Kunzmann)
Lepidium campestre	Ecology Group, DE (Kunzmann)	Sciences, UK (Thompson) Leda Database -	
	Leda Database - Source data from Carl von Ossietzky University of	Source data from Carl von Ossietzky University of Oldenburg,	
	Oldenburg, Landscape	Landscape Ecology	
LIGUSLICUM mutelling	(Kunzmann)	(Kunzmann)	
materima	(Kunzmann)	Leda Database -	
	Leda Database - Source data from University of Groningen, Community and	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology	
Limonium vulgare	Conservation Ecology Group, NL (Steendam) Leda Database - Source data from	Group, DE (Kunzmann) Leda Database - Source data from	
Lingrig vulgaris	University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences
	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape	Leda Database - Source data from Norwegian Institute for Nature Resaerch,	
Linnaea borealis	Ecology Group, DE (Kunzmann)	(Wilmann)	Ordonez <i>et al.</i> 2010
		· ·	

Lotus corniculatus Lupinus arcticus	Leda Database - Lavergne, Sébastian(2003): Do rock endemic and widespread plant species differ under the Leaf-Height- Seed Leathem 2014	Leda Database - Source data Garnier, E.(2001): Consistency of species ranking based on functional leaf traits	Leda Database - Garnier, E.(2001): Consistency of species ranking based on functional leaf traits
Medicago lupulina	Leda Database - den Dubbelden, Koen C.(1996): Inherent allocation patterns and potential growth rates of herbaceous climbing plants	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)
Malilatus alba	Crains at al 2001	Shipley 1005	Leda Database - Shipley, B.(2002): Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily
Melliotus alba	Craine <i>et al.</i> 2001	Shipley 1995	irradiance[16]
Mertensia paniculata Mertensia	Grainger and Turkington 2013	Leathem 2014	
paniculata var. paniculata	Grainger and Turkington 2013	Leathem 2014 Leda Database -	
	Leda Database - Source data from Norwegian Institute for Nature Research, NINA-Trondheim, NO	Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK
Nardus stricta	(Rusch)	(Thompson)	(Thompson)
Olea europa	Ordonez <i>et al.</i> 2010		
Oxalis europaea	Shipley 1995		
Oxalis stricta	Shipley 1995		

Leda Database -

			Meziane, Driss(2001): Direct and Indirect Relationships Between Specific Leaf Area, Leaf Nitrogen and Leaf Gas Exchange. Effects of Irradiance and
Panicum capillare	Craine <i>et al.</i> 2001	Tjoelker <i>et al.</i> 2005	Nutrient Supply [88]
Pennisetum			
clandestinum	Ordonez <i>et al.</i> 2010 Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant	Leda Database - Source data from University of Sheffield, Dept. of Animal and
Phalaris	Sciences, UK	Sciences, UK	Plant Sciences, UK
arundinacea	(Thompson)	(Thompson)	(Thompson)
Phleum alpinum	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Leda Database - Source data from Norwegian Institute for Nature Resaerch, NINA-Trondheim, NO (Rusch)	Caccianiga <i>et al.</i> 2006
,	Poorter and De jong	Poorter and De jong	U
Plantago lanceolata	1999	1999	Siefert <i>et al.</i> 2014
Plantago maritima	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson) Leda Database - Keller,	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson) Leda Database -	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)
Poa alpina	Franziska(2003): The Role of Photoperiodism in Alpine Plant Development [35]	Source data from Norwegian Institute for Nature Resaerch, NINA-Trondheim, NO (Aarnes)	Caccianiga <i>et al.</i> 2006

