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Original article

Big plants — Do they affect neighbourhood species richness and composition in herbaceous vegetation?



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A R T I C L E I N F O

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ABSTRACT

According to traditional theory, success in competition between plant species generally involves a 'sizeadvantage'. We predicted therefore that plants with larger body size should impose greater limits on the number of species — especially relatively small ones — that can reside within their immediate neighbourhoods. Species composition was compared within local neighbourhoods surrounding target plants of different sizes belonging to one of the largest herbaceous species found within old-field vegetation in eastern Ontario Canada — Centaurea jacea. Resident species density was generally greater within immediate 'inner' target neighbourhoods than within adjacent circular 'outer' neighbourhoods, and mean body size of resident neighbour species was unrelated to increases in target plant size. As target plant size increased, the proportion of resident neighbour species that were reproductive increased. Relatively big plants of C. jacea do not limit the number or the proportion of reproductive species that can coexist within their immediate neighbourhoods, nor do they cause local exclusion of relatively small species from these neighbourhoods. These results fail to support the 'size-advantage' hypothesis and are more consistent with the 'reproductive economy advantage' hypothesis: success under intense competition is promoted by capacity to recruit offspring that — despite severe suppression — are able to reach their minimum body size needed for reproduction, and hence produce grand-offspring for the next generation. The latter is facilitated by a relatively small minimum reproductive threshold size, which is generally negatively correlated with a relatively large maximum potential body size.

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1. Introduction

Plant communities, barring frequent disturbance, generally plateau at densities near carrying capacity where competition for space, light and/or soil nutrients is inevitably intense (Grime, 1979; Schoener, 1983; Aarssen and Epp, 1990; Goldberg and Barton, 1992; Gurevitch et al., 1992). Consequently, resident plants experience strong selection for competitive ability, and a wealth of experimental studies has been carried out with the goal of predicting the species characteristics involved. The most common result of these studies supports a body size-advantage, such that smaller species are generally competitively inferior, particularly when competition is for above-ground resources like light and space (e.g., Gaudet and Keddy, 1988; Keddy and Shipley, 1989; Goldberg and Landa, 1991; Keddy et al., 1994; Rosch et al., 1997; Keddy, 2001; Keddy et al., 2002; Warren et al., 2002; Violle et al., 2009; Wang et al., 2010). These results, however, cannot be reconciled with the fact that large and small species routinely coexist within natural vegetation (Aarssen and Schamp, 2002), and relatively small plant species are in fact numerically dominant, in terms of both individuals and species — a pattern that holds across floras, and down to the local community scale (Aarssen et al., 2006). A size-advantage in competition, if it functions within crowded vegetation, should generally exclude small plant species, limiting them to more frequently disturbed sites, where competition is less important.

It is not just the omnipresence of small species within plant communities that signals the lack of a functioning size-advantage in plant competition. Were a size-advantage functioning within communities, large and small species would not generally be found growing in close proximity. However, several studies have found no evidence that coexisting plant species are more similar in maximum height than would be expected by chance in grasslands (Schamp et al., 2011), old field vegetation (Schamp et al., 2008), wetlands (Weiher et al. 1998), temperate forests (Schamp and Aarssen, 2009), and tropical forests (Swenson and Enquist, 2009). Additionally, no evidence of species size convergence along a successional gradient was found in a dune succession system, despite





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that species size asymmetry increases greatly along this gradient (Waugh and Aarssen, 2012). Finally, in a study examining the diversity of species found growing beneath large woody species in temperate forests, no evidence was found for a consistent reduction in diversity beneath larger species (Keating and Aarssen, 2009). Together, these results do not support the functioning of a general size-advantage in competition within these natural communities.

