Relationships between body size, reproduction, and abundance in natural vegetation

By

Amanda Jane Tracey

A thesis submitted to the Graduate Program in Biology

in conformity with the requirements

for the Degree of Master of Science

Queen's University

Kingston, Ontario, Canada

July, 2012

Abstract

According to traditional theory, superior competitive ability in plants generally requires a relatively large plant body size. Yet, within natural, crowded vegetation, most resident species are small, and species size distributions are right-skewed at virtually all scales. I aim to provide a potential explanation for this paradox: small species are able to coexist with and outcompete larger species because smaller species have greater 'reproductive economy'—the ability for some seed production despite severe size suppression when under intense competition. Tracey and Aarssen (2011) found an isometric relationship between minimum reproductive threshold size (MRTS) and maximum resident plant size (MAX); however, a more accurate measure of maximum potential body size (MPBS) was needed (without competition), as typically the effects of competition are size-dependent. An isometric relationship, similar to Tracey and Aarssen (2011) was seen. Tracey and Aarssen (2011) also found that, contrary to the predictions of traditional theory, larger species were not more abundant (based on plot occupancy) in an old-field community. A more accurate measure of abundance was obtained by locating random 1 x 1 m plots and counting the number of ramets for each species in the plot. A significant negative relationship was seen between abundance and MRTS. This suggests that the most abundant plants in communities are not those that are bigger, or smaller, they are those with the smallest MRTSs. To test whether this relationship exists in other habitats, plots were located in different old-field, shrub-land and wood-land communities. Ramets for each species within the plots were counted, and the largest plant of each species was measured. Significant negative relationships between abundance and MAX plant body size were seen in the shrub-land and woodland sites; however, no relationship was detected in this old-field site. The data support the idea that smaller

species have greater reproductive economy, but the mechanism remains unknown. These results suggest that a smaller plant body size results in more effective gene transmission into future generations in all habitat types and stages of succession and indicates a suggested paradigm shift in the predicted selection effects of competition on the evolution of plant body size.

Acknowledgements

I want to thank my supervisor, Lonnie Aarssen for his guidance throughout this whole process from start to finish. For his input, his assistance, for letting me endlessly bother him, for his "light bulb" moments and for all his support I am very grateful.

A million thanks to Sarah Dombroskie for making every rainy or scorching field day (so *every* field day) fun and every long thesis-writing day bearable.

Many thanks also to Emily Black, Tomo Nishizawa and Stephanie Wight for their assistance with collecting the data for this project.

Thank you to my committee members, Paul Martin and Shelley Arnott, for always pointing me in the right direction when I needed help. Also, many thanks to Bob Montgomerie, Anneli Jokela, Dale Kristensen and Liam Revell for their help throughout this process.

Table of Contents

List of Tables

List of Figures

versus: standardized maximum recorded plant size index; maximum recorded resident plant height (cm); and (**g**)-(**i**) maximum recorded resident plant canopy area (cm^2).

Chapter 1

Introduction

Competition and plant body size

Competition is widely regarded as the most important force affecting plant community structure and assembly (Tilman 1982). Light and soil resources are generally limiting within natural vegetation, and resource acquisition is usually asymmetric—highly dependent on relative plant size (Craine 2009). Many previous experimental studies have confirmed that smaller species routinely experience more suppressed growth than larger species when they compete together (Gaudet and Keddy 1988, Keddy and Shipley 1989, Goldberg and Landa 1991, Keddy et al. 1994, 2002, Rosch et al. 1997, Keddy 2001). According to traditional theory therefore, superior competitive ability in plants is generally regarded as requiring a relatively large plant body size (Grime 1973, Grace 1990, Goldberg 1996), and virtually all published data that quantify and compare plant competitive ability involve size metrics (mass, height, etc.) (Aarssen and Keogh 2002).

The structure of natural vegetation, however, presents a paradox: most species are small, i.e. species size distributions are right-skewed at virtually all scales (Aarssen and Schamp 2002, Niklas et al. 2003, Aarssen et al. 2006, Poorter et al. 2008, Moles et al. 2009, Schamp and Aarssen 2009, McGlone et al. 2010, Dombroskie and Aarssen 2010). Even in later stages of succession, as larger species accumulate over time and cause the local competitive exclusion of some smaller species, other relatively small species take their place and body size distributions typically remain strongly right-skewed (Schamp and Aarssen 2009, Waugh and Aarssen 2012).

Right-skewed body size distributions are also the norm for animals, and several potential explanations have been proposed, including the obvious effects of multi-trophic energy transfer efficiencies, with fewer larger species supported at higher trophic levels—but this interpretation does not apply to body size distributions for plants which are all on the same trophic level (Aarssen et al. 2006). According to the 'left wall' effect, because size cannot be less than zero, the evolution of organismal complexity would be expected to generate a right-skewed, unimodal distribution of species sizes *if body size was selectively neutral* (Stanley 1973, Gould 1988). The latter, however, conflicts with the interpretation from traditional plant competition theory, and countless empirical studies, where 'big is better'.

The 'habitat availability' hypothesis suggests that larger plant species are relatively rare because the origination of larger species has been historically limited by the availability of habitat conditions to which larger species are adapted—i.e. relatively undisturbed, with deep fertile soil—habitat types which have themselves been relatively rare in terms of global area across evolutionary time (Aarssen and Schamp 2002, Aarssen et al. 2006). The 'physical-space-niche size distribution' hypothesis suggests that larger species—precisely because of their larger physical sizes required to reach reproductive maturity—have niche requirements that include a relatively large physical space within which to grow as a rooted unit. This space will necessarily encompass a greater number of local environmental 'patch types' represented by different local combinations of physical, chemical, and biotic (e.g. soil microbe) characteristics. In comparison, a smaller species might be capable of reproducing successfully within just a single patch type. If no species can occupy the same niche, then smaller species may occur in greater numbers simply because they can 'carve up' the environment into a greater number of smaller niches (Aarssen et al. 2006).

Other explanations recognize that smaller species may have generally enjoyed lower extinction rates over evolutionary time because they may normally have larger population sizes with a greater chance therefore—through sheer numbers—of having at least some resident individuals that survive the effects of large-scale catastrophic disturbances (McKinney 1990, Fenchel 1993, Niklas 1994). Accordingly, perhaps more descendants of plants are smaller simply because their ancestors were also smaller (Purvis et al 2003). Again however, for crowded species competing intensely all on the same trophic level, i.e. for a typical natural plant community, species with larger body sizes are traditionally regarded as having superior competitive ability and more likely therefore to recruit offspring for the next generation, and so to have *greater*— not smaller—local population sizes.

An objective of the present study was to test this latter prediction. Rejection would have one or more of three profound implications: (i) recruitment success is not as limited by competition as is usually assumed for most natural vegetation; or (ii) competition intensity is weak because of niche differentiation mechanisms that are still poorly understood; or (iii) relatively small plant body size—contrary to traditional theory—does not impose inferior competitive fitness (ability to recruit offspring under intense competition). The latter is of particular interest in the present study, based on a hypothesis involving greater 'reproductive economy' in smaller species, i.e. a capacity for at least some offspring (seed) production despite severe plant size suppression under competition (Aarssen 2008). Reproductive economy may be linked to a number of traits associated with relatively small species body size in plants, including selection for increased selfing rates, increased clonality, smaller seed size, earlier reproduction or smaller size at reproductive maturity (Aarssen et al. 2006, Aarssen 2008).

If, as traditional theory predicts, having a larger plant body size confers greater success under competition, then we should expect larger plants within populations or communities to be generally responsible for producing most of the offspring available to form the local population in the next generation. However, recent evidence indicates that this is not the case. Chambers and Aarssen (2009) found that under the most crowded conditions within herbaceous angiosperm populations, the vast majority of the total offspring (seeds) available to represent the population in the next generation were produced by resident plants belonging to the second, third and fourth smallest deciles of the plant size distribution. In addition, a recent multiple-species competition experiment with annuals (Neytcheva and Aarssen 2008) found that 97% of the variation in reproductive (seed) output under intense competition, was explained by variation in the number of survivors that, although suppressed weaklings, still managed to reproduce. These studies challenge the traditional view that evolution of competitive ability in plants, under selection from intense competition, has generally favoured a capacity for large plant body size.

Chapter 2

Literature Review

Maximum potential versus minimum reproductive threshold

Plants obviously vary in size, both between and within-species. They differ not only in the maximum potential body size (MPBS) that they can achieve, but also in their minimum reproductive threshold size (MRTS)—the minimum size a plant must be to reproduce (Bonser and Aarssen 2009). This variation in MRTS is expected given the well-known positive between-species relationship for life span versus age at first reproduction (Lacey 1986). For perennials, however, age and size are often poorly correlated, and older plants are not necessarily larger. Because of the enormous capacity for plasticity in plants, variation in plant size within natural vegetation will usually be affected more by variation in the intensity of crowding/neighbor effects than by variation in age (Harper 1977). Few studies have documented relationships for size at first reproduction versus maximum potential body size (Thomas 1996, Davies and Ashton 1999) and only one (Tracey and Aarssen 2011) has documented this relationship within a plant community, where several resident species were coexisting and competing together. Severe crowding limits attainable plant size for most resident species, yet larger size will generally promote greater competitive ability in terms of capacity to deny resources to neighbours. A central question therefore remains unresolved: does selection under intense competition favour larger MPBS or smaller MRTS (Tracey and Aarssen 2011)? Traditional theory predicts the former, but the research conducted here was designed to test for evidence of the latter.

MRTS has been previously infered from studies of reproductive allocation. Allocation studies with plants assume that there is a limited supply of critical resources available that a plant must

divide between competing functions: growth and reproduction. Reproductive allocation is the proportion of biomass that a plant allocates to reproductive versus vegetative growth and is commonly interpreted as reproductive effort (reproductive biomass/total biomass) (Evenson 1983, Wilson 1983, Samson and Werk 1986, Hancock and Pritts 1987, Weiner 1988, Wilson and Thompson 1989).

Reproductive allocation may be allometric, i.e. where the proportion of biomass that a plant allocates to reproduction varies with plant size (Weiner 2009). Samson and Werk (1986) were the first to address the latter with a simple, graphical model of the relationship between allocation to reproduction and plant size. Biomass allocated to reproductive tissues (Reproductive (R): flowers, fruits, seeds) is shown as a linear function of vegetative plant biomass (Vegetative (V): stems, leaves, roots). In any case where the slope of this regression is not equal to 1.0, reproductive effort is always a function of plant size. A regression between biomass allocated to vegetative versus reproductive growth with a positive x-intercept allows one to infer a MRTS (Samson and Werk 1986, Weiner 1988). This model has held true for many herbaceous perennials (Hartnett 1990, Thompson et. Al 1991, Schmid and Weiner 1993, Schmid et al. 1995, Sugiyama and Bazzaz 1998, Echarte and Andrade 2003). Weiner at al. (2009) however, suggest that it is possible for a plant to have a MRTS and not a positive x-intercept.

Studies of reproductive allocation therefore can yield inferences about fitness only in terms of biomass measures (Weiner 2009). Yet, fitness is not about biomass production. It represents success in the transmission of gene copies to future generations. Accordingly, fecundity (number of offspring) or more precisely, 'fecundity allocation'—number of offspring (seeds) produced per unit plant biomass per unit time—is a more direct estimate of fitness (Aarssen and Taylor 1992, Aarssen and Keogh 2002). The latter provides a meaningful measure for

comparing genotypes or species for their potential in transmitting gene copies to future generations. Few studies however, have so far measured MRTS in terms of fecundity. Claus and Aarssen 1994 measured plant size and fecundity in *Arabidopsis thaliana*, where, under light limitation the smallest remained vegetative and so a MRTS could then be measured. A similar "smaller than the smallest non-reproductive" approach was used by Worley and Harder (1996) to identify MRTS in several species.

Other studies have monitored rosette size in plants while counting the mean number of seeds per carpel and concluded that there was a threshold rosette size required for reproduction (Werner 1975, Van der meijden and Van der waals 1979, Auspurger 1985). Hanzawa and Kalisz (1993) identified a minimum leaf size for reproduction using data collected for seed counts, rhizome volume, leaf area and age. Similarly, Inouye and Taylor (1985) recorded seed count and leaf size in *Frasera speciosa* populations to determine a minimum leaf number for reproduction. A few allocation studies have counted seeds or used seed mass as opposed to total mass of reproductive structures and correlated this with plant body size (Hickman 1977, Klinkhamer et al. 1999). Fecundity allocation has also been studied in crop species by examining dry shoot matter and grain yield (e.g. Vega et al 2000).