Poa annua	Leda Database - Storkey, J.(2004): Modelling Seedling Growth Rates of 18 Temperate Arable Weed Species as a Function of the Environment and Plant Traits [93] Leda Database - Source data from	Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson) Leda Database -	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)
Poa compressa	Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences
Pod pratensis	Craine <i>et al.</i> 2001	Siefert <i>et al.</i> 2014	I Joeiker <i>et al.</i> 2005
Polygonum	Domec et ul. 2010	Leda Database - Source data from Storkey, J.(2004): Modelling Seedling Growth Rates of 18 Temperate Arable Weed Species as a Function of the Environment and	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences LIK
convolvulus	Craine <i>et al.</i> 2001	Plant Traits [93] Leda Database -	(Thompson)
	Leda Database - Bruun, Hans Henrik(2005): Distinct patterns in alpine vegetation around	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape
Polygonum	dens of the Arctic fox	Group, DE	Ecology Group, DE
viviparum	[28]	(Kunzmann)	(Kunzmann)
Populus deltoides	Reich <i>et al.</i> 1998	Ordonez <i>et al.</i> 2010 Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Ordonez <i>et al.</i> 2010
Populus tremuloides	Reich <i>et al.</i> 1998	(Kunzmann)	Ordonez <i>et al.</i> 2010

	Leda Database -	Leda Database -	Leda Database -
	Source data from	Source data from	Source data from Carl
	University of	University of	von Ossietzky
	Sheffield, Dept. of	Sheffield, Dept. of	University of
	Animal and Plant	Animal and Plant	Oldenburg, Landscape
	Sciences, UK	Sciences, UK	Ecology Group, DE
Potentilla recta	(Thompson)	(Thompson)	(Kunzmann)
	Leda Database -	Leda Database -	
	Source data from	Source data from	Leda Database -
	University of	University of	Source data from
	Sheffield, Dept. of	Sheffield, Dept. of	University of Sheffield,
	Animal and Plant	Animal and Plant	Dept. of Animal and
	Sciences, UK	Sciences, UK	Plant Sciences, UK
Primula veris	(Thompson)	(Thompson)	(Thompson)
	Leda Database -	Leda Database -	
	Source data from	Source data from	
	University of	University of	
	Groningen,	Sheffield, Dept. of	
	Community and	Animal and Plant	
	Conservation Ecology	Sciences, UK	
Puccinellia maritima	Group, NL (Steendam)	(Thompson)	
Rubus			
allegheniensis	Ordonez <i>et al.</i> 2010		
		Leda Database -	
	Leda Database -	Source data from Carl	
	Source data from Carl	von Ossietzky	
	von Ossietzky	University of	
	University of	Oldenburg,	
	Oldenburg, Landscape	Landscape Ecology	
	Ecology Group, DE	Group, DE	
Salicornia europaea	(Kunzmann)	(Kunzmann)	
		Leda Database -	Leda Database -
		Bruun, Hans	Source data from Carl
		Henrik(2005):	von Ossietzky
		Distinct patterns in	University of
		alpine vegetation	Oldenburg, Landscape
		around dens of the	Ecology Group, DE
Salix herbacea	Baptist <i>et al.</i> 2010	Arctic fox [28]	(Kunzmann)
	Lada Databasa	Leda Database -	
	Leda Database -	Dormann,	Lude Database
	Dormann,	Carsten.F.(2002):	Leda Database -
	Carsten.F.(2002):	Flowering growth	Source data from Carl
	Flowering growth and	and defence in the	VOIT USSIELZKY
		two sexes:	Oldonburg Londoorne
	sexes: consequences	consequences of	Coology Crown DC
Saliv polaria	for Salix polaria [16]	for Soliv poloria [16]	Ecology Group, DE
Suitx polaris	TOT SAILX POTATIS [10]	TOT SAILX POTATIS [10]	(KullzIllallil)