There are several possible explanations for the fact that natural systems do not appear to conform to the expectations of a competitive size-advantage in competition that is regularly found in competition experiments. First, it is possible that support for a size-advantage arises principally from methodologically limited or flawed approaches to understanding the characteristics associated with competitive superiority. For example, most studies have measured competitive effects in terms of reduction in biomass production, rather than as a reduction in reproduction (Aarssen and Keogh, 2002). Neytcheva and Aarssen (2008), however, found that total reproductive output for a species emerging from high density seed mixtures was best predicted, not by potential body size, but by the number of survivors that — although suppressed in size by the high density -could nevertheless attain at least some reproduction because of relatively small reproductive threshold sizes. Large potential body size can rarely be achieved under severe crowding. Accordingly, competitive suppression under high density/crowded conditions may instead select for relatively small reproductive threshold size, which may include capacity to reproduce at a relatively small fraction of maximum potential body size (Aarssen, 2008: Chambers and Aarssen, 2009: Tracev and Aarssen, 2011). This greater reproductive economy for small species has been suggested by allometric studies of annual plant species (Weiner et al., 2009) and by a recent analysis indicating that reproductive efficiency increases under increased competition intensity (Bonser, 2013). Finally, experimental derivations of competitive ability have universally focused on competing species that have started growing at the same time yet interspecific competitive relationships have been shown to vary with plant age (Grace, 1985; De Steven, 1991; Lamb and Cahill, 2006; Zhang and Lamb, 2012). Thus, experimentally derived hierarchies are probably poor predictors of the likely more complex competitive outcomes that occur in natural vegetation, which may respond to the order in which individuals of different species establish (Kennedy et al., 2009). It is clear that more work is required to explain why the competitive size-advantage so often observed in experimental studies is not clearly manifested in the size distributions of resident species within natural plant communities.

In this study, we explicitly explore the impact of a large 'target' plant on the composition of its immediate neighbourhood in old-field vegetation. We examine the immediate neighbourhoods of different sized *C. jacea* L. (Asteraceae) plants to assess whether: a) the size of a target *C. jacea* plant is associated with the density of species growing in its immediate neighbourhood; b) whether the size variation of species in the target neighbourhood changes with target plant size; and c) whether *C. jacea* plant size is related to the proportion of neighbouring species achieving reproduction.

2. Materials and methods

2.1. Study site and study species

The study was conducted during August (late summer) 2010, in an old-field community — approximately 10ha in size and bordered by woodland — at Queens University Biological Station (44°33'N, 76°21'W), located north of Kingston, Ontario, Canada. The field is highly productive with deep, mesic, fertile soil, that originally (prior to European colonization) supported mixed deciduous forest. The site had been used historically for having and some cattle grazing but had otherwise been left mostly undisturbed for at least ten years prior to the start of the study. The species composition was typical of eastern Ontario old-field habitats, with a mix of native and introduced grasses, legumes and other forbs, numbering about 35 species in total. The target species, *C. jacea*, native to Eurasia, was by far the largest species in the study field in terms of biomass production and lateral extent, and it was the third tallest (unpublished data). C. jacea is one of the largest herbaceous perennial species found in old-field habitats of eastern Ontario, Canada. It flowers from June–October and has an openly branched growth form, commonly reaching heights of up to 1.5 m. Variation in target plant size is likely to be related to a combination of variation in plant age, genotype, and variation in local soil nutrient status within the study community. We were not concerned with possible interference from the influence of soil nutrient variation as a size-advantage in competition reflects asymmetric competition for light rather than soil nutrients (Schwinning and Weiner, 1998).

2.2. Selection of 'target' plants

The three largest plants of *C. jacea* within the population were selected, and 16 additional C. jacea plants were selected to obtain a large range of body size among 'target' plants — based on visual estimation, taking account of both height and lateral extent. The three largest plants were easily more than twice as large as the largest plants of any other resident species within the community. For the 16 target plants with a broad range of sizes, individuals were chosen without bias, with the exception that the target plant could not have any other relatively large near-neighbouring plants that belonged to any other species. In other words, within both the inner (TA) and outer (TB) target plant neighbourhood (see Fig. 1), there were no other resident plants belonging to any other species that were any larger than half of the size of the target plant-based on visual estimation, and taking both height and lateral extent into account. This was done in order to ensure that potential effects on the composition of the resident species within the target neighbourhoods could not be attributed to any other relatively large plants nearby. If this condition was not satisfied, then the potential target plant was rejected for sampling. In addition, the objective was to assess the effect that a relatively large individual (not a large clump of individuals) of the study species has on the composition of



Fig. 1. Diagram illustrating the target neighbourhood at two scales — TA and TB. See text for details.