Abundance and plant body size

If, as traditional theory predicts, superior competitive ability in plants generally requires a larger plant body size, then larger species should recruit offspring more successfully under conditions of intense crowding /competition. A recent review of relationships between body size and abundance suggests that most research in this area has been conducted on animals with little data

available for plants, particularly for the relationship of interest here—the local size-density relationship (LSDR), where the abundance of each species is measured at the same location (White et al 2007). In general, LSDRs show that body size explains little variation in abundance, possibly because LSDRs typically examine a relatively small range of body sizes (compared with global scales), thus accounting for relatively low r^2 values (White et al 2007). A few studies of forest vegetation, however, have shown significant negative between-species relationships for species body size versus local stem density (Condit 1988, Muller-Landau et al 2006). Tracey and Aarssen (2011) measured abundance (based on plot occupancy) in an old-field plant community and found that generally, species with smaller MRTSs were more abundant throughout the community—consistent with some of the earlier studies of forest vegetation. No other comparable data for herbaceous vegetation or mixed (herbaceous plus woody) vegetation are published to my knowledge. Do resident species within early stages of succession—which generally host relatively small species—also display this negative local size/density relationship? How general is this relationship and does it depend on successional stage? These questions inspired the objectives developed for the present study.

Chapter 3

Study Objectives

Tracey and Aarssen (2011) is the first study to suggest a fundamental between-species trade-off between MRTS and MPBS under natural field conditions. However, the measurement of MPBS from this study was only a crude estimate based on the largest resident plant of each species. Thus, the first objective of the present study was to obtain a more accurate measure of MPBS for coexisting species within the same old-field plant community. A large portion of the variation in resident plant body size is likely to be explained by the local crowding/competition effects from neighbouring plants. Although smaller species, based on previous experimental studies (e.g. Gaudet and Keddy 1988), are generally expected to experience greater suppression from neighbouring vegetation, competition is likely to still have some effect on large species. To address this, the present study includes a neighbour removal experiment in order to obtain a more accurate between-species comparison of MPBS—thus allowing a more confident analysis and interpretation of the relationship between MPBS and MRTS.

Tracey and Aarssen (2011) found that smaller species within the community have smaller MRTS, and that—across species—the size of the smallest reproductive individual recorded, MIN, was a constant proportion of MAX, the size of the largest individual recorded (Fig 1a); i.e. isometric, with a slope of 1.0 for log-transformed data. However data for MAX in this study could not be recorded in the absence of competition from neighbours. Figure 1(b) shows the hypothesized relationship, tested in the research presented here, when MAX represents true maximum potential body size (i.e. recorded without competition). Here, a slope greater than 1.0 is predicted since, if smaller species are generally more suppressed by competition, then they

should be expected to show a greater 'release' from the removal of neighbor effects. In other words, they should display a greater increase in MAX when competition is removed, indicated by the relative lengths of the blue arrows in Fig. 1(b). Accordingly, the hypothesized slope greater than 1.0 in Figure 1(b) would suggest that a smaller species generally has greater reproductive economy; i.e. under competition, it is capable of reproducing at a smaller fraction of its MPBS.

Tracey and Aarssen (2011) found that MRTS was a better predictor of species abundance than MPBS. Species abundance however, was based only on plot occupancy, i.e. the number of 1 x 1 m plots, out of 155, that the species was found in. The second objective of the present study, therefore, was to record a more informative measure of species abundance for the same community, based on individual ramet counts—thus providing a more direct estimate of offspring recruitment success. This together with the first objective allowed a more confident analysis and interpretation of the relationship between species body size and local density (reflecting recruitment success).

Traditional plant competition theory is based on a '*size advantage'* hypothesis, i.e. under intense competition, natural selection will generally favour larger plant body size. This implies that larger species should generally transmit more genes into future generations than smaller species do. The greater transmission of genes would be reflected by a higher recruitment success, manifested in turn by greater local (per plot) density (Fig 2a). In contrast, according to the 'fecundity allocation premium hypothesis' (Aarssen et al. 2006), smaller species generally have higher local resident plant density, reflecting greater local recruitment success (Fig. 2b), because they have smaller reproductive size thresholds. Under intense competition, therefore, smaller species have greater 'reproductive economy'—i.e. they are able to produce offspring that,

although severely crowded and/or suppressed in size by competition with larger species, are nevertheless able to achieve sufficient size to produce at least a few offspring of their own, and thus collectively they are more successful in transmitting genes from the parent plant into future generations (Tracey and Aarssen 2011).

A final objective of this study was to test the body size / abundance relationships in Figure 2 for resident plants within natural vegetation representing different stages of succession—in order to explore the generality of this relationship within plant communities, and to consider possible interpretations in terms of the relationship between MPBS and MRTS for different stages of succession.

Chapter 4

Methods and site descriptions

Wire Fence old-field study site

Field work was conducted from May to September in both 2010 and 2011 at the Queen's University Biological Station (QUBS), Chaffey's Locks, Ontario, Canada (44°33'N, 76°21'W). The field—known locally as the 'Wire Fence' field was last tilled and sown about 70 years ago with a hay mixture of timothy (*Phleum pratense* L.) and red clover (*Trifolium pratense* L.), and has been mown for hay periodically, up until summer 2008. The field was otherwise undisturbed with the exception of some hikers and occasional specimen collection by QUBS researchers. The plant community consists of mostly perennial dicots, grasses and sedges, all typical of old-field vegetation in the south-eastern Ontario region. The most common species in the field (measured in terms of frequency of occurrence in plots) are *Phleum pratense* L., *Poa pratensis* L., *Vicia cracca* L., *Trifolium pratense* L., and *Ranunculus acris* L. A total of 43 resident species (Appendix 1) have been recorded.

Data collection—abundance

Abundance data in 2009 (Tracey and Aarssen 2011) was calculated based on plot occupancy, i.e. the number of plots out of 155 that the species occurred in. In summer 2010, abundance data was measured as counts of individuals (or 'ramets') within 1x1 m quadrats for all vascular plant species present. For tufted, non-creeping sedges and grasses (e.g. *Phelum pratense* L.), both an individual tiller and a tuft of tillers was counted as an individual ramet. For clonal rhizomatous

species (e.g. *Poa pratensis* L.), just the local tiller or tuft of tillers that was visible above ground was regarded as an individual ramet. For stoloniferous species (*Fragaria virginiana* L, *Trofolium repens* L.), all connected tissue that could be seen above ground was regarded as an individual ramet. Three separate vegetation surveys were conducted—spaced out across the growing season: from June 8 to 15; from July 12 to 16; and from August 10 to 20. In each survey, 1 x 3 m plots (consisting of three contiguous 1 x 1 m quadrats – to help coordinate a work crew of three people) were positioned randomly across the field using a table of random number coordinates. Within each 1 x 1 m quadrat, all individuals of each species were clipped at ground level and counted. The counts were separated into two main categories: reproductive or non-reproductive. A reproductive individual was defined as one displaying flowers or indications of present or recent seed/fruit production. In each survey, as many quadrats as could be completed over the course of about one week, were sampled: June (45 quadrats); July (18 quadrats); August (15 quadrats).

Data collection—maximum potential body size

During May 2011, the field was surveyed using visual inspection to locate the five largest individuals (target plants) of each of the 35 species studied by Tracey and Aarssen (2011). Neighbouring plants were clipped at ground level (with clippings left in place) to a distance of 1m in diameter around each target plant. Metal wire cages 1 m in diameter and 1 m in height were constructed and placed around each individual plant in order to prevent herbivory by deer and rabbits . The cages were held in place (attached to the ground) with tent pegs. A spade was inserted 30cm deep around the exterior of the cage in order to sever any roots of other plants that might extend within the confines of the cage. Hay was applied around the base of the plant (2 to 3 inches high) and filled the entire area of the cage, to minimize re-growth of cut vegetation, and

to minimize any increased moisture evaporation from the soil surface resulting from the reduced ground cover caused by removing neighbouring vegetation. Flagging tape was also tied across the tops of the cages to deter deer from reaching inside of the cages to graze. For species that were climbers (i.e. *Vicia cracca* L., *Cerastium arvense* L., etc.) the plant was able to climb up the side of the cage. The plots were visited weekly over the growing season to monitor the plots and clip any re-growth of neighbouring vegetation.

Processing

Target plants were harvested after they showed signs of reproduction (flower, fruit, seed production) and once they started to show visible signs of senescence (e.g. withering/brown tissue; fallen leaves). The plant was cut at ground level and all aboveground biomass (including leaves that had fallen off) for each target plant was placed into a labeled brown paper bag. The plants were dried in a drying oven for 7 days at 70°C. The plants were then weighed to obtain their dry mass (MAX2, i.e. maximum potential plant body size).

Methods for recording the minimum (MIN) and maximum (MAX1) resident plant size (dry mass)—i.e. with natural competition in the field—are described in Tracey and Aarssen (2011).

Data analyses

Type-1 linear regression analysis was applied to MAX2 versus MIN (log-transformed). If significant, then type-II (reduced major axis) regression was applied to test for proportionality, i.e. with slope=1.0 as the null hypothesis. Type-1 linear regression analysis was also applied to test for relationships between abundance (both plot occupancy and ramet counts) and MIN, MAX1 and MAX2 (log-transformed).

Bracken study site

This field work was conducted in July and August 2011 at the QUBS Bracken tract near Westport, Ontario, Canada, involving three different habitat types: old-field, shrub-land and wood-land. The shrub-land and wood-land have been largely undisturbed for about a century, with the exception of occasional grazing by low density free-ranging cattle in recent decades. The old-field site was last tilled early in the last century and had been used for cattle grazing up until 2008. Resident species in the old-field included mostly perennial dicots, grasses and sedges typical of the south-eastern Ontario region, as well as occasional young tree saplings. The most common species (measured in ramet counts) were *Bromus inermus* L., *Cerastium arvense* L, *Poa pratensis* L, and *Vicia cracca* L. A total of 54 vascular species (Appendix 2) were collected. The shrub-land site included most of the same species as in the old-field with some additional herbaceous species plus various shrub and tree species. The most common species in the shrub-land were *Fragaria virginiana* L., *Phleum pratense* L., *Poa compressa* L. and *Vicia cracca* L. The most abundant woody species were *Rhamnus catharticus* L. and *Prunus virginiana* L. A total of 69 vascular species (Appendix 3) were recorded there. Wood-land species included mostly sedges and perennial dicots typical of shaded or forested areas in south-eastern Ontario. The most common species in the habitat were *Carex hirtifolia* Mackenzie, *Hepatica Americana* (DC.) KerGawler. and *Carex albursina* Sheldon. The most abundant woody species were *Ostrya virginiana* (Miller.) K.Koch. and *Acer saccharum* Marshall. A total of 27 vascular species (Appendix 4) were recorded there.

Sampling – old-field habitat

The area of the field used for sampling had roughly level topography. A metre tape was run along the longest axis of the habitat to create a transect (See **Appendix 5**). To choose a plot, we started 10m from the edge, and used random numbers to move along the transect to point A (and later points B, C, D and E). The random numbers were between 5 and 20 to distribute plots reasonably well across the community. At point A, a coin flip determined whether the plot would be located to the left or the right of the transect, and another set of random numbers (1 to 10m) was used to measure the perpendicular distance to the bottom right corner of the 10 x 10 m plot. Within each 10 x 10 m plot, five plots in total, using a set of random numbers 1 to 10m, the five 1 x 1 m plots were located.

Within each 1 x 1 m plot, all of the vascular plant species were recorded and the largest individual ramet of each species was measured for height and lateral canopy extent in 2 dimensions, i.e. along the longest axis, and then the second longest axis, perpendicular to the first axis. These two dimensions were multiplied together to obtain an estimate of canopy area. The number of resident ramets of each species was counted and recorded.

Sampling – shrub-land and wood-land habitats

In both habitats, a transect was set up and 10 x 10 m plots were positioned along the transect in the same way as in the old-field (**Appendix 5**). Once the plots were set up, the tallest herbaceous plant within each 10 x 10 m plot was found and measured ('h').

Within each 10 x 10 m plot, 1 x 1 m plots were located using random numbers (with the condition that a 1 x 1 m plot could not contain any woody plants taller than 'h'). Within each 10 x 10 m plot, all of the woody plants taller than 'h' were identified and the largest individual of

each species was measured for height, and its canopy area was estimated as in the old-field habitat. The number of plants that were taller than 'h' for each species were then counted and recorded.

Within each 1 x 1 m plot, all of the vascular plant species were recorded and the largest individual of each species was measured for height, and its canopy area was estimated as described above. The number of resident ramets of each species was counted and recorded (See **Appendix 5**).