	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK		
Satureja vulgaris	(Inompson)		
Schizachyrium scoparium	Craine <i>et al.</i> 2001	Siefert <i>et al.</i> 2014	Tjoelker <i>et al.</i> 2005
	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE	Leda Database - Source data from University of Groningen, Community and Conservation Ecology
Scorzonera humilis	(Kunzmann)	(Kunzmann)	Group, NL (Steendam)
Senecio pauperculus Serratula tinctoria	Laurin 2012 Msc Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann) Leda Database - Source data from University of Sheffield, Dept. of	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)
Sesleria caerulea	Animal and Plant Sciences, UK (Thompson)	Leda Database -	
Setaria viridis	Leda Database - Source data from University of Sheffield, Dept. of Animal and Plant Sciences, UK (Thompson)	Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)	Ordonez <i>et al.</i> 2010
Sibbaldia procumbens	Leda Database - Eriksson, Ove(2003): Recruitment and life- history traits of sparse plant species in subalpine grasslands [81]	Leda Database - Bruun, Hans Henrik(2005): Distinct patterns in alpine vegetation around dens of the Arctic fox [28]	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)

	Leda Database -	Leda Database -	
	Source data from	Source data from	Leda Database -
	University of	University of	Source data from
	Sheffield, Dept. of	Sheffield, Dept. of	University of Sheffield,
	Animal and Plant	Animal and Plant	Dept. of Animal and
	Sciences, UK	Sciences, UK	Plant Sciences, UK
Solanum dulcamara	(Thompson)	(Thompson)	(Thompson)
Solidaao altissima	Siefert <i>et al.</i> 2014		
Solidago canadensis	Shinley 1995	Ordonez et al. 2010	Laurin 2012 Msc
Solidago nemoralis	Craine et al 2001	Tioelker et al. 2005	Ordonez et al 2010
Solidago ricida	Craine et al. 2001	Tjoelker et al. 2005	Ordonez et al. 2010
Solidayo Tigida		1 joeiker <i>et ul.</i> 2005	Ordonez et al. 2010
Solidago rugosa	Siefert <i>et al.</i> 2014		
Solidago virgaurea	Austrheim <i>et al.</i> 2005	Ordonez <i>et al.</i> 2010	
Stipa comata	Ordonez <i>et al.</i> 2010		
Stipa neomexicana	Ordonez <i>et al.</i> 2010		
		Leda Database -	
	Leda Database -	Source data from Carl	
	Source data from	von Ossietzky	Leda Database -
	University of	University of	Source data from
	Groningen,	Oldenburg,	University of Sheffield,
	Community and	Landscape Ecology	Dept. of Animal and
	Conservation Ecology	Group, DE	Plant Sciences, UK
Suaeda maritima	Group, NL (Steendam)	(Kunzmann)	(Thompson)
		Leda Database -	
		Source data from Carl	
		von Ossietzky	
		University of	
		Oldenburg,	
Tanawaana	Dearter and De ione	Landscape Ecology	
officinale	Poorter and De Jong	Group, DE	Ordonaz at al 2010
ojjicinale	1999	(KUNZINANN)	
Terminalia coricoa	Scholos at al 2004	(2017)	
renninunu senceu	Scholes et ul. 2004	(2017) Loda Databaso	
	Lada Databasa -	Source data from Carl	Loda Databaso -
	Bruun Hans	yon Ossietzky	Source data from Carl
	Henrik(2005): Distinct	University of	von Ossietzky
	natterns in alnine	Oldenhurg	University of
	vegetation around	Landscane Ecology	Oldenburg Landscape
	dens of the Arctic fox	Group DF	Ecology Group DE
Trientalis euronaea	[28]	(Kunzmann)	(Kunzmann)
inentano caropaca	[20]	Leda Database -	(Runzinum)
	Leda Database -	Source data from Carl	Leda Database -
	Source data from Carl	von Ossietzky	Source data from Carl
	von Ossietzky	University of	von Ossietzky
	, University of	, Oldenburg,	, University of
	Oldenburg, Landscape	Landscape Ecology	Oldenburg, Landscape
	Ecology Group, DE	Group, DE	Ecology Group, DE
Trifolium agrarium	(Kunzmann)	(Kunzmann)	(Kunzmann)