Fig. 2. Neighborhood size and Target plant size effects on neighborhood diversity. Resident neighbour species richness versus target plant neighbourhood area (a, b, c); resident neighbour species richness versus target plant dry mass (d, e, f); and resident neighbour species density versus target plant dry mass (g, h, i) — for inner target neighbourhoods only (a, d, g); outer target neighbourhoods only (b, e, h); and total neighbourhoods (c, f, i). Note log-scales in some plots. *r*- and associated *P*-values are from Pearson Product Moment correlation analyses with log transformation applied to neighbourhood area, dry mass, and species density to achieve normality.

its immediate neighbourhood; accordingly, dense clumps were avoided by selecting only target plants that had no conspecific neighbours that were larger than half of the target plant size residing within its inner or outer target neighbourhood (see Fig. 1). We used dry biomass as our measure of target plant size; however, biomass was strongly positively correlated with height (r = 0.931, P < 0.0001) and lateral extent (r = 0.933, P < 0.0001) which determined the radius of the inner target neighbourhood (all variables log transformed).

2.3. Delineation of target neighbourhood (Fig. 1)

The target plant's immediate neighbourhood was defined at two scales, delineating an 'inner' versus 'outer' target neighbourhood:

TA – the circular area defined by a radius rA centered on the rooted location of the target (C) and extending to the outermost limit of the lateral leaf/branch canopy extent (point A);

TB – the circular area defined by a radius $rB = (rA + \frac{1}{2} rA)$, extending to point B, centered on the rooted location of the target (C; Fig. 1).

2.4. Data collection

For each of target plant, data collection involved 4 stages:

- (1) When the study species (*C. jacea*) was in the flowering stage (with visible open flowers, but before any flowers/dry mass was lost), a suitable target plant (see criteria above and Fig. 1) was located and its lateral extent (distance from the rooted location to the point of the furthest reaching outer shoots) was recorded. Flag A (see Fig. 1) was inserted at this point and then the target plant was cut at ground level and placed in a paper bag for later dry-weight measurement in the lab. A flag (C, Fig. 1) was placed where the target plant was rooted; then flag B (Fig. 1) was inserted and the radius rA and radius rB were recorded (see above and Fig. 1).
- (2) The perimeter for the two scales of the target neighbourhood was delineated, TA and TB, as described above (Fig. 1): The radius measurements rA and rB were used to calculate the circumferences $(2\pi r)$ for TA and TB and these circular perimeters were marked with large adjustable metal hose clamps.



Fig. 3. Species density in inner versus outer neighbourhoods. Relationship for resident neighbor species density (per cm²) in outer neighbourhoods versus inner neighbourhoods for target plants of *Centaurea jacea* ranging in size — coded in the graph from smallest to largest dry mass by the numbers 1 to 19 respectively. Dashed lined is shown only to indicate the 1:1 line. Variables were log-transformed to achieve normality. *t*- and associated *P*-values are from a paired *t*-test.

- (3) A list of all species residing within TA (the 'inner' target neighbourhood), was recorded, with notes indicating, for each species, whether or not at least one of the individuals were reproductive (showing flowers or fruits or evidence of their recent attachment to the plant, e.g. a peduncle).
- (4) A list of all species residing within the donut-shaped 'outer' target neighbourhood was recorded, with notes indicating, for each species, whether or not at least one of the individuals was reproductive.

2.5. Data for resident neighbourhood species body sizes

The typical maximum adult plant heights for resident species recorded within target neighbourhoods were obtained from published data reported in Gleason and Cronquist (1991).