Data Analyses

All data were $\log_{10}$-transformed to normalize distributions. For each habitat type, the total abundance for each species was scaled up to the whole community level (the entire 50 x 50 m area) and each species' estimated abundance was plotted as a Y coordinate with the maximum height recorded for each species, and separately with the maximum canopy area (lateral spread) recorded for each species, as X coordinates. Type-I linear regression analysis was used to test for a significant departure of slope from zero.

For each species within each habitat type, height and canopy area were combined in a composite measure of maximum plant body size—a standardized plant body size index—as follows:

(1) For each resident species within the site, identify the replicate plant—the 'MAX plant'—with the largest relative body-size 'volume' estimate, i.e. (measured height) x (measured canopy area) (Appendix 14).

(2) For each species, calculate *standardized height*: Using LOG (height) values only for the 'MAX plants', calculate the grand mean and standard deviation across all species. Then, for

each of the species, subtract this grand mean from the individual species LOG (height) value, and divide this result by the above standard deviation.

(3) For each species, calculate *standardized canopy area*: Repeat (2) using LOG (canopy area) values only from the 'MAX plants'.

(4) For each species, calculate:

Standardized maximum body size index = [standardized height] + [standardized canopy]. Values range between negative and positive values, with larger positive values indicating a larger plant body size.

The old-field sites at both Wire Fence and Bracken were geographically close (approximately 30 km apart) and had overlapping species composition. Thus, the MIN values from 2009, MAX1 values from 2009, and MAX2 values from 2011—all recorded at the Wire Fence old-field—were combined with maximum height and maximum canopy area values for the same species recorded at the Bracken old-field, and used as multiple regression variables for predicting ramet count abundance data from both the Wire Fence and Bracken study sites. Multiple regression analyses using automated model selection in R were performed to determine the top models with the best predictors.

Phylogenetic independent contrasts (PIC analyses) were performed for relationships involving Bracken abundance data. A tree was created using the online program 'Phylomatic' and the subsequent NEXUS file was used to create phylogenetic contrasts using the 'ape' package in R version 2.14.2.

Chapter 5

Results

Wire Fence old-field study site

Maximum potential body size

Type I linear regression of MAX1 (with natural competition in the field) versus MAX2 (without competition; near neighbours removed) shows a significant relationship (**Fig. 3**). A paired t-test confirms that there is a significant difference between MAX1 and MAX2 ($t=-4.868$ $P < 0.0001$). The ratio of MAX1 to MAX2 for all 35 species indicates that even the largest resident plants are suppressed by 28%, on average, due to competition with near neighbours. After removing the seven species where MAX1 was greater than MAX2, this value increased to 69%. Type II regression analysis shows that the slope of the Type II line does not differ from 1.0, suggesting an isometric relationship. In other words, on average, the maximum plant body size when competition is removed is greater than but proportional to the maximum recorded body size under natural field conditions.

MIN versus MAX relationships

The ratio of MIN to MAX2 for all 35 species indicates that the smallest reproductive plants are suppressed by 98%, on average, due to competition with near neighbours. The Type I regression for MAX2 versus MIN was significant and Type II regression analysis showed that the slope was not significantly different from 1.0 (**Fig. 4b**). This indicates that the between-species relationship for MAX2 versus MIN is isometric. These results are consistent with the regression results for MAX1 versus MIN reported by Tracey and Aarssen (2011) (**Fig. 4a**).

Species abundance – plant size relationships

More abundant resident species were generally those with smaller reproductive size thresholds (i.e. smaller MIN), and this is true regardless of whether abundance was measured by plot occupancy (**Fig. 5a**) or ramet counts (**Fig. 5b**). In contrast, species abundance in the field was unrelated to maximum resident plant body size (MAX1), regardless of whether abundance is measured as plot occupancy (**Fig. 5c**) or ramet counts (**Fig. 5d**). MAX2 also showed no significant relationship with plot occupancy (**Fig. 5e**), but had a significant negative relationship with abundance measured as ramet counts (**Fig. 5f**). In multiple regression analysis, however, the top model for ramet count abundance includes only MIN as a predictor variable (**Table 1**).

The MIN, MAX1 and MAX2 data from Wire Fence were compared with ramet counts for the same species recorded at Bracken, and the only significant relationship was between MAX2 and abundance ($P = 0.0464$, **Appendix 9**). A multiple regression confirms this— the top model is abundance with MAX2 and height as predictor variables (**Table 2**).

Species reproductive abundance – plant size relationships

More abundant reproductive resident species were generally those with smaller reproductive size thresholds (i.e. smaller MIN), and this is true regardless of whether reproductive abundance was expressed as percent of ramets that were reproductive (**Fig. 6a**) or as reproductive ramet counts (**Fig. 6b**). In contrast, species reproductive abundance in the field was unrelated to maximum resident plant body size (MAX1), regardless of whether reproductive abundance is expressed as percent of ramets that were reproductive (**Fig. 6c**) or as reproductive ramet counts (**Fig. 6d**). MAX2 showed a nearly-significant negative relationship with percent of ramets that were reproductive (**Fig. 6e**) and a significant negative relationship with abundance as reproductive

ramet counts (**Fig. 6f**). A simple product moment correlation confirms that there is a significant, positive correlation between reproductive and non-reproductive ramet abundance ($P < 0.0001$).

Bracken study site

Species abundance – plant size relationships

In all three habitat types at the Bracken tract, species that were taller, greater in area, or had greater overall (standardized) maximum plant body size were not more abundant (**Fig. 7**). In the old-field habitat, no significant relationship was found for abundance (measured in ramet counts) versus maximum height, maximum plant canopy area or standardized maximum body size index. However, in the shrub-land habitat, significant negative relationships were found with standardized plant body size ($P < 0.0001$), maximum plant height ($P = 0.0001$) and maximum plant area ($P < 0.0001$). Similarly, in the wood-land habitat, significant negative relationships were found with standardized maximum plant body size ($P = 0.008$), maximum plant height ($P = 0.014$) and maximum plant area ($P = 0.006$).

Controlling for phylogeny

Since there was no relationship between MAX plant body size and abundance in the Bracken old-field site, I controlled for phylogeny using phylogenetic independent contrasts (PIC) for the relationships between abundance and standardized maximum plant body size ($r^2 = 0.0001$, $P = 0.815$), maximum plant height ($r^2 = 0.030$, $P = 0.271$) and maximum plant area ($r^2 = 0.009$, $P = 0.551$) in the old-field habitat did not significantly change. In the shrub-land habitat, the relationships between abundance and standardized maximum plant body size ($r^2 = 0.381$, $P <$

0.0001), maximum plant height ($r^2 = 0.232$, $P = 0.0004$) and maximum plant area ($r^2 = 0.493$, $P < 0.0001$) all remained significantly negative. In the wood-land habitat, the relationships between abundance and standardized maximum plant body size ($r^2 = 0.075$, $P = 0.196$), maximum plant height ($r^2 = 0.039$, $P = 0.350$) and maximum plant area ($r^2 = 0.108$, $P = 0.117$) were no longer significant. The trees used (Appendix 10, 11, 12) were topologies with branch lengths of zero. A code for the 'ape' package *multi2d( )* was used to randomly resolve the polytomies in the old-field and shrub-land trees.

Table 1: Multiple regression (variables identified by automated model selection) for predicting LOG [Abundance] (ramet counts) in Wire Fence old-field (summer 2010). Predictor variables are LOG [MIN] (smallest reproductive plant mass; g), LOG [MAX1] (largest resident plant mass; g), LOG [MAX2] (largest recorded plant mass (g) with near neighbours removed), LOG [Maximum plant height] (recorded from overlapping species measured at Bracken old-field site) and LOG [Maximum plant canopy area] (recorded from overlapping species measured at Bracken old-field site). Only top model and models with ΔAICc values ≤ 2 are presented. ΔAICc = difference in corrected akaike information criteria, Weight = akaike weight, β = unstandardized coefficient (i.e. slope), SE = standard error, Evidence ratio = best fit model weight/ next best model weight. Bolded P values are significantly different than zero.

Model	**Variable**	**ΔAICc**	**Weight**	**R^2**	**P (model)**	**β**	**SE**	**t**	**Evidence ratio**	**P**
LOG [Abundance]	LOG [MIN]	0	0.27	0.337	**0.0018**	-0.7195	0.206	-3.492	- -	**0.00188**
LOG [Abundance]	LOG [MIN]	1.0	0.16	0.379	**0.0041**	-0.9070	0.252	-3.599	1.7	**0.00151**
	LOG [MAX1]					0.3196	0.253	1.262		0.21958

Table 2: Multiple regression (variables identified by automated model selection) for predicting LOG [abundance] (ramet counts) in Bracken old-field study site (summer 2011). Predictor variables are LOG [MIN] (smallest reproductive plant mass (g), recorded from overlapping species at Wire Fence old-field), LOG [MAX1] (largest resident plant mass (g) recorded from overlapping species at Wire Fence old-field), LOG [MAX2] (largest recorded plant mass (g) with near-neighbours removed for overlapping species at Wire Fence old-field), LOG [Maximum plant height] and LOG [Maximum plant area]. Only top model and models with ΔAICc values ≤ 2 are presented. ΔAICc = difference in corrected akaike information criteria, Weight = akaike weight, r = partial coefficient of determination, β = unstandardized coefficient (i.e. slope), SE = standard error, Evidence ratio = best fit model weight/ next best model weight. Bolded P values are significantly different than zero.

Model	**Variable**	**ΔAICc**	**Weight**	**R^2**	**P (model)**	**R**	**β**	**SE**	**t**	**Evidence ratio**	**P (coefficient)**
LOG [Abundance]	LOG [MAX plant height]	0	0.33	0.4466	**0.00824**	0.18	1.342	0.364	3.685	--	**0.00116**
	LOG [MAX2]					0.22	-0.844	0.207	-4.078		**0.00043**
LOG [Abundance]	LOG [MAX plant height]	1.0	0.31	0.5039	**0.00092**	0.15	1.462	0.359	4.061	1.1	**<0.0001**
	LOG [MAX2]					0.22	-0.356	0.219	-1.630		0.11168
	LOG [MIN]					0.03	-0.705	0.217	-3.242		**0.00481**
LOG [Abundance]	LOG [MAX plant height]	1.7	0.11	0.4632	**0.00219**	0.15	1.241	0.386	3.216	2.8	**0.00383**
	LOG [MAX2]					0.20	-0.968	0.255	-3.793		**0.00093**
	LOG [MAX plant area]					0.02	0.182	0.216	0.842		0.40867
LOG [Abundance]	LOG [MAX plant height]	1.9	0.07	0.4484	**0.00296**	0.17	1.389	0.410	3.387	4.7	**0.00254**
	LOG [MAX2]					0.21	-0.834	0.214	-3.390		**0.00073**
	LOG [MAX1]					0.01	-0.057	0.214	-0.268		0.79075

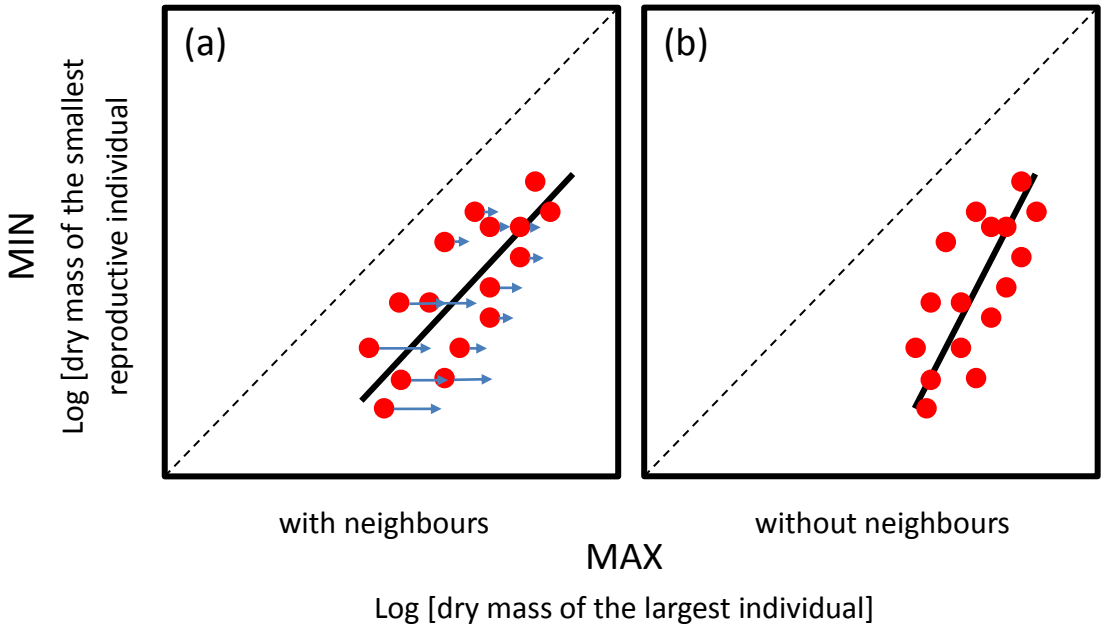


Figure 1: Possible between-species relationships for the sizes of the largest (MAX) individual versus the smallest (MIN) reproductive individual for resident species competing within natural vegetation. The leading diagonal is shown only for reference to a hypothetical 1:1 relationship (isometry). In (a) MAX is measured in the presence of competition from natural- occurring near neighbours. In (b) MAX is measured with near neighbours removed, and thus represents the 'true' maximum potential body size (MPBS). The relative lengths of blue arrows in (a) show predicted effects of neighbour removal depending on differences in species body sizes (see text).

