



Plant species size and density-dependent effects on growth and survival

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Keywords

Competitive equivalence; Inter-specific competition; Intra-specific competition; Seed size; Species size

Nomenclature

Gleason & Cronquist (1991)

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Abstract

Question: Experimental evidence suggests that competition among plant species is generally hierarchical and that relatively large species are at a competitive advantage when competition is predominantly above-ground. However, regional species pools are dominated numerically by relatively small plant species, and small species generally have higher local densities of resident plants within natural communities. One explanation is that larger plant species suffer disproportionately more under effects of intra-specific competition (i.e. greater density dependence). We tested this prediction using ten herbaceous plant species in a competition experiment.

Location: Kingston, Ontario, Canada, glasshouse.

Methods: Using a glasshouse experiment, we tested whether relatively large species suffer disproportionately more in monoculture relative to mixtures of all ten herbaceous plant species. We measured the effects of competition on biomass production and survival by monitoring both in monocultures and mixtures of our species.

Results: Larger plant species suffered more under intra-specific relative to diffuse inter-specific competition in terms of survival; however, the slope of this relationship was not significantly greater than one, indicating that larger species did not suffer disproportionate density-dependent suppression.

Conclusions: Our results support a role for size in plant competition, but also indicate that this role is reduced because relatively larger species suffer greater density-dependent mortality when competing with other, equally large plants. As such, size-based competitive hierarchies may not function as clearly in natural systems because the increased negative density dependence for larger species contributes to balancing out competition across size hierarchies.

Introduction

The relative importance of competition in driving community assembly has been debated since the introduction of the ‘assembly rules’ concept by Diamond (1975). This debate has expanded in recent years with the emergence of several ‘neutral’ models of community assembly, emphasizing the strong role of regional-scale processes and highlighting the potential for competitive ‘equivalence’ among species (Taylor et al. 1990; Hubbell 2001; Zobel 2001). It is therefore necessary to more clearly understand mechanisms for species co-existence that directly involve the competitive process (e.g. Gilpin 1975; Aarssen 1983; Buss 1990; Bengtsson et al. 1994; Huisman & Weissing 1999; Laird & Schamp 2006).

Theoretical models have consistently found that co-existence can occur when species suffer most under competition with conspecifics and therefore inevitably experience higher fitness when in competition with heterospecifics (e.g. Molofsky et al. 1999; Chesson 2000; Adler et al. 2007). The basis for this co-existence is niche differentiation, with niche partitioning among species contributing to all species experiencing greater intra-specific competitive effects compared to inter-specific competitive effects. However, evidence from competition studies suggests that there is no consistent tendency for intra-specific competition to be higher than inter-specific competition (Goldberg & Landa 1991; Goldberg & Barton 1992; Gurevitch et al. 1992). In fact, studies of pair-wise competition have detected strong evidence of clear transitive competitive

relationships among species (reviewed in Shipley 1993). Furthermore, experimental evidence suggests that traits related to species size are important in determining relative competitive ability (Goldberg 1987; Gaudet & Keddy 1988; Keddy & Shipley 1989; Goldberg & Landa 1991; Rosch et al. 1997; Keddy et al. 2002; Warren et al. 2002; Fraser & Keddy 2005; Jumpponen et al. 2005; Violette et al. 2009; Wang et al. 2010). An advantage of larger size may be most important in communities where size differences can lead to asymmetric competition for light (Weiner 1990; Schwinnig & Weiner 1998). The difficulty in accepting that asymmetric inter-specific competition among plant species is based largely on plant size differences comes from evidence that large and small plant species routinely co-exist (e.g., Aarssen & Schamp 2002; Aarssen et al. 2006). Also, trait-based community assembly studies have not uncovered the convergence in maximum height predicted by a size advantage in competition (Weiher et al. 1998; Stubbs & Wilson 2004; Schamp et al. 2008; Schamp & Aarssen 2009; Swenson & Enquist 2009). Thus, while experiments tend to repeatedly uncover a size advantage in plant competition, there is little evidence of such a size advantage in natural communities.