Trifolium repens	Poorter and De jong 1999	Poorter and De jong 1999	Siefert <i>et al.</i> 2014
	Leda Database -	Leda Database - Source data from	Leda Database -
	Source data from Carl	University of	Source data from
	von Ossietzky	Groningen,	University of
	University of	Community and	Groningen,
	Oldenburg, Landscape	Conservation Ecology	Community and
	Ecology Group, DE	Group, NL	Conservation Ecology
Triglochin maritima	(Kunzmann)	(Steendam) Leda Database -	Group, NL (Steendam)
	Leda Database -	Source data from Carl	
	Source data from Carl	von Ossietzky	Leda Database -
	von Ossietzky	University of	Source data from
	University of	Oldenburg,	University of Sheffield,
	Oldenburg, Landscape	Landscape Ecology	Dept. of Animal and
Trolling ouronsour	Ecology Group, DE	Group, DE	(Therease)
-	(Kunzmann)	(Kunzmann)	(mompson)
Empetrum		Lagerstrom <i>et al.</i>	
hermaphroditum	Lagerstrom <i>et al.</i> 2013	2013	Lagerstrom <i>et al.</i> 2013
		Leda Database -	Lada Databasa
		Ninemets,	Lega Dalabase -
		010(2003): Leal	Bruun, Hans Honrik(2005): Distinct
		rolationship yany with	nettorns in alnino
		soil conditions in	vegetation around
		temperate shruhs	dens of the Arctic fox
Vaccinium myrtillus	Reich et al 1998	and trees	[28]
i deelindin niyi cindo		Leda Database -	[=0]
	Leda Database -	Source data from Carl	Leda Database -
	Bruun. Hans	von Ossietzky	Source data from Carl
	Henrik(2005): Distinct	University of	von Ossietzky
	patterns in alpine	, Oldenburg,	University of
	vegetation around	Landscape Ecology	Oldenburg, Landscape
Vaccinium	dens of the Arctic fox	Group, DE	Ecology Group, DE
uliginosum	[28]	(Kunzmann)	(Kunzmann)
	Leda Database -		
	Niinemets, Ülo(2003):	Leda Database -	Leda Database -
	Leaf structure vs.	Bruun, Hans	Source data from Carl
	nutrient relationship	Henrik(2005):	von Ossietzky
	vary with soil	Distinct patterns in	University of
	onditions in	alpine vegetation	Oldenburg, Landscape
	temperate shrubs and	around dens of the	Ecology Group, DE
Vaccinium vitis-idea	trees	Arctic fox [28]	(Kunzmann)

Veronica alpina	Leda Database - Eriksson, Ove(2003): Recruitment and life- history traits of sparse plant species in subalpine grasslands [81]	Leda Database - Bruun, Hans Henrik(2005): Distinct patterns in alpine vegetation around dens of the Arctic fox [28] Leda Database -	Leda Database - Source data from Carl von Ossietzky University of Oldenburg, Landscape Ecology Group, DE (Kunzmann)
	Leda Database - Source data from Carl von Ossietzky	Source data from Carl von Ossietzky University of	Leda Database - Source data from Carl von Ossietzky
	Oldenburg, Landscape Ecology Group, DE	Landscape Ecology Group, DE	Oldenburg, Landscape Ecology Group, DE
Vicia cracca	(Kunzmann) Leda Database -	(Kunzmann) Leda Database -	(Kunzmann)
	Source data from University of	Source data from University of	Leda Database - Source data from
	Sheffield, Dept. of Animal and Plant	Sheffield, Dept. of Animal and Plant	University of Sheffield, Dept_of Animal and
	Sciences, UK	Sciences, UK	Plant Sciences, UK
Vulpia myuros	(Thompson)	(Thompson)	(Thompson)

Appendix D: Reference list of sources for functional traits used in data-synthesis