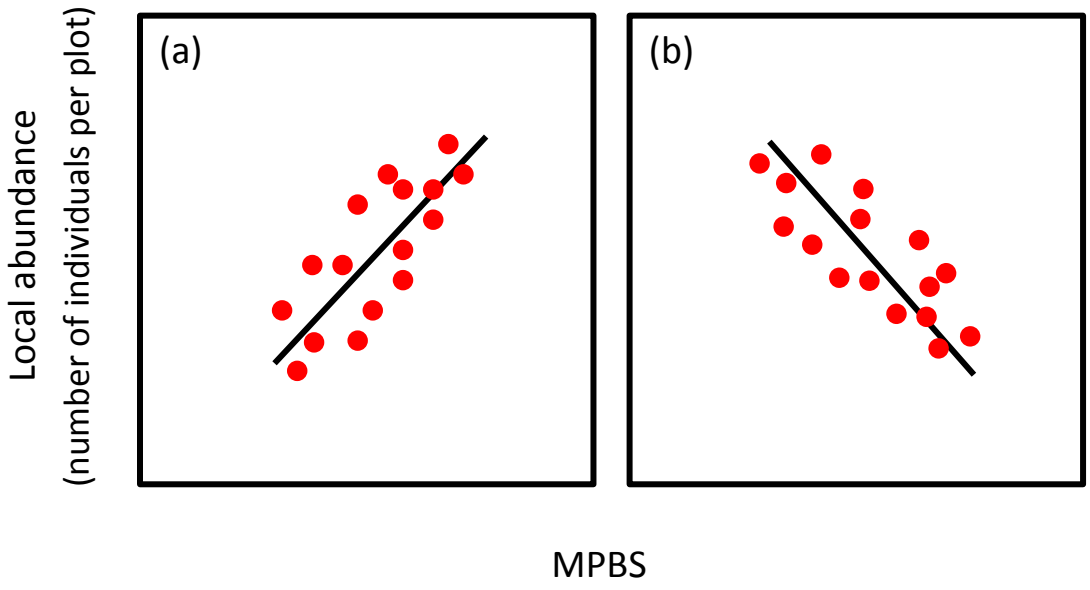


Figure 2: Possible between-species relationships for maximum potential species body size (MPBS) versus local abundance (number of individuals per plot, reflecting local recruitment success) for resident species competing within natural vegetation, predicted by (a) the traditional 'size advantage' hypothesis; and (b) The 'fecundity allocation premium' hypothesis (see text).

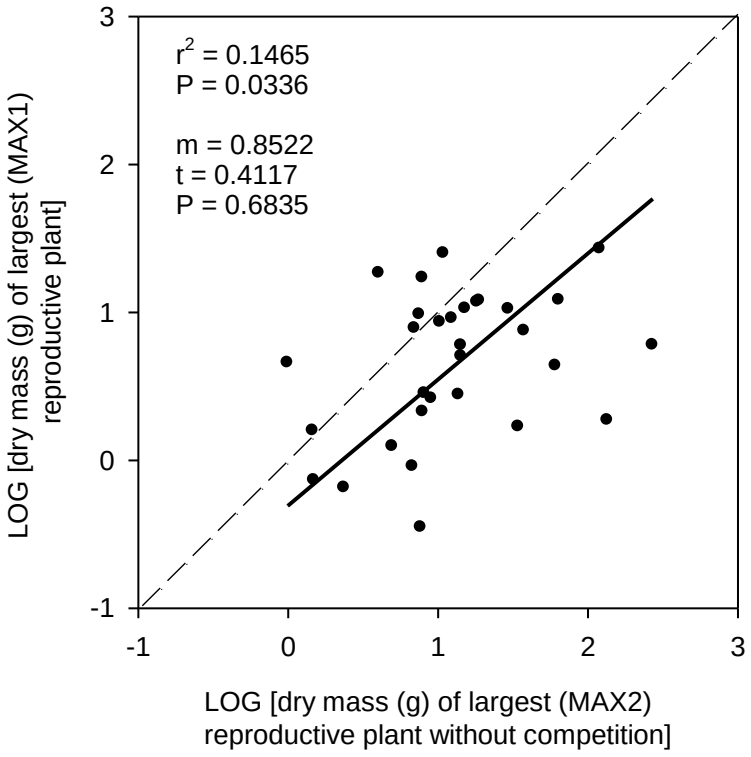


Figure 3: Between-species relationship (for log-transformed data; n = 35 species) for dry mass (g) of the largest (MAX2) reproductive plant growing without competition recorded in 'vegetation removal' plots (selected from 5 treatment replicates per species) in 2011 versus dry mass (g) of the largest (MAX1) reproductive plant recorded within randomly positioned plots surveyed during the 2009 growing season at the Wire Fence old-field study site. r^2 and associated P value are from Type I linear regression analysis. Solid line is from RMA regression analysis; m = RMA slope; t and associated P value test for deviation from the null hypothesis of m = 1.0 (isometry). Dashed line is shown only for reference to the hypothetical 1:1 relationship.

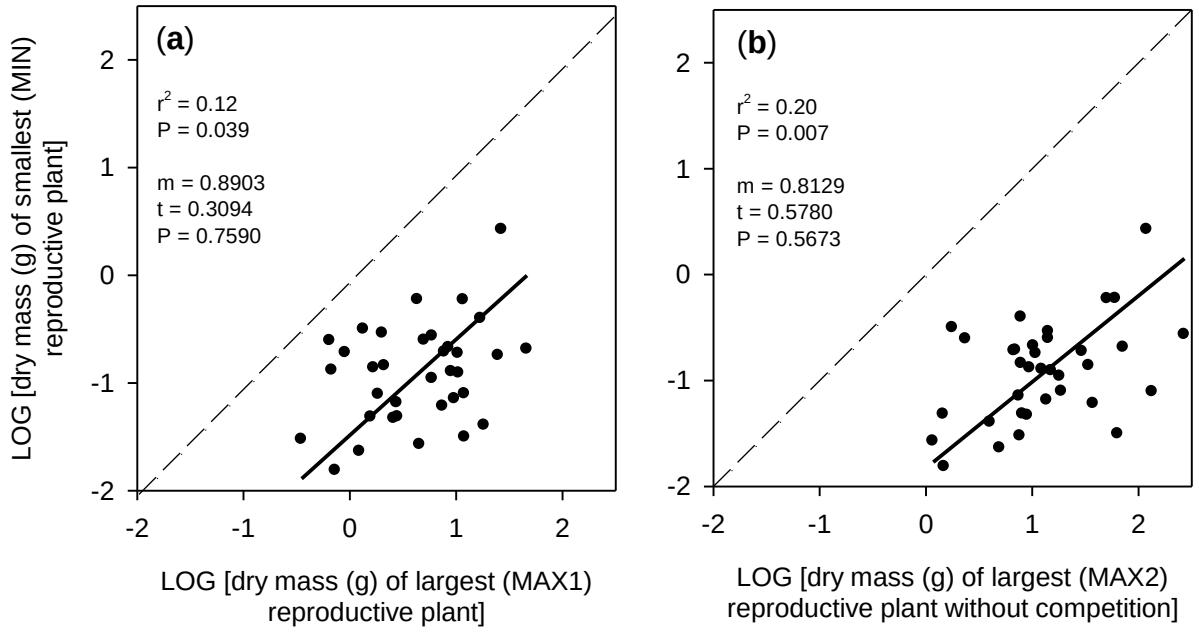


Figure 4: Between-species relationship (n = 35 species) for (**a**) dry mass (g; log-transformed) of the largest (MAX1) versus the smallest (MIN) resident reproductive individuals recorded within surveyed plots at the Wire Fence old-field study site in the 2009 growing season (from Tracey and Aarssen 2011); and (**b**) dry mass (g; log-transformed) of the largest (MAX2) reproductive individual growing without competition recorded in 'vegetation removal' plots (selected from 5 treatment replicates per species) in 2011 versus MIN. r^2 and the associated P values are from Type I linear regression analysis. Solid line is from RMA regression analysis; m = RMA slope; t and associated P value test for deviation from the null hypothesis of m = 1.0 (isometry). Dashed line is shown only for reference to a hypothetical 1:1 relationship.

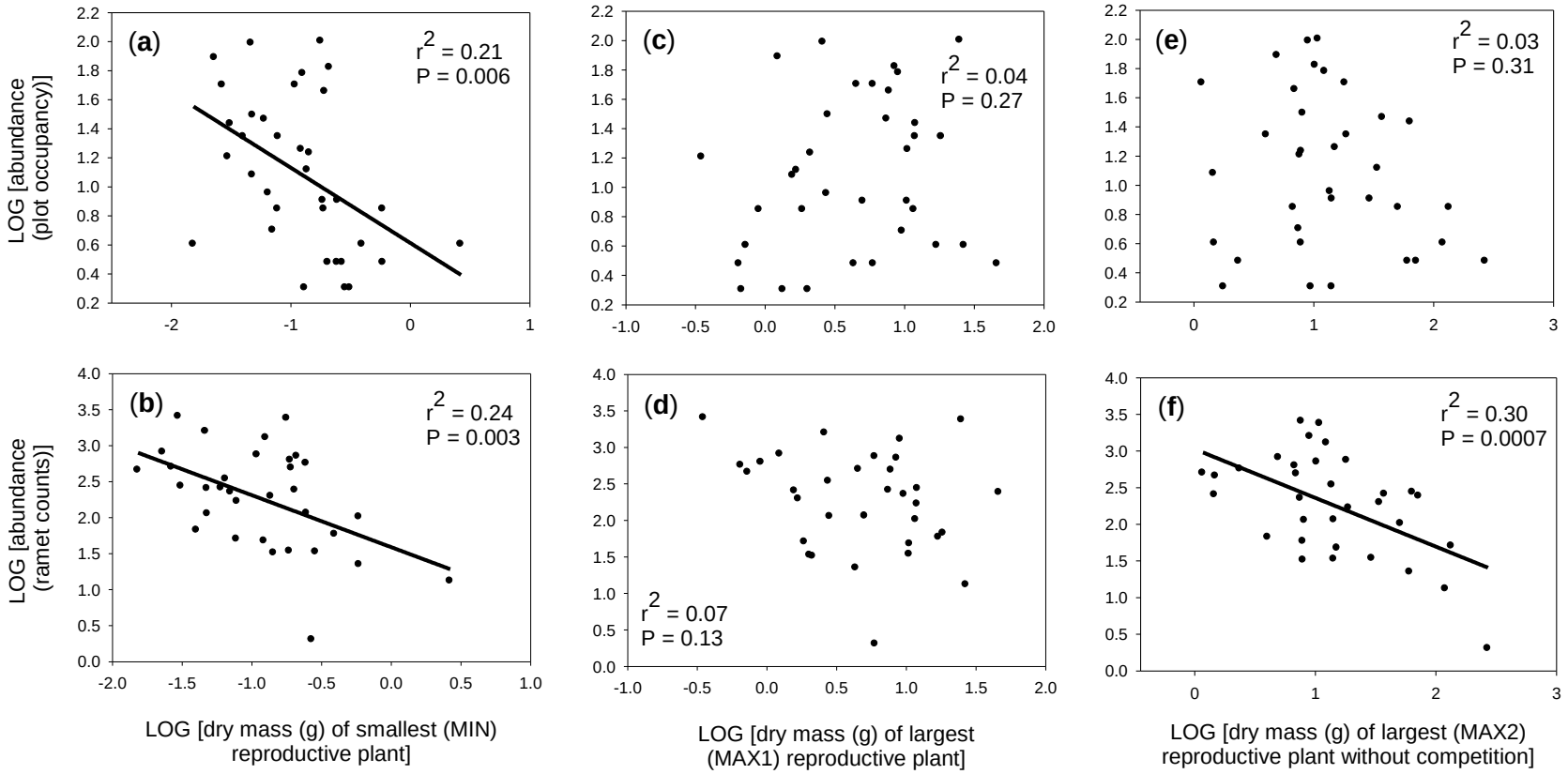


Figure 5 (**a**) (**c**) (**e**): Between-species relationships (for log-transformed data; n = 35 species) for species abundance (plot occupancy, out of 155, recorded summer 2009; data from Tracey and Aarssen 2011) at the Wire Fence old-field study site versus: (**a**) dry mass (g) of the smallest (MIN) reproductive plant recorded across all surveyed plots in 2009 (from Tracey and Aarssen 2011); (**c**) dry mass (g) of the largest (MAX1) reproductive plant recorded across all surveyed plots in 2009 (from Tracey and Aarssen 2011); (**e**) dry mass (g) of the largest (MAX2) reproductive plant growing without competition in 'vegetation removal' plots (selected from 5 treatment replicates per species) in 2011. (**b**) (**d**) (**f**): Between-species relationships (for log-transformed data; n = 33 species) for species abundance (ramet counts per 75 m^2, recorded summer 2010) within surveyed plots at the Wire Fence old-field study site versus: (**b**) MIN; (**d**) MAX1; (**f**) MAX2. r^2 and associated P values are from Type I linear regression analyses.