2.6. Data analyses

We used Pearson Product Moment correlations to test whether species richness increased with area and with target plant size, and also to test whether neighbourhood species density declined with target plant size. We used similar correlation analyses to assess whether target neighbourhood species mean body sizes changed with target plant mass, and to determine whether target mass was associated with a change in the reproductive status of species in associated inner and outer neighbourhoods. We used a paired *t*-test to examine whether inner neighbourhood plant species density was greater than outer neighbourhood plant density across our 19 target plant neighbourhoods. Variables were log transformed where necessary to meet the requirement that data be normally distributed.

3. Results

Resident species richness increased with both increasing target neighbourhood area (Fig. 2a–c) and increasing target plant size

(Fig. 2d–f), whereas resident species density decreased with increasing target plant size (Fig. 2g–i). Resident species density was significantly greater (P < 0.001) within inner (compared with outer) target neighbourhoods (Fig. 3). Mean body size of resident neighbour species (based on published height data) was unrelated to increases in target plant size (Fig. 4). As target plant size increased, the number of reproductive resident species increased (Fig 5a–c), and for inner target neighbourhoods (but not outer or total, Fig 5e and f),



Fig. 4. Target plant height in relationship to the height distribution of neighbour species. Relationship between target plant dry mass (g) and mean resident neighbor species maximum height (based on published data). (a) inner neighbourhoods only; (b) outer neighbourhoods only; (c) total neighbourhoods. Target dry mass is plotted on a log scale. *r*- and associated *P*-values are from Pearson Product Moment correlation analyses with dry mass log-transformed (to achieve normality).

the proportion of resident neighbor species that were reproductive increased with target plant size (P = 0.045, Fig 5d).

4. Discussion

According to traditional plant competition theory, larger plant body size generally confers superior competitive ability, particularly in competition for light (Grime, 1979; Grace, 1990; Goldberg, 1996). Based on this 'size-advantage hypothesis' we predicted that plants with larger body size should impose greater limits on the number of species—especially relatively small ones—that can reside within their immediate neighbourhoods. We tested this prediction by comparing neighbourhood composition for target plants of different sizes belonging to one of the largest herbaceous species found within old-field vegetation in eastern Ontario Canada — *C. jacea.*



Fig. 5. Target plant size in relation to the number/proportion of reproductive neighbour species. Relationship between target plant dry mass (g) and the number of reproductive (a, b, c), and proportion of reproductive (d, e, f) resident neighbours species — for inner neighbourhoods only (a, d); outer neighbourhoods only (b, e), and total neighbourhoods (c, f). Dry mass is plotted on a log scale. r- and associated *P*-values are from Pearson Product Moment correlation analyses with dry mass log-transformed (to achieve normality).

We found no evidence to support this prediction. Resident species density within target neighbourhoods decreased with increasing target plant size (Fig. 2g-i) — however, this is accounted for by the relatively small (only 2.5-fold) increase in species richness across about a 28-fold increase in target neighbourhood area (Fig. 2a-c), involving about a 280-fold increase in target plant dry mass (Fig. 2d-f). Across the vast majority of the range of target plant sizes—i.e. across the 14 largest target plants—species density decreases (Fig. 2g-i) only because neighbourhood area increases with no net change in species richness (Fig. 2a-c). In other words, increasing neighbourhood species richness plateaus at a relatively small neighbourhood area (Fig. 2a-c), associated with a relatively small target plant size (Fig. 2d-f). Resident species density was also generally higher (not lower as the size-advantage hypothesis would predict) within inner target neighbourhoods compared with outer target neighbourhoods (Fig. 3).

Larger plant size may also confer an advantage (proportional to size) in competition for below-ground resources, particularly in less productive ecosystems. But our old-field study site is productive, having originally (prior to European colonization) been mixed deciduous forest over deep mesic, fertile soil. Competition, especially for light therefore, is expected to be important here, and this should-according to the 'size-advantage' hypothesis-promote local competitive exclusion of relatively small species. Yet, we did not find this. It is possible that our larger target plants may be partially indicative of more favorable local substrate conditions, and so higher diversity in the inner neighbourhoods of larger target plants may be partially associated with variation among neighbourhoods in soil resource levels. However, target plant size variation is just as likely, or more likely to be, we suggest, indicative of variation in plant age, or variation in genotype or history of local impacts by consumers.