Here, we propose an alternative explanation for the co-existence of large and small plant species: because plant size reflects the growth component of competitive ability, larger species experience much more intense intra-specific competition and are prevented from completely dominating plant communities by density-dependent regulation. Indirect evidence in support of this prediction can be found from data on the species size-density relationship, i.e. larger species self-thin to a lower density per unit area than smaller species (White 1980). Furthermore, research indicating that the slope of this relationship may be closer to -4/3 than -3/2 (Enquist et al. 1998) suggests that a twofold decrease in density during thinning (i.e. decrease in two-dimensional area) is accompanied by less than a three-fold increase in biomass (i.e. increase in three-dimensional volume), thus suggesting a lower efficiency of space/resource use for larger species. This decreased efficiency in space use by larger plants has also been supported by evidence that monocultures of larger plant species are more readily invaded than are those of smaller plant species (Schamp & Aarssen 2010). Effectively, through intra-specific self-thinning, larger plant species may leave 'parcels' of resources free for use by smaller species with lower minimum resource requirements, thus allowing co-existence through differentiation in the sizes of 'physical space niches' (Aarssen et al. 2006). Intra-specific density dependence has also been observed to contribute to the maintenance of diversity in forest community models (Lischke & Löffler 2006).

Plant size has received a great deal of attention in the plant competition literature; however, seed size has also

been implicated as an important determinant of seedling competition (Eriksson 1997; Turnbull et al. 1999; Leishman 2001; Moles & Westoby 2004a). While evidence suggests that large-seeded species may be increasingly likely to survive shading or herbivory (Moles & Westoby 2004a), it has been suggested that this advantage might not be strong enough to play a primary role in determining species composition in plant communities (Leishman 2001; Moles & Westoby 2004b). Given the shape of the seed size/plant size relationship, intra-specific density dependence should be most prominent for large-seeded species, which also tend to be large in general (Aarssen 2005). For this reason, we hypothesize that large-seeded species will also suffer more under intra-specific competition.

To examine the above hypotheses, we investigated the relationship between species size/seed size and inter- and intra-specific competition using a glasshouse competition experiment involving ten old-field plant species known to co-exist. We tested the prediction that intra-specific competition is more important in terms of limiting growth and survival of relatively large/large-seeded species. We explore the implications of our results for the interpretation of experimentally derived evidence of a competitive size advantage and the role of density-dependent regulation of species size/seed size distributions in understanding mechanisms of co-existence of plant species varying in these traits.

Methods

Ten study species were chosen — all herbaceous perennials that commonly co-exist in old-field vegetation in eastern Ontario — with a range of species sizes and abundances spanning about two orders of magnitude (Fig. 1), and a range of seed sizes (mass) spanning three orders of magnitude (Table 1). These included two perennial grasses, seven non-nitrogen fixing forbs, and one nitrogen-fixing forb. Sufficient seed for these species was purchased from commercial suppliers (Prairie Moon Nursery, Winona, MN, USA; Ontario Seed Company, Kitchener, ON, Canada). All seeds were stored in refrigerated conditions (three were stored wet as recommended) for a period of 6 wk prior to starting the experiment to simulate natural over-wintering conditions. Germination tests were conducted to determine the percentage of seeds expected to germinate for each of the ten species. These tests used five replicates of 50 seeds per species placed in pots and soil similar to those used in the experiment and monitored for 4 wk in a growth chamber. Growth chambers were maintained on a 16:8 h light:dark schedule at 25 °C, similar to greenhouse conditions for the experiment. For each species, the number of seeds sown experimentally was

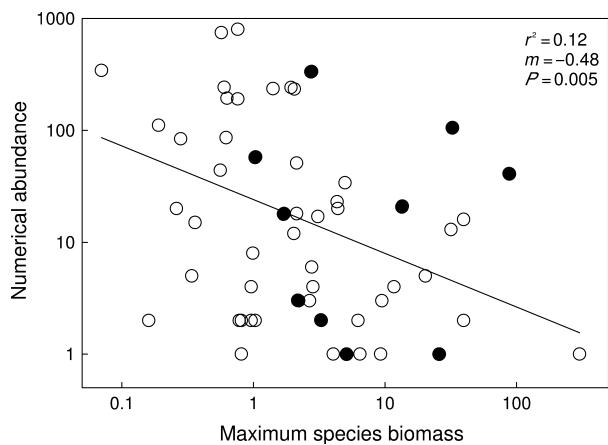


Fig. 1. Relationship between biomass and numerical abundance. Linear regression of numerical abundance vs. maximum above-ground biomass for $n = 56$ plant species recorded from an old field at Queen's University Biology Station, Chaffey's Locks, Ontario, Canada ($44^{\circ}34'N$, $76^{\circ}20'W$). Abundance data were determined by counting the number of rooted units per species in 100 randomly located $25 \times 25\text{-cm}$ plots, and maximum biomass per species was determined as the maximum dry mass accumulation (g) at flowering among 25 randomly selected samples per species. Filled circles represent those species chosen for the experiment in the present study, while open circles represent all other resident species identified in the field.

adjusted to species-specific germination rates such that we could expect approximately the desired number of seedlings of each species for each treatment (1, 100, 1000 individuals).