Maximum Height

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Specific Leaf Area

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CHAPTER 6

CONCLUSION

In this thesis I tested the predictions of traditional strategy theory on the role of competition in the evolution of plant strategies and life histories. Traditional strategy theories have remained the foundation of much of the research into plant-plant competitive interactions even if there have been difficulties finding consistent evidence to support them and difficulties reconciling the different predictions of theories on the role of competition in the evolution of plant strategies and traits (Grime 1973; 1977; Tilman 1982; 1988). Recent investigations of competition have revealed that in addition to the ability to acquire resources for growth, the ability to reproduce under competition can be important in determining species distributions and relative abundance in environments (Neytcheva and Aarssen 2008; Bonser and Ladd 2011). However, the assumptions of existing theoretical frameworks (and thus much of the research on plant competition which was built upon these theoretical foundations) have focussed on the ability to acquire resources for growth and neglected the ability to reproduce under competition in measuring performance under competition and in their predictions of which species evolved under competition. These issues suggest that we need to reappraise a number of the influential theories and models in plant ecology regarding the evolution of traits in which competition plays a predominant role in. I presented four studies where I collated the data from the extensive plant competition literature to test how aspects of plant strategies are related to performance under competitive conditions. Here, I provide a summary of these findings and their implications on existing theory.

This thesis started by testing whether seed size, a trait that is predicted to affect plant performance from the earliest stages and link reproduction and seedling establishment with vegetative growth strategies (Grime *et al.* 1988; Leishman *et al.* 2000) is related to

competitive ability (chapter 2). Traditional ecological theory predicts that seedlings emerging from large seeds would have the advantage in environments of dense vegetation. The higher amount of resources contained in the large seed would allow for rapid growth to reach a large size to capture more resources whilst the large number of seeds smallseeded species can produce would allow them to be better colonisers than large-seeded species (Geritz 1995). However, finding experimental evidence to support these predictions has been difficult and newer theories have predicted that this may be because seed size is not important for competition (Falster *et al.* 2008). By performing a synthesis of the literature, I found that large seed size was associated with competitive ability but only in the environments where other competitors were also seedlings and did not provide any competitive benefits for seedlings against adult plants. This may partly explain the discrepancies between previous tests of the effect of seed size on competitive performance. My findings offer a new interpretation of seed size strategies suggesting that seedlings have little chance of establishing in dense communities but rather mainly emerge in open spaces.

The findings of chapter 2 have important implications for competition-colonisation theory which has often been used to explain the evolution of seed size, and the maintenance of the coexistence of different seed size strategies (Geritz 1995; Rees and Westoby 1997; Geritz *et al.* 1999). The findings of this study suggest that large seeds are not as poor colonisers and that small seeds are not as poor competitors as predicted by the competition-colonisation theories. In contrast to theory, species do not exist on a strict continuum of colonisation to competition strategies. Species large and small-seeded are able to outcompete

each other depending on the timing of establishment. These findings will be important to make realistic predictions on competition and colonisation scenarios. The findings of this chapter demonstrate that competition is important in the evolution of all life histories including small-seeded, short-lived species.

In the third chapter, I tested whether shade avoidance plasticity was an adaptive response under competition. Shade avoidance responses have often been thought of as a strategy plants use to outcompete their neighbours for light resources (Givnish 1982; Falster and Westoby 2005). In contrast to traditional predictions of theory, my analysis showed that shade avoidance did not confer any increase in competitive performance, rather we found that shade avoidance plasticity was associated with a decrease in performance under competition. Interestingly, shade avoidance was found to instead confer higher reproductive efficiency in our dataset of mostly short-lived plants. These findings demonstrated that shade avoidance responses are adaptive under competition. However, the adaptive value lies in gathering resources to allow earlier reproduction under competition rather than for gathering resources to increase growth and outcompete neighbours as has been predicted by theory.