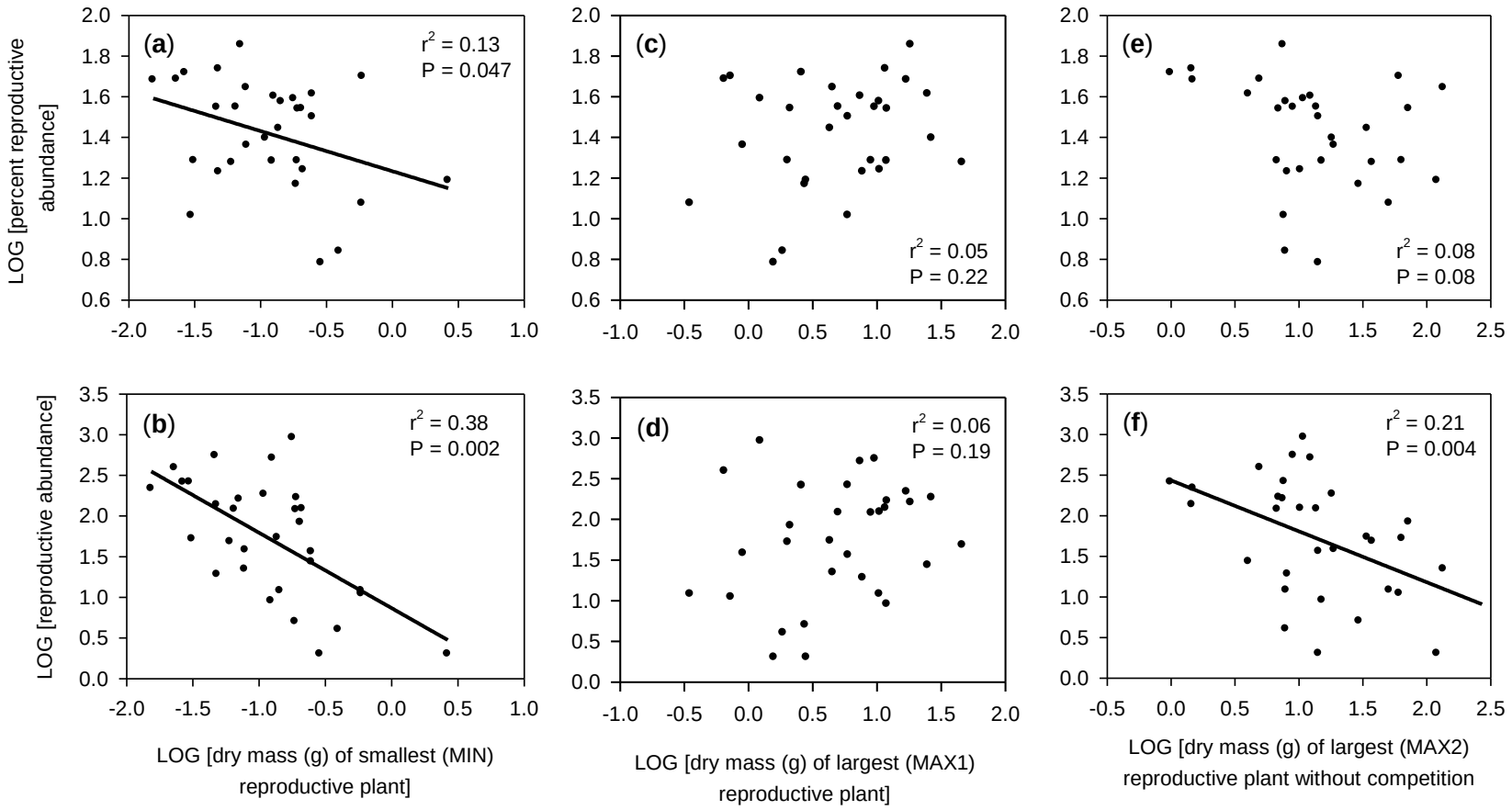


Figure 6 (**a**)(**c**)(**e**): Between-species relationship (for log-transformed data, n=31 species) for percent reproductive abundance (i.e. percent of counted ramets per 75 m^2 that were reproductive) within surveyed plots at the Wire Fence old-field study site in 2010 versus: (**a**) MIN (minimum resident reproductive plant size recorded within surveyed plot in 2009); (**c**) MAX1 (maximum resident reproductive plant size recorded within surveyed plots in 2009); (**e**) MAX2 (reproductive plant size growing without competition in 'vegetation removal' plots in 2011). (**b**)(**d**)(**f**): Between-species relationship (for log-transformed data, n= 31 species) for reproductive abundance (actual counted number of reproductive ramets per 75 m^2) versus: (**b**) MIN; (**d**) MAX1; (**f**) MAX2. r^2 and associated P values, and regression lines are from Type I linear regression analyses.

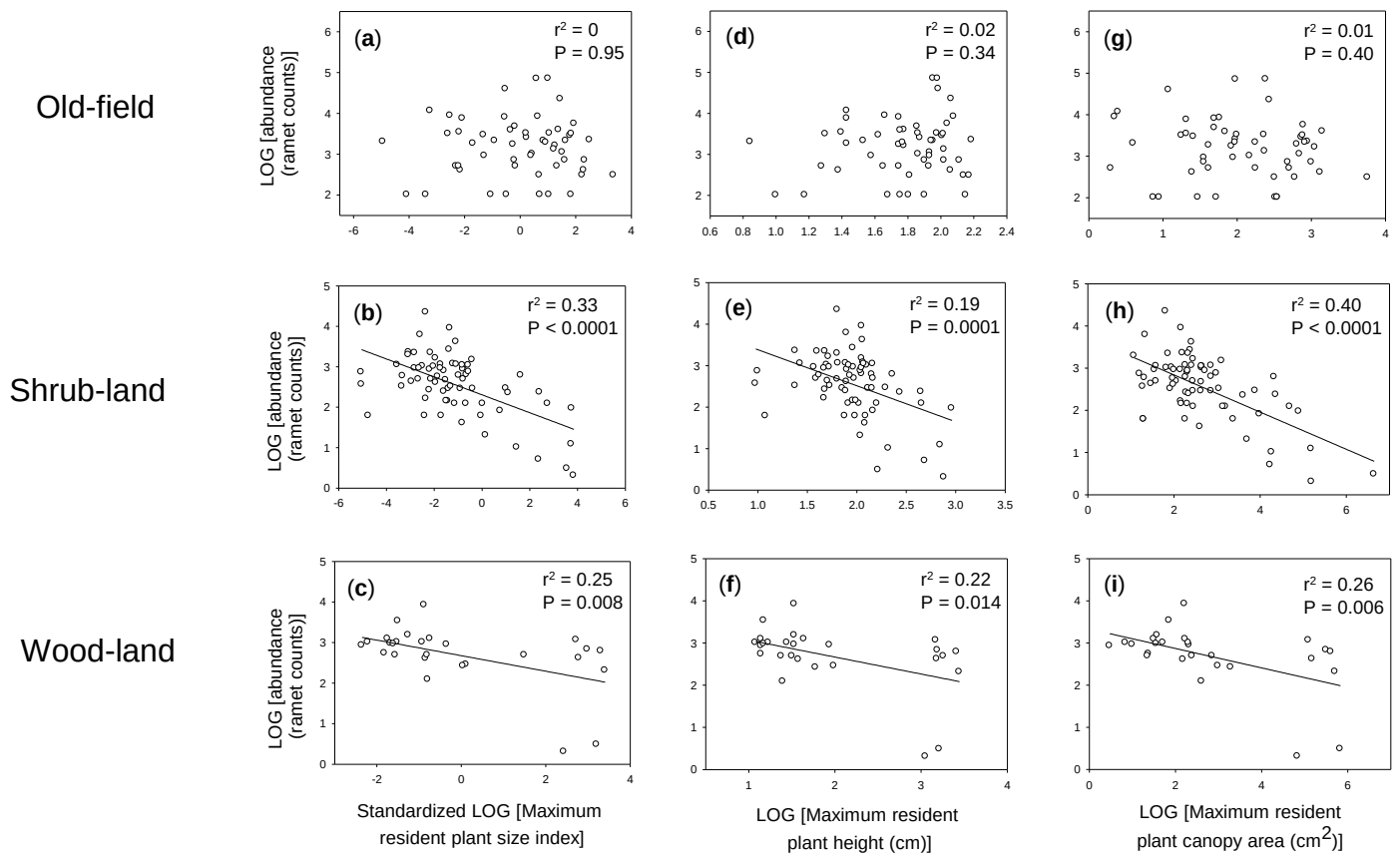


Figure 7: Between-species relationships (for log-transformed data) for species abundance (based on ramet count estimates per 500 m^2) at the Bracken study site within old-field (n=54 species; a, d, g), shrub-land (n=69 species; b, e, h) and wood-land (n=27 species; c, f, i) habitats versus: (**a**)-(**c**) standardized maximum recorded plant size index; (**d**)-(**f**) maximum recorded resident plant height (cm); and (**g**)-(**i**) maximum recorded resident plant canopy area (cm^2). Standardized LOG [maximum resident plant size index] is the sum of standardized LOG [maximum resident plant height] and standardized LOG [maximum resident plant canopy area] (see text). r^2 and associated P values, and regression lines, are from Type I linear regression analyses.

Chapter 6

Discussion

Neighbour removal experiment

Figure 3 clearly shows that the experiment I set up in Wire Fence field to remove competition was successful. The dashed line in Figure 3 shows the hypothetical 1:1 relationship and the majority of the species I collected fell below that line, meaning that when competition was removed, most plants increased significantly in size ($t=-4.868$ $P < 0.0001$). By looking at the ratio of MAX1 to MAX2 you can see that with competition MPBS is suppressed by 28% (considering all species) and 69% (considering only species whose MPBS increased after neighbour removal). This is consistent with other studies that have looked at competitive abilities in plants. Taylor and Aarssen (1990) reported a 75-85% average reduction in size (dry mass) due to competition; however it is important to note that Taylor and Aarssen (1990) collected plants randomly, whereas I targeted the biggest plants. The aforementioned give me confidence that I was able to measure very close to the true MPBS for most species.

In Tracey and Aarssen (2011), an isometric relationship was seen between MRTS and MAX reproductive plant size (**Fig. 4a**). However, upon examination of the new MPBS data with the old MRTS data, the same isometric relationship was seen (**Fig. 4b**). There could be several implications of these results:

Species that did not increase in size

It is important to look at the traits and strategies of species that did not fall below the 1:1 line (**Fig. 3**). These included two grasses: *Phleum pratense* and *Agrostis stolonifera*, and five other herbaceous angiosperms: *Cerastium arvense* and *vulgatum*, *Trifolium repens* and *dubium*, and *Tragopogon pratensis*.

Many grass species that tiller benefit from being grazed as herbivory can promote increased tillering. For example, a study using *Schizachyrium scoparium* found that there were greater tiller numbers per cm^2 of the remaining basal area after greater damage from livestock (Butler and Briske 1988). Other studies have also reported evidence of increased grass tillering following grazing (Owen 1980, Owen and Wiegert 1982b). In fact, many studies show support for overcompensation for growth following herbivory for many plant species (McNaughton 1979, Belsky 1983, 1986, Hendrix 1989, Agrawal et al. 2000, Ruiz et al. 2008, among others). In order to prevent target plants from being eaten, it was necessary to cage them to deter herbivores. If some of these species overcompensate, which many have the potential to, I prevented this from happening. However, overcompensation is widely debated in ecology, and often the phenomenon of overcompensation is dependent on various abiotic conditions including nutrient availability, light, etc. Thus it is difficult to conclude that overcompensation would be the main reason why some species (i.e. grasses) did not increase in size after removal of competition.