Experimental design

Growth and survival of the ten species were compared based on relative performance in monocultures and polycultures (henceforth mixtures) with the same plant density. Five monoculture replicates with projected initial densities of 1, 100 and 1000 individuals per pot (4.87 L volume; 25.4 cm diameter; 125.3 cm^2 area) were produced

for each of the ten species (150 pots). Additionally, using the same pot size, 30 mixtures were prepared with projected total initial densities of 1000 individuals per 125.3 cm^2 and projected per-species initial densities of 100 individuals. Densities of 1000 individuals per pot were chosen to exceed the maximum density of individual plants (rooted units) observed in the field (B.S. Schamp and L.W. Aarssen unpublished data). Field abundance was determined by counting the number of rooted units per species in 100 randomly located $25 \times 25\text{-cm}$ plots, and maximum biomass per species was determined as the maximum dry mass accumulation (g) at flowering among 25 randomly selected samples per species. Rooted units were counted by enumerating the number of transitions between above-ground shoot and below-ground roots for each species. Densities of 100 individuals per pot were used to confirm that 1000 plant monoculture pots were indeed undergoing competition for space and/or light (Fig. 2) and to track germination success. A total of 180 pots were filled with a mixture of Premiere ProMix[®] consisting of 75–85% Sphagnum peat moss, perlite and vermiculite, mixed 3:1 with autoclaved sand.

All pots were seeded on 24 May 2005 in the greenhouse at Queen's University. Pots were initially top watered carefully to minimize the movement of seeds, avoid pooling and prevent the formation of soil topography in pots. All 180 pots were placed on two greenhouse tables. Pots were aligned in six rows of 15 per table, with the long axis (15 per row) oriented approximately east-west, and were spread to four tables after germination and randomized alternately within, and then between tables, biweekly. Pots were top watered daily with RO water for the first 2 wk of growth and bottom watered thereafter (in an individual tray for each pot). Additionally, all pots were given approximately the same volume of 20-20-20 NPK solution weekly. The greenhouse was maintained at 16 h of daylight at 25°C and at 20°C for the remaining 8 h.

Table 1. Characteristics of the study species. Numerical abundance rank refers to the rank of abundance (number of rooted units) observed at the Queen's University Biology Station, Chaffey's Locks, Ontario, Canada ($44^{\circ}34'N$, $76^{\circ}20'W$).

Species	Life form	Max. field dry mass (g)	Seed mass (mg)	Numerical abundance rank
<i>Asclepias syriaca</i> L.	Forb	128.00	5.13	4
<i>Aster novae-angliae</i> L.	Forb	16.80	0.38	5
<i>Chrysanthemum leucanthemum</i> L.	Forb	2.21	0.517	7
<i>Dactylis glomerata</i> L.	Grass	1.40	1.16	6
<i>Eupatorium perfoliatum</i> L.	Forb	5.11	0.163	9
<i>Lycopus americanus</i> Muhl.	Forb	2.50	0.325	3
<i>Phleum pratense</i> L.	Grass	2.40	0.478	1
<i>Rumex crispus</i> L.	Forb	25.82	1.308	10
<i>Solidago canadensis</i> L.	Forb	33.80	0.065	2
<i>Trifolium pratense</i> L.	N-Fixing Forb	3.28	1.86	8