For short-lived plants, allocating to earlier reproduction is likely to be more important than allocating to increased growth to outcompete neighbours because these short-lived plants only have short timeframes within which to live and reproduce. This means that using resources towards outgrowing neighbours would not be a strategy that would allow these species which are unlikely to outlive or outgrow longer-lived species to achieve

competitive dominance. Additionally, under increasing levels of competitive suppression which can severely limit growth and reproduction, there is a high risk of dying without producing offspring. Reproducing earlier ensures sufficient time and resources for fruits to mature under intense competition. The ability to obtain resources for growth is a key part of competitive strategies predicted by traditional strategy theories (Grime 1973). The findings of chapter 3 challenge these traditional predictions and suggest obtaining resources to reach a large size may not be important for all plants to achieve fitness under competition. This major finding suggests that obtaining resources for reproduction is also an important part of plant strategies under competition. Future studies will be required to determine whether the same relationships between shade avoidance plasticity and reproductive efficiency exist for long-lived species as extremely few studies measured these species until reproductive maturity. However, these findings indicate that competition played an important role in the evolution of the strategy of short-lived species.

Following on from the findings of chapter 3, in the fourth chapter I examined whether plasticity in general is associated with competitive ability. Like shade avoidance plasticity, plasticity has been thought to be an important trait in competitive strategies for maximising resource acquisition (Grime 1979; Grime *et al.* 1986; Bazzaz 1991; de Kroon and Hutchins 1995; Huber *et al.* 1999). Contrary to the predictions of theory, I found that plasticity was linked with lower competitive performance in both short and in long-lived species. In addition, although I found that overall plasticity was not significantly related to reproductive efficiency, plasticity was positively associated with reproductive efficiency in the short-lived species whilst there was no such association with reproductive efficiency in the long-lived species. These findings show that whilst plasticity is adaptive under

competitive environments for short-lived species, the advantage of expressing high plasticity is not in conferring high competitive ability by allowing the plants to obtain higher fecundity than their competitors but by allowing short-lived plants to acquire resources to expedite their reproduction. This is consistent with the findings of chapter 3 where I also found that shade-avoidance plasticity did not increase the competitive performance of short-lived species but was related to increased reproductive efficiency in short-lived species. In this chapter there was sufficient data to test if there was any such relationship between plasticity and reproductive efficiency in the long-lived species. I found no association between plasticity and reproductive efficiency in long-lived species in contrast to the findings for short-lived species.

The findings of chapter 4 suggest that in line with our predictions, plasticity is too costly to maximise competitive ability in environments which are not variable such as highly competitive environments. Competitive ability is more likely to evolve under high and persistent competition where specialised competitive strategies would be favoured whilst plasticity in resource acquisition traits would be favoured and should evolve in variable environments. The findings also suggest that plasticity is either not adaptive in long-lived species or its adaptive value could be in another component of fitness I was unable to assess in this study which was survival. The lack of relationship between plasticity and reproductive efficiency of long-lived species could be a result of the larger threshold size required by long-lived species to reproduce than short-lived species. This would allow short-lived species greater flexibility to adjust the timing of their reproduction than long-lived species. In this case, under intense competition where greater fitness than long-lived

species for which it would take more time and resources to reach the large size required for them to reproduce. Together, the findings of chapter 3 and 4 have important implications on what traditional theory predicts to confer high competitive ability in plants. These findings illustrate that short-lived species could potentially perform better than long-lived species under intense competition. This also indicates that not only long-lived species but short-lived species evolved under competitive environments too.

In the fifth chapter, I examined whether functional traits were good predictors of competitive ability. Increasing numbers of studies utilise functional traits to predict the competitive ability of species across communities and ecosystems. I focussed on two of these traits, specific leaf area and maximum height. Competition experiments have not previously been synthesised to assess the role of plant functional traits in defining competitive ability. I found that neither maximum height nor specific leaf area were particularly good predictors of competitive performance. My findings suggest that whilst functional traits such as maximum height can be good indicators of competitive performance under certain circumstances, this is often because of the strong links between other life history traits such as life span and not just due to the height of the plant. Other functional traits such as specific leaf area may be linked to life history traits as well but their links with other external environmental factors is often stronger leading them to be too variable to be good predictors of competitive ability across large scales.