The *Trifolium* species (clovers) are typically creeping species that spread via rhizomes (Gleason and Cronquist) and the roots of these plants (especially white clover) are typically very delicate. Although care was taken to ensure that the target was isolated without damage, the plants often didn't survive long after being targeted. The flower stems were also not able to stay upright as they had no neighbouring vegetation to rely on for structural support. In Wire Fence field in particular, the clovers could be considered 'understory plants' with most of their supporting

biomass shaded for a large part of the day by neighbours. Thus, removing these neighbours changed this. Similar circumstances likely affected the *Cersatium* species (chickweeds), as these species tend to climb on other species, and without that support, they did not survive long after being targeted. Without neighbouring vegetation to lean on *Tragopogon pratensis*' stem would also often snap.

Introducing other factors

The goal of this experiment was to remove neighbouring vegetation and find the MPBS a plant could achieve without competition *specifically*. However, it is important to consider the other factors that come into play once I removed competition. As previously mentioned, plants were more exposed to the sun, especially smaller species and creeping species, which are accustomed to living below the 'canopy' (i.e. *Oxalis corniculata*, *Prunella vulgaris*, etc.). Species were also more exposed to the elements with no surrounding, supportive vegetation. This caused taller species (i.e. *Erigeron strigosus*, *Ranunculus acris*, etc.) to frequently snap, bend, lose biomass, or become damaged from wind exposure. Without neighbours, target plants would have increased access to the resources in the soil (i.e. water, nutrients, etc.) which could have important implications for species that are very limited by competition for soil resources.

Removing competition (and more)

Although, I believe I successfully removed the majority of competition surrounding the target plants, in most cases I removed more than just competition. When you remove competition, you are also removing other important ecological mechanisms that drive stability and succession in communities including facilitation, inhibition and tolerance. Many plants benefit from neighbours which either facilitates their growth or reproduction, or they do not suffer in the

presence of neighbours as they are able to inhibit their neighbour's growth. In fact, in Chu et al. (2008), their results show that facilitation can affect density-biomass relationships in plants. Therefore it is important to consider that in addition to competition, I also removed other important mechanisms from the picture, which may affect the MPBS a plant could achieve.

Variation affecting plant size

Another possible reason that we could not detect a slope of greater than 1.0 is that there are simply too many variables that affect plant size and it is impossible to control for all of them in a natural setting. Some of these variables could include (but are not limited to): plant viruses and pathogens, differences in local soil conditions, the habitat's history, insect infestations and importantly, genetic variation.

Plant diseases are frequently overlooked by Ecologists, as there are often no signs that the plant is diseased. If there are signs, there is little that can be done to remedy the problem. For example, when collecting species in Wire Fence field, *Trifolium pratense* (red clover) showed visible signs that it was badly diseased. However, there is no easy way to determine what the disease was, what caused it, and what effect it had on plant size, if any. A study looking at white clover, *Trifolium repens*, found that infecting the species with different strains of viruses specific to *other* plants in all cases decreased growth of white clover (Gibson 1981). On the other hand, in some potato plants, viruses specific to that species do not affect growth, or tuber production at all in certain genotypes (Frankhauser 2000). Jones (1924) was the first to suggest that plant diseases can be dependent on environmental conditions and that one field could be devastated by a disease and an adjacent field remain unaffected (Colhoun 1973).

Similarly, in previous field seasons, different insects have infested specific species at varying times throughout the growing season. Sometimes these tiny herbivores would cause physical damage to the plant, but sometimes, they wouldn't. In either case it is hard to assess whether the damage is critical, the damage is negligible or if it could per chance benefit the plant. Many of these could be mutualistic relationships. For example, in summer 2009 *Asclepsias syracia* was badly eaten by a *Tetraopes* species (milkweed beetles); however studies have shown that although these beetles can significantly reduce leaf biomass, this doesn't affect the growth or reproduction of the plant (Agrawal 2004). Interestingly enough, the presence of these beetles often depends on the neighbours of the plant itself (Agrawal 2004). For example if the milkweed plant has grass species near it, they are going to be more affected by the beetles as the beetles breed on the neighbouring grass species. It is obvious how hard it would be to control for insect infestation in a natural setting, when each species is associated with different herbivores, which in turn have different effects on the plant's growth and size.

Moreover, no growing season ever has the exact same conditions as the previous year. Differences in nutrient and water supply as well as climatic conditions can affect species in different ways (Craine 2009). The summer of 2011 in which MPBS was measured, early in the growing season conditions were abnormally wet, and the species composition of the field began to change. It is difficult, if not impossible, to predict how these variable conditions could affect plant body size for each species and the overall community.

Genetic variation is an important factor that is not controlled for as well. It is unlikely, but possible that the largest targets for each species were all from the same genotypes. Moreover, beyond genetic variation related to size, there is genetic variation related to a species' ability to deal with varying abiotic conditions, disease, etc.

Experimental setup and error

Although the outside of target cages were trenched with a 12 inch spade, this did not sever roots of all of the neighbouring plants or the plants that were removed from within the target area. If only aboveground clipping is applied, then belowground parts of the severed plants could still continue to grow and utilize resources (Silander 1976). The degree to which this would affect plant growth and MPBS is difficult to measure, and would likely depend on the species composition of the target plant's neighbourhood. Removing the neighbouring plants by digging them up would have caused more issues as manual removal of belowground vegetation disturbs the soil environment and potentially the roots of the target plant (Aarssen and Epp 1990). Using herbicides to kill off surrounding vegetation was an option but this can leave unknown residues (Aarssen and Epp 1990) and have differential effects on growth and size of target species i.e. some forbs may be killed, but other grass species could benefit from herbicide application.

Thomas' (1996) paper

One reason for predicting a slope greater than 1.0 was that there had been one reported case showing evidence of this relationship. Thomas (1996) used a set of Malaysian rainforest trees to answer several questions about reproductive size and relative size at onset of maturity (RSOM). They found that large-statured trees reproduced very close to their asymptotic heights and intermediate trees at relatively smaller sizes. The formula they used to calculate RSOM is seen below:

$$RSOM = SOM \div asymptotic\ maximal\ size$$

RSOM is thus only a dimensionless constant (Charnov 1991, Thomas 1996) and is not as accurate as other size metrics are. His data suggested that large-statured trees reproduced very

close to their asymptotic heights and intermediate-statured trees at relatively smaller sizes; however, for the smaller species there was too much variation in RSOM seen due to greater error in estimates for smaller species to make any conclusions. It would have been very interesting if they were able to draw conclusions about the smaller-statured species, and this would be most relevant to my project. The data also don't relate to all trees he sampled, just Malaysian rainforest trees in which reproduction was not strongly contingent on crown exposure, which eliminated several species from the equation (Thomas 1996). Moreover, this may suggest that the relationship between MRTS and MPBS could be habitat-specific.

Although all of the above reasons could contribute to my inability to detect a slope greater than 1.0, indeed, the isometric relationship between MRTS and MPBS could very well be true and real. This data I collected show no support for greater reproductive economy (the ability for some seed suppression despite severe size suppression under competition) in smaller species in the sense that smaller species do not reproduce at a smaller fraction of their MPBS. That being said, my data are also contradictory to traditional theory. Traditional theory suggests that smaller species are more suppressed by competition than larger species; however, you can see by comparing Figure 4a with 4b that large species enjoyed release from competition just as much as smaller species did. Most previous research in the size-dependent effects of competition has been under unnatural or experimental conditions and not in a natural community (Gaudet and Keddy 1988, Keddy and Shipley 1989, Grace 1990, Goldberg and Landa 1991, Keddy et al. 1994, 2002, Rosch et al. 1997, Keddy 2001).

Body size and abundance

Tracey and Aarssen (2011) was the first to suggest that the most abundant plants in communities were not those that were bigger, or smaller, they were those which had the smallest reproductive threshold size (MRTS). However, the measure of abundance was not entirely accurate, and thus a new measure of abundance (ramet counts) was obtained. This new measure of abundance provided us with the same results (**Fig.5**). The measures of abundance with plot occupancy (**Fig.5 c,e**) showed no relationship with maximum plant size whether that be MAX1 measured with competition or MPBS (MAX2) measured without competition. In one way it is surprising that there is no relationship between MPBS and abundance when we know there is a relationship between MIN and MPBS. However, the r^2 value for the MIN-MAX regressions (**Fig. 4**) is not particularly high, especially with competition and therefore it may not be surprising that we did not see a relationship.

With the new measures of abundance (**Fig. 5d and e**) MPBS has a strong relationship with abundance, and this is likely because I was able to control for all of the variation that competition was causing—it really is just a more accurate measure of MPBS. You can see that the r^2 is improved when competition is removed (**Fig. 5**). Moreover, even with the older, less accurate measure of maximum plant size (MAX1), when you remove the outliers, the relationship is significantly negative (Appendix 8).

These data suggest that smaller plants do have greater reproductive economy; however, the mechanism is unknown. In addition, this is contrary to what traditional theory would predict (**Fig. 2**). Clearly, those plants with the highest recruitment rates are not bigger in size, they are those that have the smallest reproductive threshold sizes.

Figure 7 really drives the above point home. Plants with smaller MRTSs have greater reproductive abundances and a greater percent of their total abundance is reproductive. This shows more support for reproductive economy in smaller species; however, once again the mechanism is not understood. MPBS is also negatively related to abundance and this shows support not only for greater reproductive economy in smaller plants (plants with smaller MPBSs are recruiting more offspring) but also refutes traditional theory. Wright et al. (2005) suggest that in tree species from Barro Colorado, the proportion of individuals that are reproductive increases more slowly with size (DBH); however, their figures clearly show that the highest proportion of reproductive plants is in the higher DBH size classes and runs contrary to what my data suggest.

Interestingly, this relationship may be habitat-dependent, or even site-dependent. When I tried to relate Bracken abundance with Wire Fence measures of MIN and MAX, only a marginally significant relationship was seen with MPBS, and no relationship with the other two size measures.

Given the consistent relationship between MIN and abundance (measured by both plot occupancy and ramet counts) (**Fig.5**) in Wire Fence field, it was important to see if this pattern translated to other old field communities as well as other habitat types. Figure 7 shows that at the Bracken old field site, similar patterns were not seen. There is no relationship between body size (whether that be standardized maximum resident plant size index, maximum resident plant height, or maximum resident plant canopy spread) and abundance (measured in ramet counts).

There are two important factors to consider regarding the differences in relationships across the two sites. Firstly, the metrics for body size are different. At Wire Fence field, plants were harvested and weighed and mass (g) was the metric used for body size. However, at the Bracken

old field site, height (cm) and canopy spread (cm^2) and a combination of the two into a standardized size index were all independently used as size metrics. It is not always clear what approach should be taken when measuring plant size. Due to the scale of the experiment at the Bracken field, obtaining measures for mass was not feasible. Height is one of the most frequently used size metrics in plants and thus that, and canopy spread were more easily attainable measures of plant size in this study. In addition, for woody species, which come into play in other habitats, mass would be impossible to measure.

The second factor to consider was the differences in species composition of the two fields. Species at Wire Fence field are very evenly distributed but in the old field site at Bracken, *Bromus inermus* or smooth brome, a non-native grass species, is invading the site. When the site was first chosen, it was not obvious that it could be a potential problem; however, early on in the growing season smooth brome is not very noticeable. Like many grass species found in south eastern Ontario, it does grow quite large, but this is not until at least mid-June. Environment Canada lists smooth brome grass as a "moderate invasive alien" (Environment Canada). Many studies have examined the effects that smooth brome has on other plants. A study of the effects of invasive plants on native plants found that *Anenome patens* can persist in native grass patches but that extinction probabilities were much higher in patches of smooth brome grass (Williams and Crone 2006). Survival, growth, size in the next year, number of flowers and fecundity of *A. patens* was also lowest in patches of smooth brome (Williams and Crone 2006). A later study examined the impact of smooth brome on patch dynamics of *Spartina pectinata*, a dominant, native grass species (Dillemuth et al. 2008). They found that there was a significant negative relationship between the amount of smooth brome present and the growth of *S. pectinata* (Dillemuth et al. 2008). Establishment of a new patch of *S. petinata* is almost 1.5 times more

likely in areas with no or low smooth brome coverage and existing patches of *S. pectinata* were almost 8 times more likely to go extinct in areas of high smooth brome coverage than areas of low smooth brome coverage (Dillemuth et al. 2008). Another study which took place in prairie grasslands found that plant-soil feedbacks were contributing to persistence of smooth brome across the prairies, where smooth brome invasions are becoming a serious issue (Vinton and Goergen 2006). In soils that were higher in nitrogen, they found that smooth brome had greater tiller density and canopy interception of light (Vinton and Goergen 2006). This is interesting as cattle-grazing was very common in and around this site for many years and thus, there may be a surplus of N at this Bracken old-field site. Moreover, species that fix nitrogen, for example the clovers, are very abundant in Wire Fence, but not as abundant at Bracken. This could also imply that there was a surplus of nitrogen at the Bracken site. The soil at Bracken is also mostly clay, which holds a lot more nitrogen than sandy or loamy soils would. From these studies it is evident that smooth brome can strongly impact community structure, and thus, it is very likely that with the great abundance of smooth brome in this field, that it biased the ability to detect a similar relationship between body size and abundance as was seen in Wire Fence field.