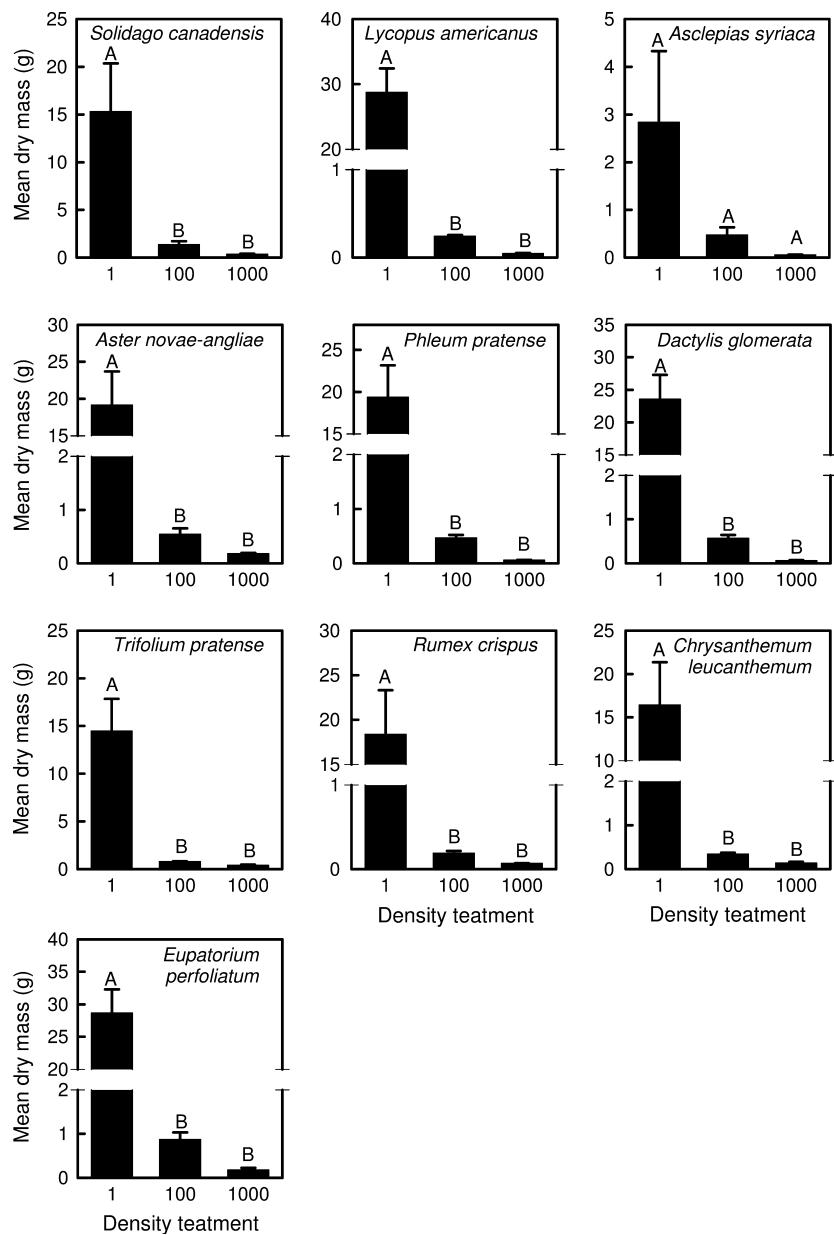


Fig. 2. Biomass per species in monoculture treatments. Bar plots and SE of mean dry mass accumulation per individual in three monoculture density treatments per species ($n = 5$ for each treatment). Separate plots indicate this pattern for each of the ten study species. Density treatments topped with different letters (i.e. A, B, C) indicate those for which dry mass per individual is significantly different at $\alpha = 0.05$ using ANOVA with Tukey–Kramer multiple comparison tests.

Harvest

All pots were harvested between 24 Sept and 15 Oct 2005 after ca. 4 mo of growth. During harvest, all individuals (i.e. genets) were enumerated and each was measured for above-soil fresh weight. Mean dry weight/individual/species/pot was later calculated using the dry weight (after 7 d in a drying oven at 80 °C) per species divided by the number of individuals of that species in a particular pot.

Data analyses

Survival per species per pot was calculated as the number of individuals alive at the end of the experiment, divided by the mean estimate of germination for each species. This mean estimate was determined as the mean number of seeds germinating in each of the five replicate monocultures, per species (Density 100). To measure germination, weekly counts were done for each of the

50 monoculture pots (Density-100) for the first 8 wk of the experiment. It is assumed in this study that germination rates of all species in monoculture reflect germination rates in mixture.

In all cases, the results of competition were measured in terms of both biomass production and survival per species, which represent two important components of fitness. The relative effects of intra- and inter-specific competition on species were assessed both in terms of mean biomass production per individual, per species and mean survival per species in monocultures relative to mixtures.

Using linear regression, we tested the prediction that growth (mean biomass production) and survival in monoculture relative to mixture was a negative function of species/seed size. Maximum species size was used as a measure of species size and was taken as the maximum wet/dry biomass produced among the five replicates per species when grown at a density of one plant per pot. Maximum size here reflects the maximum growth rate for the duration of the experiment rather than the actual maximum size of the species. Dry mass and fresh mass were uncorrelated for the ten test species, and all analyses were therefore done in consideration of both measures as dry mass reflects resource capture while fresh mass likely better reflects the ability of a plant to compete for light. Regression analyses were one-tailed tests based on previous work highlighting the competitive advantage of plant and seed size, as well as the self-thinning literature. Based on these studies, as well as self-thinning research, it is not possible for these relationships to be positive. We then tested our prediction that the slope of these relationships would be <-1 using a *t*-test. Data were log transformed as necessary to approximate normal distributions and improve variance homogeneity.