The findings of the fifth chapter show that to make accurate predictions about the outcomes of competitive interactions it is important to consider life histories as a whole.

They also demonstrate that we need to work on an improved theoretical foundation for our understanding of competitive ability taking into account the entire life history including reproduction under competition and differences in the strategy short and longlived species would utilise before we will be able to effectively predict competitive ability. A major problem with testing the general rules predicted by theory of whether certain functional traits are related to competitive ability is that there is little consensus about the definition of competitive ability and the definition of competition. This chapter (chapter 5) showed that whilst functional traits can influence the performance of plants under competition and can be used as a guide when predicting the results of competitive interactions, they do not effectively define competitive ability. The results of competitive interactions are affected by many different environmental factors which makes it difficult to determine competitive ability across environments. Additionally, competitive performance is determined by many different life history traits which makes it difficult to use any single trait to define competitive ability. Trait-based approaches remain potentially useful as we have still not reached a stage where we have enough data to be able to predict the competitive performance of species in every community but traditional taxonomic based approaches and detailed experiments will be required to first understand how the effect of traits on competitive ability varies under different conditions when selecting for traits to be used for predicting competitive ability.

Further implications

Plants have evolved a diverse range of ecological and life history strategies to succeed in the conditions they encounter in their lives. Some have adapted a strategy of living quickly, growing to a small body size, producing small seeds through one reproductive event and

dying quickly after. Others live more slowly, taking time to grow to a larger size before their first reproduction, and producing large seeds often over more than one reproductive event over their lifetime. Traditional strategy theories have predicted competition to only be important in the evolution of plants with the slow life strategies because their traits allow them to obtain a larger share of the contested resources (Grime 1973; 1977). This emphasis on resource acquisition in defining success under competition has led most experimental measurements of competitive ability to have focussed on plant size (e.g. ability to not have size be suppressed, ability to suppress the size of others). However, the findings of this thesis have suggested that the ability to reproduce under competitive conditions can also be an important part of plant competitive strategies especially where there is a high chance of mortality. For example in chapters 3 and 4, I showed the adaptive values of shade avoidance plasticity and of plasticity in general in short-lived species were not in increasing body size under competition but rather in increasing reproductive efficiency. In Chapter 4, I also demonstrated that even in the long-lived species (the species traditionally predicted to have higher competitive ability because they would be able to obtain a larger share of the contested resources) the adaptive value of plasticity did not lie in increasing body size under competition. In chapter 2, large seed size was found to only confer greater competitive ability under open environments where their competitors were other seedlings, rather than lead to a general increase in competitive ability as predicted under plant strategy theory. Other findings suggest that seed number may provide a greater advantage for successful establishment in dense environments of mature vegetation than seed size (e.g. Tilman 1997; Foster 2001; Williams et al. 2007) suggesting that small-seeded species which are able to produce more offspring in a reproductive event may be more advantaged in competition in these dense environments. These findings have all provided support for how the ability to reproduce can be more

important than the ability to grow to large sizes under competition. The ability to grow to a large size could instead limit the ability to reproduce earlier as larger-sized species are unable to reproduce until they reach a larger size. Thus, being able to grow to the size required for reproduction may be more important than being able to grow to a large size under competition. I demonstrated that contrary to traditional theory, small plants are not inferior to large plants at passing on their genes when under intense competition.