Interestingly, out of the 54 species in the old-field, 47 of those species are seen in the shrub-land site as well. When you use the shrub-land abundance counts and measures of MAX plant size, but just for the species that overlap with the old-field site, in all cases you see negative relationships, two of which are significant (**Appendix 15**). These results would indicate that all or some of the aforementioned factors could be affecting my ability to detect this relationship in the Bracken old-field site.

The shrub-land and wood-land sites (**Fig.7**) on the other hand were consistent with the results seen in Figure 5 showing a strong negative relationship between maximum plant size and

abundance. This was not surprising as I had anticipated a 'woody effect' coming into play later in succession. However, after removing the woody species from the shrub-land site and re-analyzing the data, you see the same relationship (**Appendix 17**). This means that there is indeed no 'woody effect' causing this relationship. Similar reanalysis was not performed on the woodland data as the sample size was initially much lower than the other habitats and upon removal of the woody species there would be little power remaining in the analysis.

Thus, if you imagine the three Bracken sites as a successional gradient, you can see that in all stages of succession, there is a strong negative relationship between maximum plant size and abundance. Traditional theory would predict the opposite. Higher local recruitment rates are seen in the species that are able to reproduce at smaller sizes meaning that most of the offspring must be coming from those plants with smaller MRTSs.

Multiple regression analyses

Multiple regression analyses from Wire Fence confirmed that indeed MIN is the best predictor of abundance, and thus, local recruitment, in the plant community (**Table 1**). In all multiple regression analyses there were several models that were close to the top model and it is important to consider all of them as feasible. All models whose ΔAICc values ≤ 2 were reported. This is the method suggested by Anderson and Burnham (2001). This method is appropriate for smaller sample sizes (sample sizes that are less than 40 times the number of explanatory variables). This criterion prevents ignoring models that are almost as good as the best model. Smithwick et al. (2009) also suggest that you should only present models whose akaike weights are within 10% of each other and this prevents having too many top models to choose from. In either case I

reported all models whose ΔAICc values ≤ 2 and in some cases the weights were different by more than 10%.

Controlling for phylogeny

In plant communities, it is inevitable that many species will be related to some extent. Therefore it was important to perform PIC analyses which would determine whether or not phylogeny played a role in these relationships. This proved to be very difficult for the old-field and shrub-land in particular. The phylogenies for many grass species in the family *Poaceae, Asteraceae* and *Rosaceae* are not resolved (Tree of Life, http://tolweb.org/tree/). Therefore, when doing PIC analysis it was impossible to use the 'ape' package in R version 2.14.2 for any analysis, as trees must be dichotomous and fully rooted.

There is a code, multi2d( ), for R which by default resolves polytomies randomly by inserting a branch of zero length (Personal correspondence Liam Revell). When using this approach, I found that phylogeny did not play a role in either the old-field or the shrub-land (Appendix 10, 11). Abundance and any of the three size metrics still had no relationship and in the shrub-land, all size metrics showed significant relationships with abundance (**Fig. 7**). A more accurate way to analyze the data with PIC would be to examine studies that have attempted to resolve these relationships, and edit the trees to reflect the most widely-accepted relationships (Jansen et al. 1991, Hsaio et al. 1995, Potter et al. 2007, Rodger Evans). After editing the NEXUS files manually, R consistently provided the error message "phy is not fully rooted and dichotomous" even though from what I can see the tree is fully dichotomous (Appendix 11). Further research is

needed to determine why R provides this error message and what is wrong with the object "phy" (Personal correspondence Liam Revell).

The multi2d( ) code was not used for the wood-land site, as the tree was fully dichotomous and functional in R. The relationship between abundance and body size changed from being significantly negative to being insignificant when the regressions were redone using the phylogenetically independent contrasts. This does not mean that the relationship does not exist; it simply means that phylogeny plays some sort of role in the relationship. This is surprising; however, given that there are only 2 sets of species that are in the same genus, yet, this may not be surprising, as the sample size was already low to begin with, and after PIC the analysis lost power. It would be interesting to have fully resolved trees for the other 2 sites and see if this changed the outcome of the PIC analysis.

It is also important to note that my PIC analysis used branch lengths of 1.0, as the trees were strictly topologies. Not having accurate branch lengths and missing branch length transformations can cause highly variable and inflated Type I error rates (Diaz-Uriarte and Garland Jr 1998). In the future it would be useful to use a tree with branch lengths that represent genetic differences, or even time, and see if the outcome changes.

Chapter 7

Interpretations and Conclusions

A suggested paradigm shift

If all plants existed without any competition from neighbours, most plants would likely survive and reproduce regardless of their body size. This would mean that more genes would be transmitted into future generations by producing offspring with larger MPBSs. This is best illustrated using a fitness model from Tracey and Aarssen (2011) (Appendix 18). You can see in Appendix 18 that fitness in this case would be a straightforward function of MPBS. This is consistent with previous research (Claus and Aarssen 1994, Aarssen and Jordan 2001, Chambers and Aarssen 2009) which suggests that the relationship between plant body size and fecundity is positive and isometric.

Most natural vegetation is crowded though. Even my research suggests that just MPBS is suppressed by nearly 70% by neighbouring vegetation. Plants with a larger MPBS will necessarily take longer to reach a size at which they can reproduce (have larger MRTS Fig.1) and thus, their offspring will also have a larger MPBS. Under severely-crowded conditions most of these plants with larger MPBSs will get big enough soon enough and will likely die before reproducing. The probability therefore of any reproduction is a decreasing function of MPBS (**Appendix 18(b)**) (Tracey and Aarssen 2011).

So, if vegetation is crowded most of the time, and in crowded vegetation, selection favours plants that have smaller MRTS and smaller MPBS, this raises the question: does being big really matter? Albeit there are many advantages to having a larger plant body size, if plants with

smaller MRTSs are better at transmitting genes into future generations, being big may not be as important as traditional theory suggests.

Future directions

My research has found many interesting patterns in natural plant communities. The relationship between MRTS and MPBS in Wire Fence field was further explored but still remains unclear; however, it is important to consider in terms of sites, my sample size was essentially one. It would be interesting to replicate this experiment in different fields and see how consistent this relationship is across different species compositions.

It would also be interesting to see the effects of different competition treatments (not just crowded or no crowding) and see the impacts this has on the relationship. That being said, it would also be useful to vary competition between inter- and intra- specific competition treatments and see the effects on MPBS.

It is generally accepted in plant body size ecology that smaller species are more suppressed by competition than larger species are. However, my research (**Fig. 4**) suggests that larger species enjoy just as much release from competition as smaller species. In the future, further competition removal experiments in natural vegetation of many types would be useful to investigate this discontinuity in findings. Should this be the case in other natural habitats, this could have critical implications for plant competition theory in ecology.

Literature Cited

1. Aarssen LW and Epp GA. 1990. Neighbour manipulations in natural vegetation: a review. Journal of Vegetation Science. 1: 13-30.
2. Aarssen LW and Jordan CY. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. Ecoscience. 8:471-477.
3. Aarssen LW and Taylor DR. 1992. Fecundity allocation in herbaceous plants. Oikos. 65:225-232.
4. Aarssen LW, Keogh T. 2002. Conundrums of competitive ability in plants: what to measure? Oikos. 96:531-542.
5. Aarssen LW, Schamp BS, Pither J. 2006. Why are there so many small plants? Implications for species coexistence. Journal of Ecology. 94: 569–580.
6. Aarssen LW, Schamp BS. 2002. Predicting distributions of species richness and species size in regional floras: applying the species pool hypothesis to the habitat template model. Persp Plant Ecol Evol Syst. 5: 3–12.
7. Aarssen LW. 2008. Death without sex — the 'problem of the small' and selection for reproductive economy in flowering plants. Evolutionary Ecology. 22: 279–298.
8. Agrawal AA. 2004. Resistence and susceptibility of milkweed : competition, root herbivory and plant genetic variation. Ecology. 85: 2118-2133.
9. Agrawal AA. 2000. Overcompensation of plants in response to herbivory. Trends in plant science. 5: 309-313.

10. Anderson DR, Link WA, Johnson DH and Burnham KP. 2001. Suggestions for presenting the results of data analysis. USGS Northern Prairie Wildlife Research Center. Paper 227.
11. Augspurger CK. 1985. Demography and life history variation in Puya dasylirioides, a long lived rosette in subalpine bogs. Oikos.45: 341-352.
12. Bayer RJ and Star JR. 1998. Tribal phylogeny of the Asteraceae based on two non-coding chloroplast sequences. Annals of Missouri Botanical Garden. 85: 242-256.
13. Belsky AJ. 1983. Small-scale pattern in grassland communities in the Serengeti National Park, Tanzania. Vegetation Science. 55: 141-151.
14. Belsky AJ. 1986. Does herbivory benefit plants? A review of the evidence. American Naturalist. 127: 870-892.
15. Bonser SP, Aarssen LW. 2009. Interpreting reproductive Allometry: Individual strategies explain size-dependent reproduction in plants. Perspectives in plant ecology, evolution and systematic. 11: 31-40.
16. Butler JL and Briske DD. 1988. Population structure and tiller demography of the bunchgrass Schizacharyum scoparium in response to herbivory. Oikos. 51: 306-312.
17. Chambers J, Aarssen LW. 2009. Offspring for the next generation: most are produced by small plants within herbaceous populations. Evolutionary Ecology. 23:737–751.
18. Charnov EL. 1991. Pure numbers, invariants and symmetry in the evolution of life histories. Evolutionary Ecology. 5: 339-342.
19. Chen H, Niklas KJ, Yang D and Sun S. 2009. The effect of twig architecture and seed number on seed size variation in subtropical woody species. New Phytologist. 183: 1212-1221.

20. Chu CJ, Maestre FT, Xiao S, Weiner J, Wang YS, Duan ZH, and Wang G. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. Ecology Letters. 11: 1189-1197.
21. Clauss MJ, Aarssen LW (1994) Patterns of reproductive effort in Arabidopsis thaliana: confounding effects of size and developmental stage. Ecoscience 1:153–159.
22. Colhoun J. 1973. Effects of environmental factors on plant disease. Annual Review of Phytopathology. 11: 343-364.
23. Condit R (1988) Tropical forest census plots. Springer-Verlag and R.G. Landes.
24. Craine JM. 2009. Resource strategies of wild plants. Princeton University Press, New Jersey.
25. Davies SJ, Ashton PS (1999) Phenology and fecundity in 11 sympatric pioneer species of Macaranga (Euphorbiaceae) in Borneo. Am J Bot 86:1786–1795.
26. Diaz-Uriarte R and Garland Jr T. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Systematic Biology. 47: 654-672.
27. Dillemuth FP, Rietschier EA and Cronin JT. 2009. Patch dynamics of a native grass in relation to the spread of invasive smooth brome. Biological Invasions. 11:1381-1391.
28. Dombroskie SL, Aarssen LW (2010) Within-genus size distributions in angiosperms: small is better. Perspectives in plant ecology, evolution and systematic 12:283–293.
29. Echarte L, Andrade FH, Vega CRC and Tollenaar M. 2004. Kernel number determination in Argentinian Maize hybrids released between 1965 and 1993. Crop Science. 44: 1654-1661.