During germination trials, it became apparent that some species germinated very quickly, while others germinated more variably through time. Because such variation in germination timing can lead to size-asymmetric competition (Howell 1981; Watkinson et al. 1983), we investigated the potential for this variation to contribute to species success in monocultures relative to mixtures in terms of biomass and survival. Given the abundance of work on the impact of seed size on community dynamics (e.g. Gross 1984; Gurevitch et al. 1990; Westoby et al. 2002), we also included an analysis of the effects of seed mass on growth and survival.

Lastly, to investigate the potential for these results to contribute to our understanding of plant community structure, we explored a possible relationship between species size as recorded in the present experiment and its abundance in the field (as observed in Fig. 1), or whether the latter was better predicted by survival in experimental monocultures relative to mixtures.

Results

Maximum biomass and seed size effects on growth and survival

Mean biomass production (fresh weight) of species in monoculture relative to mixture decreased with increasing maximum species size (maximum fresh weight of plants at density = 1; Fig. 3a), although this relationship was not statistically significant ($P = 0.22$). In an effort to improve statistical power in this analysis, as we lose a great deal due to the use of the mean of biomass production per species across replicates, we used all five monocultures for each species as replicates. To increase the independence of these measures in the face of our common mixtures, we calculated biomass production in each monoculture relative to the mean biomass production of five randomly chosen mixtures. This technique did not improve the power of analysis, and was therefore not pursued further.

Mean survival in monoculture relative to mixture was significantly negatively related to maximum species size ($R^2 = 0.23$; $P = 0.045$; Fig. 3b). Although there is a disproportionately larger impact of intra-specific competition relative to inter-specific competition on the survival of large species, the slope of this relationship was not significantly <-1 ($t = -0.58$, $P = 0.287$). The relationships in Fig. 3a and b were not significant using dry mass as a measure of species size ($P = 0.76$ and $P = 0.64$, respectively).

Seed mass was significantly negatively related to fresh mass production in monoculture relative to mixture ($R^2 = 0.302$, $P = 0.029$; Fig. 3c); however, the slope of the regression of fresh mass production in monoculture relative to mixture on seed mass was not significantly <-1 ($t = 0.1677$, $P = 0.435$). Survival in monoculture relative to mixture declined with increasing species size, but this pattern was only marginally significant ($R^2 = -0.53$, $P = 0.058$; Fig. 3d). In both of these analyses, the exclusion of *Asclepias syriaca* L. as an outlier in seed size, makes these negative relationships highly significant (fresh mass production: $R^2 = 0.744$; $P < 0.001$; survival: $R^2 = 0.886$, $P < 0.001$).

Germination variation

Both mean biomass production and mean survival in monocultures relative to mixtures were unrelated to variation in germination timing (calculated as the coefficient of variation) (biomass production: $P = 0.492$; survival: $P = 0.325$).

Predictions for community structure

Neither maximum biomass (fresh) nor mean survival in monoculture relative to mixture were predictive of