The findings of this thesis suggest that contrary to predictions of traditional strategy theories that competition was only important in the evolution of long-lived plants (Grime 1973), the strategies of both short and long-lived plants have evolved under competition. Differing strategies have emerged to maximise fitness under competition within the different constraints and limitations of the two life history types. For example, short-lived species are limited by their small maximum sizes and short lifespans and thus would need to increase allocation to reproduction to increase fitness whilst long-lived species are limited by a large minimum reproductive threshold size and so for them, growing to large sizes would be important (however it is not yet clear whether this would be for the plants to reach the size required for reproduction or not). This change in way of thinking suggests short-lived plants can potentially perform better than longer-lived species under competition where lives can be curtailed early in contrast to the predictions of traditional strategy theories. Under severe levels of competition, the strategy of short-lived species could allow them to be better at ensuring they are represented in the community in the future than long-lived species which may not be able to reach the minimum required size for reproduction before death.

The demonstration of the importance of reproduction as part of a strategy that evolved under competition would call for a change in the way we measure competitive ability to incorporate reproductive performance. Next steps would be to determine the best way to measure reproductive output of the plants. The reproductive output of a single reproductive event is only a good estimate of the lifetime reproductive output of annual plants and monocarpic perennials. For long-lived plants, reproductive performance can only be accurately assessed over lifetime reproductive events until the plant reaches its natural demise. All these issues will need to be clearly defined in our theoretical foundations before we will be able to make and test predictions about the competitive abilities of species based on their traits or strategies. In order to be able to make predictions about the outcomes of all competitive interactions that occur in natural communities with the interactions of other environmental factors, we need to first understand what we need to measure as competitive ability for plants with different life history strategies.

Conclusion

In this thesis I have assembled results from the competition literature on a large number of individual cases of species and environments to test theoretical ideas on competitive ability. In doing so, I have made findings that will serve useful in refining the existing theoretical foundations upon which much of the work on competition is based. My thesis has helped refine models such as the competition-colonisation model on seed size, highlighted the important role reproduction can play in the competitive strategies of plants and demonstrated the current limitations of trait-based methods. Most importantly, my research has challenged some of the important notions about how plants compete

under or evolve competitive strategies predicted by traditional theories and shown competition has had an important role in the evolution of plants with different life history strategies including small, short-lived species. The role of competition in selecting for different traits and strategies will be important for understanding species' distributions and abundances. This improvement of our understanding is necessary in order to help us to predict with more certainty the ranges where species will move and where they will persist in a changing environment (for instance under species invasions).

Although many advances have been made over the years in competition theory, there have remained numerous questions which we have struggled to answer, differences between theories which we have struggled to reconcile. Theoretical models on competition have remained difficult to find consistent experimental evidence to support. Despite extensive research, our understanding of this complex force is still limited. My thesis has been about challenging traditional ways of thinking about competition (e.g. challenging the ideas on whether seed size confers greater competitive ability or if seed size is associated with growth prior to the onset of competition). Importantly, these traditional ways of thinking about plant responses to competition are written into the ecological theory with which they are associated. For example, the perception of size as a good measure of competitive ability is so deeply entrenched in competition theory that almost all competitive indices and experiments which have followed have focussed on size and measured competitive ability in this way without considering any other measures. The results of this thesis suggest that a fundamental change in the way we think about adaptive evolution in plants under competition is necessary e.g. the importance of reproduction in plant responses to competition. Reproduction has been largely sidelined until recent studies (Neytcheva and Aarssen 2008; Bonser and Ladd 2011; Tracey and

Aarssen 2011; 2014). Moving forward, an evolutionary competitive ability approach such as that suggested by Tracey and Aarssen (Tracey and Aarssen 2014; Tracey and Aarssen, in press) which recognises the importance of reproduction in community composition in crowded environments will be necessary. When considering whether traits are adaptive, it is important to consider the entire life history of a plant (e.g. plant size, lifespan, reproductive schedule). This thesis demonstrates that taking into account reproduction and fecundity under competition will help to fill in a lot of the critical gaps in knowledge in competition theory. Only by taking into account the entire life histories of plants in our future research on competition can we gain a true understanding of plant performance under competition.
Conclusion

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