In addition, larger target plants did not exclude relatively small species from their neighbourhoods (as predicted by the sizeadvantage hypothesis); mean size of resident neighbour species (based on published species maxima) was unrelated to increases in target plant size (Fig. 4). While we did not measure actual sizes of species within target neighbourhoods, and some suppression of individuals through light restriction by the target plants is possible, across our samples, this effect should have been visible through the exclusion of smaller species. It would have been preferable to have field-determined mean and maximum potential size data for the species resident within our study site, but we note that these are likely to be significantly correlated with the size data that we used from the standard flora for the study region. Our analysis of unpublished data from nearby sites (with similar species composition) shows that both the mean and maximum potential sizes of resident species are significantly positively correlated with the maximum heights obtained from local floras.

The size-advantage hypothesis would also predict that, as target plant size increases, the number of resident species should increase or remain constant (simply because of the effect of greater area to contain more species) but the proportion that are reproductive should decrease because of greater suppression in the presence of a larger target plant. This was not supported by our data (Fig 5), and in fact the proportion of resident neighbor species that were reproductive increased with target plant size for inner neighbourhoods, where proximity to the target plant was greatest (P = 0.045, Fig 5d). The observed coexistence of large and small species may be explained by canopy partitioning between large and small species (Nevai and Vance, 2007; Kohyama and Takada, 2009). However, the increased density of reproductive species in the neighbourhood of increasingly large target plants is consistent with evidence supporting a higher reproductive efficiency for relatively small species (Weiner et al., 2009, Bonser, 2013).

These data are more consistent with what might be called the 'Reproductive-Economy-Advantage' hypothesis: the ability of a species to persist within vegetation that has intense crowding/ competition from neighbours is promoted by 'reproductive economy' — the ability to produce offspring in spite of severe size suppression (caused by crowding/competition) (Aarssen, 2008). This may be especially facilitated by a relatively small minimum reproductive threshold size (MRTS), which is generally negatively correlated with a relatively large maximum potential body size (MPBS); and recent research has shown, for old-field vegetation, that resident species with smaller MRTS (and hence generally smaller MPBS) have generally higher numerical abundance (i.e. a greater number of individuals) (Tracey and Aarssen, 2011).

A reproductive economy advantage for species with smaller body size may involve two possible mechanisms (Aarssen et al., 2006). The first involves an interpretation of differences in competitive fitness — the relative abilities to transmit genes to future generations when plant size is severely suppressed under intense crowding of similar-sized neighbours or competition from larger neighbours. Under these conditions, species with relatively large MPBS only rarely manage to recruit offspring that are able to reach their relatively large minimum body size needed for reproduction, and so-unlike smaller species-they commonly die without producing any grand-offspring for the next generation (Tracey and Aarssen, 2011). The second mechanism involves a form of niche differentiation, with two components: (i) smaller species (because of their smaller MRTS) have smaller 'physical space niches' — i.e. the physical space containing enough resources for an individual to produce at least one offspring; and (*ii*) larger species because they are less efficient at harvesting all of the resources within their immediate neighbourhoods - generate a variety of relatively small physical space niches within these immediate neighbourhoods that contain small parcels of these 'unused' resources that are sufficient in quantity for individuals of smaller species to reproduce successfully. The present results support the above interpretations, as resident species density was generally higher within inner target neighbourhoods compared with outer target neighbourhoods (Fig. 3), and the proportion of resident neighbour species that were reproductive within the inner target neighbourhoods increased with target plant size (P = 0.045, Fig 5d).

In conclusion, our data for old-field vegetation parallel the findings of a recent study in mixed woody vegetation (Keating and Aarssen, 2009), in showing that relatively big plants do not limit the number of species that can coexist within their immediate neighbourhoods, nor do they cause local exclusion of relatively small species from these neighbourhoods. Future studies are required to identify the relative importance of the above two mechanisms for explaining why/how species that vary widely in body size routinely interact and coexist together within natural vegetation, and why the vast majority of them are relatively small, even when crowding/ competition is intense and persistent.

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