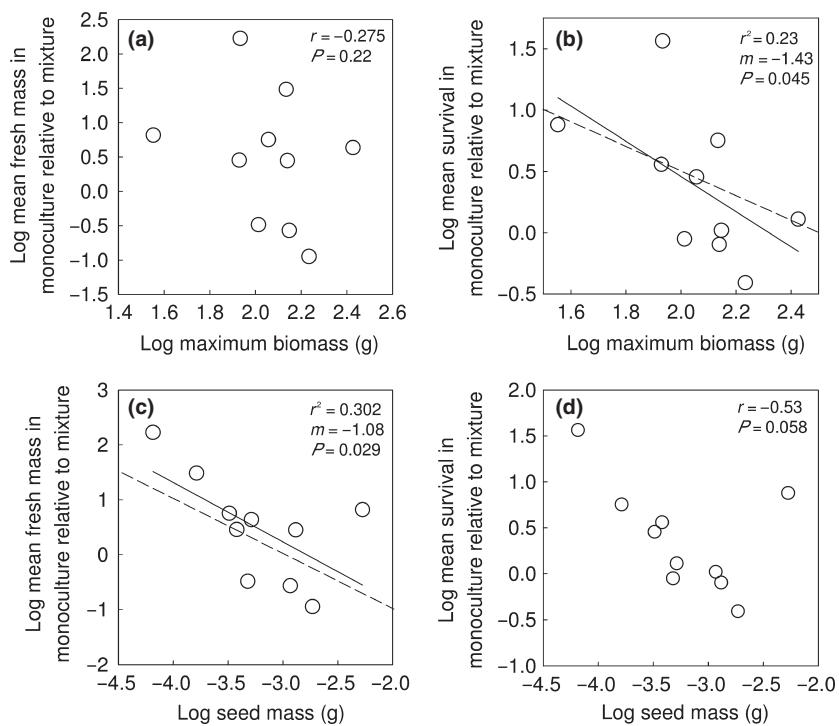


Fig. 3. Intra- relative to inter-specific competitive effects in relation to maximum biomass and seed mass. Regression analyses for two components of fitness, growth (panels **a**, **c**) and survival (panels **b**, **d**) vs. maximum biomass (g) (panels **a**, **b**) and seed size (g) (panels **c**, **d**). Maximum biomass is the maximum accumulation of fresh mass (g) over the course of the experiment. All variables were \log_{10} transformed to meet normality, and homogeneity of variance requirements of regression. Dashed lines have a slope of -1 , for comparison.

patterns of species abundance in a local target community (maximum biomass: $R^2 = 0.30$, $P = 0.103$; survival in monoculture relative to mixture: $R^2 = 0.13$, $P = 0.306$). There was a weak negative relationship with maximum biomass, although power is low for establishing this relationship given the number of data points and scatter observed.

Discussion

Our results suggest that plant performance under intra-specific competition relative to inter-specific diffuse competition is negatively related to maximum biomass and seed size. Survival in monoculture relative to mixture was significantly negatively related to maximum biomass (Fig. 3a,b). Although this relationship had a slope <1 , as predicted, it could not be statistically distinguished as such, likely due to relatively low statistical power resulting from the significant scatter observed. Seed size was also significantly negatively related to biomass production in monocultures relative to mixtures, and marginally significantly negatively related to survival in monocultures relative to mixtures; (Fig. 3c, d). Although slopes of these relationships were <-1 , this was again not supported by statistical

testing. The degree to which larger/larger-seeded species experience disproportionately higher intra-specific competitive effects relative to inter-specific effects will require further confirmation with a larger sample size. While we did not find a significantly negative relationship between species size and mean biomass production in monoculture relative to mixture, this is perhaps not surprising as competition studies examining biomass production do not account for differences in survival rate with increasing size that will inevitably result from the increasing effect of self-thinning on relatively large plant species. This draws attention to a problem among competition studies that will require a larger forum for further discussion.

We believe that these results signal the potential for greater negative density-dependent regulation of relatively large plant species, such that large species suffer greater competitive stress when densely surrounded by conspecifics, while smaller species will do best under such conditions. This is of particular relevance given that the majority of plant communities can be characterized by a strongly right-skewed distribution of maximum species size, in which very large species, as well as large individuals, are rare relative to small species/individuals (Aarssen & Schamp 2002; Aarssen et al. 2006). This kind of trait-mediated

negative density dependence may therefore help prevent large species from forming monocultures, excluding smaller competitor species entirely. This is consistent with previous findings that monocultures of larger herbaceous plant species are more susceptible to invasion, and that invasion tends to be by smaller species (Schamp & Aarssen 2010). Thus, this effect may enhance the co-existence of old-field plant species that compete for a similar set of limiting resources (Molofsky et al. 1999; Chesson 2000).

To investigate the generality of this pattern, we explored previously published data on pair-wise competitive relationships among seven old-field plant species (Goldberg & Landa 1991). We explored the relationship of both per individual, and per gram competitive effect on conspecifics relative to the average effect of heterospecific neighbours in relation to maximum relative growth rate (RGR_{max}), and maximum final mass as defined by Goldberg & Landa (1991). Species with a higher RGR_{max} had significantly larger per gram effects on conspecifics than they did, on average, on heterospecifics (Fig. 4a). The slope of this relationship was also significantly >1 ($t = 2.75$, $P = 0.035$), indicating that species with higher RGR_{max} have a disproportionately greater intra-specific per gram effect relative

to the average inter-specific effects. No significant per individual effect of RGR_{max} was observed (Fig. 4c). Species with a larger final mass had a much greater intra-specific per individual competitive effect (Fig. 4c), and the slope of this relationship was significantly greater than 1 ($t = 4.003$, $P = 0.005$), in support of the predicted disproportionately greater intra-relative to inter-specific competitive effect of larger species.

Pair-wise competition data from Goldberg & Landa (1991) emphasize that the relative size of competitors (intra- or inter-specific) can predict the outcome of competition. Similar-sized species will have similar inter- and intra-specific competitive effects on one another. Hence, larger species within a community context will *necessarily* experience greater intra- than inter-specific competitive effects until a more competitive species arrives in the community. The degree to which relatively larger species experience a *disproportionately* greater effect of intra-specific relative to inter-specific competitive effects will be important in determining the degree to which density dependence regulates the dominance of large species in plant communities. It remains to be seen, using larger groups of species, what the shape of this relationship is at the

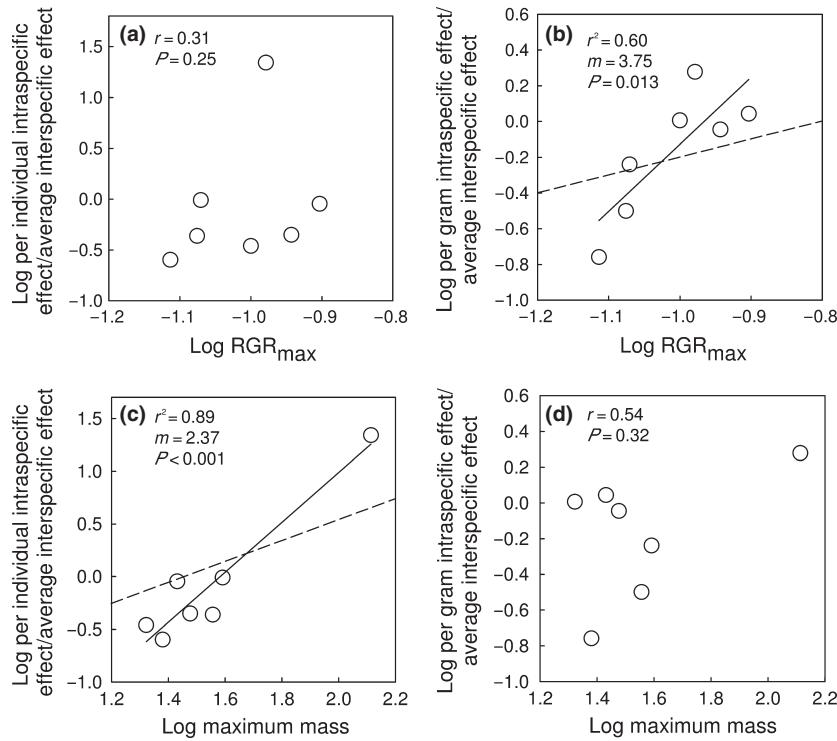


Fig. 4. Re-analysed data from Goldberg & Landa (1991). Regression analyses of intra- relative to mean inter-specific competitive effect on RGR_{max} (panels a, b) and maximum plant mass (panels c, d). Relative competitive effects (intra-/mean inter-specific effect) were considered both as per individual effects (panel a, c) and per gram effects (panel b, d). RGR_{max} was reported in Goldberg & Landa (1991) as the log of maximum dry mass accumulation in mg per mg seed mass, per day. Maximum mass was reported as the maximum above- + below-ground biomass accumulated when grown alone for 5 wk (Goldberg & Landa 1991). Variables were \log_{10} transformed as necessary. Dashed lines have a slope of 1 for comparison.

community scale. Combined with the results of this study, these data demonstrate that larger/larger-seeded herbaceous plant species, species that are frequently found to sit at or near the top of competitive hierarchies, are more highly impacted by intra-specific competition than inter-specific competition. This may be of increasing importance when species tend to form aggregations, such that most individuals predominantly interact with conspecifics (e.g. Rees et al. 1996; Monzeglio & Stoll 2005).

Our results indicate that both pair-wise and diffuse competition are impacted by variation in species size. It can therefore be expected that size variation will also have consequences in natural vegetation (i.e. the species size distribution; Goldberg 1990; Aarssen & Schamp 2002). Thus, two distinct processes may contribute to the co-existence of large and small species in plant communities. First, for relatively small species, which make up the bulk of individuals in plant communities that have characteristically right-skewed species size distributions (Aarssen et al. 2006), competitive equivalence may be a general rule (Aarssen 1983; Pacala 1988; Freckleton & Watkinson 2001). This notion is clearly most relevant to collections of species within a single guild that overlap significantly in niche (Aarssen 1983; Goldberg & Werner 1983). Second, species that are very different in size may co-exist because small species can avoid competition with larger species by occupying 'physical space niches' that result from density-dependent mortality among relatively larger species. This interpretation conforms to the general predictions of Scheffer & van Nes (2006), that evolution can result in sets of species that compete similarly/interact neutrally (Aarssen 1988; Hubbell 2001, 2005), as well as others that are sufficiently different to avoid competition through niche separation.

The degree to which the observed potential for size-mediated negative density dependence may contribute to the co-existence of large and small species remains uncertain, and it is not clear that this effect is sufficient to explain the ubiquitous presence and abundance of small species in natural communities. There are other factors that may contribute to the co-existence of large and small species. Some evidence supports a trade-off between herbaceous species size and susceptibility to invasion (Schamp & Aarssen 2010), which supports the notion that larger species, through self-thinning when abundant, will yield space for colonization and growth by small species. It has also been suggested that smaller species are more efficient at channelling resources to reproduction to ensure fitness under competitive suppression (Aarssen 2008); some data have accumulated in support of this prediction (Weiner et al. 2009; Bonser 2013). Hence, the observation in this study that large species suffer more under intra-specific competition, while smaller species suffer less when

growing with conspecifics, appears to contribute, along with other factors, to the co-existence of large and small plant species.

Larger plant species self-thin to a level where they appear to be more inefficient in their use of space/resources. For this reason, we suggest that relatively small species may be able to successfully use these 'physical space niches', thereby improving resource use efficiency through a form of post-thinning complementarity (Aarssen et al. 2006). This is one possible explanation for the observation that large and small species either co-exist more frequently than expected by chance (Weiher et al. 1998; Swenson & Enquist 2009), or no more or less than expected by chance (Schamp et al. 2008). If the percentage of variance in biomass production that is explained by diversity can be interpreted as the proportion of niche overlap characteristic of plant communities, the contribution of size differences to functional niche differentiation and complementarity represents an important line of inquiry. Future work investigating this possibility could involve examining the degree to which over-yielding is related to size differences between constituent species (Berendse 1979, 1981).

Maximum biomass in terms of fresh mass accumulation appears to be a better predictor of survival in monoculture relative to mixture than dry mass production (Fig 3), which has more traditionally been used as a measure of relative competitive success. For two reasons we believe that fresh mass is an important measure of species size. First, experimental plants received nutrient additions on a weekly basis in this experiment, and therefore, competition in this experiment would primarily have been for space and light. Fresh mass may be a better measure of a species' ability to intercept light for photosynthesis. Second, fresh mass is a more accurate, albeit imperfect, measure of the extent to which an individual takes up space in three dimensions. In natural vegetation, live plants compete with each other for space and light in terms of the effects of their relative fresh mass, not dry mass.

While plants grown singly in this study were allowed to grow for 4 mo, which is similar to the growing time available in temperate natural systems, maximum dry mass as recorded experimentally was not correlated with maximum dry mass recorded from the field (results not shown). It is possible that fresh mass from the experiment may have been correlated with fresh mass from the field; however, fresh mass data for field-collected species were not available. Also, all species measured in the field were in crowded conditions, whereas maximum size in our experiment reflects the size that species may obtain when grown without competition. When grown in absence of competition, several species quickly spread laterally through clonal extension, taking up the entire surface area of the pot. The

difference in maximum biomass obtained experimentally vs. in the field may signal a trade-off, whereby some species that do not obtain large size under crowded conditions are able to capture space quickly when it becomes available, comparable to a kind of competition/colonization trade-off (e.g. Turnbull et al. 1999). Finally, the lack of correlation between experimental dry mass and field dry mass may have been impacted by our limited sample size (ten species).

Neither maximum fresh biomass, as determined experimentally, nor survival in monoculture relative to mixture was related to numerical abundance in a local old-field community where these ten species co-exist. Predicting abundance at the community level may be difficult in the absence of estimates of competitive interaction data for all constituent species, and a better understanding of the degree to which some pair-wise competitive relationships may modify competitive dynamics in natural communities (e.g. Laird & Schamp 2006). Furthermore, our inability to predict abundance patterns from traits that drive competitive ability may result from differences in fecundity allocation patterns among species (Aarssen & Keogh 2002), the degree to which species of different size may be efficient at translating resources into reproduction (Aarssen 2008; Weiner et al. 2009; Bonser 2013) and limitations to our sample size. Finally, theoretical explorations of the community-level impact of size-dependent negative frequency dependence are required to determine what equilibrium abundance patterns can result, given typical species size distributions.

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