30. Environment Canada. 1999. Invasive plants of natural habitats in Canada. http://www.ec.gc.ca/eee-ias/78D62AA2-55A4-4E2F-AA08-538E1051A893/invasives.pdf
31. Evenson WE. 1983. Experimental studies of reproductive energy allocation in plants. In: Jones CE and Little JR, Handbook of experimental pollination biology. Scientific and academic editions. New York, pp. 249-274.
32. Fenchel T. 1993. There are more small than larger species? Oikos. 68: 375-378.
33. Frankhauser C. 2000. Seed-transmitted diseases as constraints for potato production in the tropical highlands of Ecuador. PhD Dissertation.
34. Gaudet CL, Keddy PA. 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334:242–243.
35. Gibson PB, Barnett OW, Skipper HD and McLaughlin MR. 1981. Effects of three viruses on growth of white clover. Plant Disease. 65: 50-51.
36. Gleason HA, Cronquist A. 1991. Manual of the Vascular plants of Northeastern United States and Adjacent Canada. The New York Botanical Garden, Bronx, New York.
37. Goldberg DE, Landa K. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. Journal of Ecology. 79:1013–1030.
38. Goldberg DE. 1996. Competitive ability: definitions, contingency and correlated traits. Proceedings of Royal Society B: Biological Sciences. 35:1377–1385.
39. Gould SJ. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. Journal of Paleontology. 62: 319–329
40. Grace JB. 1990. On the relationship between plant traits and competitive ability.384-385.
41. Grime JP. 1973. Competitive exclusion in herbaceous vegetation. Nature. 242: 344-347

42. Hancock JF, Pritts MP. 1987. Does reproductive effort vary across different life forms and seral environments. A Review of the literature. Bull Torey Botany Club. 114: 53-59.
43. Hanzawa FM and Kalisz S. 1993. The relationship between age, size and reproduction in Trillium grandifolorum. America Journal of Botany. 80: 405-410.
44. Hartnett DC. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. Oceologica. 84: 254-259.
45. Hendrix SD. 1979. Compensatory reproduction in a biennial herb following insect defloration. Oecologica. 42: 107-118.
46. Hickman JC. 1977. Energy allocation and niche differentiation in four co-existing annual species of Polygonum in western North America. Journal of Ecology. 65: 317-326.
47. Hsaio C, Chatterton NJ, Asay KH and Jensen KB. 1995. Molecular phylogeny of the Pooideae (Poaceae) based on nuclear rDNA (ITS) sequences. Theoretical Applications of Genetics. 90: 389-398.
48. http://labs.eeb.utoronto.ca/dickinson/rosaceaeevolution/rosaceaeevolution.htm Dickinson Lab: Rodger Evans.
49. http://tolweb.org/tree/ Tree of Life online, The University of Arizona College of Agriculture and Life Sciences and The University of Arizona Library.
50. Inouye DW and Taylor OR. 1985. Synchrony and periodicity of flowering in Frasera speciosa. Ecology. 66: 521-527.
51. Jansen RK, Michaels HJ and Palmer JD. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Systematic Botany. 16: 98-115.

52. Jones LR. 1924. The relation of environment to disease of plants. American Journal of Botany. 11: 601-609.

53. Keddy PA, Nielsen K, Weiher E, Lawson R. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. Journal of Vegetation Science 13:5–16.

54. Keddy PA, Shipley B. 1989. Competitive hierarchies in herbaceous plant communities. Oikos 54:234–241.

55. Keddy PA, Strutt LT, Wisheu IC. 1994. Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? Journal of Ecology. 85:634–643.

56. Keddy PA. 2001. Competition (2nd Edn.). Kluwer Academic Publishers, Dordrecht, The Netherlands, 575 pp.

57. Klinkhamer PGL, Meelis E, de Jong TJ and Weiner J. 1999. On the analysis of size-dependent reproductive output in plants. Functional Ecology. 6: 308-316.

58. Lacey EP. 1986. Onset of reproduction in plants: size versus age dependency. Trends in Ecology and Evolution. 1: 72-75.

59. Liam Revell, University of Massachusetts Boston. Personal correspondence.

60. McGlone MS, Richardson SJ, Jordan GJ. 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes. New Zealand Journal of Ecology 34:137–151.

61. McKinney ML. 1990. Trends in body-size evolution. Evolutionary Trends (ed. KJ McNammara) pp. 75-118. University of Arizona Press, Tucson, AZ.

62. McNaughton SJ. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist. 113: 691-703.

63. Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, Pitman A, Hemmings FA, Frank A, Leishman MR. 2009. Global patterns in plant height. Journal of Ecology. 97:923–932.

64. Muller-Landau. 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. Ecology letters. 9: 589-602.

65. Newcomb L. 1977. Newcomb's Wildflower Guide. Little, Brown and Co.USA

66. Neytcheva MS, Aarssen LW. 2008. More plant biomass results in more offspring production in annuals, or does it? Oikos 117:1298–1307.

67. Niklas KJ, Midgley JJ, Rand RH. 2003. Size dependent species richness: trends within plant communities and across latitude. Ecology Letters. 6:631–636.

68. Niklas KJ. 1994. Plant Allometry: the scaling of form and process. University of Chicago Press, Chicago.

69. Owen DF and Wiegert RG. 1982b. Do consumers maximize plant fitness? Oikos. 27: 488-492.

70. Owen DF. 1980. How plants may benefit from animals that eat them. Oikos. 35: 230-235.

71. Poorter L, Hawthorne W, Bongers F, Sheil D. 2008. Maximum size distributions in tropical forest communities: relationships with rainfall and disturbance. Journal of Ecology. 96:495–504.

72. Potter D, Eriksson T, Evans RC, Oh S, Smedmark JEE. 2007. Phylogeny and classification of Rosaceae. Plant Systematics and Evolution. 266: 5-43.

73. Purvis A, Orme CDL and Dolphin K. 2003. Why are most species small-bodied? A phylogenetic review. Mecroecology: Concepts and Consequences (eds. TM Blackburn and KJ Gaston) pp. 155-173. Blackwell Publishing, Oxford.

74. Rosch H, Van Rooyen HW, Theron GK. 1997. Predicting competitive interactions between pioneer plant species by using plant traits. Journal of Vegetation Science. 8:489–94.

75. Ruiz NR, Ward D, Saltz D. 2008. Leaf compensatory growth as a tolerance strategy to resist herbivory in Pancratium sickenbergeri. Plant Ecology. 198:19-26.

76. Samson DA and Werk KS. 1986. Size-dependent effects in the analysis of reproductive effort in Plants. The American Naturalist. 127: 667-680.

77. Schamp BS, Aarssen LW. 2009. The assembly of forest communities according to maximum species height along resource and disturbance gradients. Oikos 118:564–72.

78. Schmid B and Weiner J. 1993. Plastic relationships between reproductive and vegetative mass in Solidago altissima. Evolution. 47: 61-74.

79. Schmid B, Bazzaz FA and Weiner, J. 1995. Size dependency of sexual reproduction and of clonal growth in two perennial plants. Canadian Journal of Botany. 73: 1831-1837.

80. Silander JA. 1976. The genetic basis of the ecological amplitude of *Spartina patens* on the outer banks of North Carolina. PhD dissertation. Duke University, Durham.

81. Stanley SM. 1973. An explanation for Cope‘s rule. Evolution. 27: 1-26

82. Sugiyama S and Bazzaz FA. 1998. Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. Functional Ecology. 12: 280-288.

83. Taylor DR, Aarssen LW. 1990. Complex competitive relationships among genotypes of three perennial grasses: Implications for species coexistence. American Naturalist 136:305–327.

84. Thomas SC. 1996. Relative size at Onset of maturity in Rain forest trees: a comparative analysis of 37 Malaysian species. Oikos. 76: 145-154.

85. Thompson BK, Weiner J and Warwick SI. 1991. Size-dependent reproductive output in agricultural weeds. Canadian Journal of Botany. 69: 442-446.

86. Tilman D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, 296 pp.

87. Tracey AJ and Aarssen LW. 2011. Competition and body size in plants: the between-species trade-off in maximum potential versus minimum reproductive threshold size. (In press)

88. Van der meijden E and van der waals kooi RE. 1979. The population ecology of Senecio Jacobaea in a sand dune system: reproductive strategy and the biennial habitat.

89. Vega CRC, Sadras VO, Andrade FH and Uhart SA. 2000. Reproductive allometry in soybean, maize and sunflower. Annals of Botany. 85: 461-468.

90. Vinton MA and Goergen EM. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairies. Ecosystems. 9: 967-976.

91. Waugh JM and Aarssen LW. 2012. Size distributions and dispersions along a 485-year chronosequence for sand dune vegetation. Ecology and Evolution. 2: 719-726.

92. Weiner J, Campbell LG, Pino J and Echarte L. 2009. The allometry of reproduction within plant populations. Journal of Ecology. 97: 1220-1233.

93. Weiner J. 1988. The influence of competition on plant reproduction: Plant reproductive ecology: patterns and strategies. 228-245. Oxford University Press, New York.

94. Werner PA. 1975. Predictions of fate in rosette size teasel. Oecologica. 20: 197-201.

95. White EP, Ernest SKM, Kerkhoff, AJ and Enquist BJ. 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution. 22: 323-330.

96. Williams JL and Crone EE. 2006. The impact of invasive grasses on the population growth of Anenome patens, a long-lived native forb. Ecology. 87: 3200-3208.

97. Willis, KJ, McElwain JC. 2002. The evolution of plants. Oxford University Press, New York, 392 pp.

98. Wilson AM, Thompson K. 1989. A comparative study of reproductive allocation in 40 British grasses. Functional Ecology. 3: 297-302.

99. Wilson MF. 1983. Plant reproductive ecology. John Wiley. New York.

100. Worley AC and Harder LD. 1996. Size-dependent resource allocation and costs of reproduction in Pinguicula vulgaris. Journal of Ecology. 84: 195-206.

101. Wright SJ, Jaramillo MA, Pavon J, Condit R, Hubbell SP, and Foster RB. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. Journal of Tropical Ecology. 21: 307-315.

102. Wright SJ, Muller-Landau HC, Condit R and Hubbell SP. 2003. Gap-dependent recruitment, realized vital rates and size distributions of tropical trees. Ecology. 84: 3174-3185.

Appendix 1: List of the 43 species recorded at Wire Fence old-field study site. Nomenclature follows Gleason & Cronquist (1991). Common names follow Newcomb (1977).

Scientific Name	Common Name
***Achillea millefolium* L.**	common yarrow
***Agrostis stolonifera* L.**	creeping bentgrass
***Asclepias syriaca* L.**	common milkweed
***Aster cordifolius* L.**	heart-leaved aster
***Barbarea vulgaris* L.**	common winter cress
***Bromus inermis* L.**	smooth brome
***Carex gracillima* Shwein.**	graceful sedge
***Carex pallescens* L.**	pale sedge
***Carex pensylvanica* Lam.**	Pensylvania sedge
***Cerastium arvense* L.**	field chickweed
***Cerastium vulgatum* L.**	mouse-eared chickweed
***Chrysanthemum leucanthemum* L.**	oxeye daisy
***Dactylis glomerata* L.**	orchard grass
***Danthonia spicata* L.**	poverty oat grass
***Dianthus armeria* L.**	deptford pink
***Erigeron strigosus* Muhl. Ex Wild.**	daisy fleabane
***Festuca rubra* L.**	red fescue
***Fragaria virginiana* L.**	wild strawberry
***Hieracium aurantiacum* L.**	orange hawkweed
***Hieracium piloselloides* Vill.**	king devil's hawkweed
***Hypericum perforatum* L.**	common St. John's wort
***Lotus corniculata* L.**	bird's foot trefoil
***Oenothera perennis* L.**	small sundrops
***Oxalis corniculata* L.**	creeping wood sorrel
***Phleum pratense* L.**	timothy
***Plantago major* L.**	common plantain
***Poa pratensis* L.**	Kentucky bluegrass
***Potentilla argentea* L.**	silver cinquefoil
***Potentilla recta* L.**	sulphur cinquefoil
***Prunella vulgaris* L.**	heal-all
***Ranunculus acris* L.**	tall buttercup
***Satureja vulgaris* L.**	wild basil
***Setaria viridis* L.**	green foxtail
***Sisyrinchium montanum* Greene.**	little Blue-eyed grass
***Solidago Canadensis* L.**	Canada goldenrod
***Taraxacum officinale* Weber.**	common dandelion
***Thlapsi arvense* L.**	pennycress mustard
***Tragopogon pratensis* L.**	meadow goat's beard
***Trifolium dubium* Sibth.**	hop clover
***Trifolium pratense* L.**	red clover
***Trifolium repens* L.**	white clover
***Vicia cracca* L.**	cow vetch
***Waldsteina fragarioides* Michx.**	barren strawberry

Appendix 2: List of the 54 species recorded at the Bracken old-field study site. Nomenclature follows Gleason & Cronquist (1991). Common names follow Newcomb (1977).

Scientific Name	Common Name
Achillea millefolium L.	common yarrow
Agrimonia gryposepala Wallr.	agrimony
Agrostis stolonifera L.	creeping bent Grass
Asclepias syriaca L.	common milkweed
Aster novae-angliae L.	New England aster
Aster umbellatus Miller.	flat-topped aster
Barbarea vulgaris L.	yellow rocket
Bromus inermus L.	smooth brome
Carex gracillima Shwein.	graceful sedge
Carex pallescens L.	pale sedge
Carex pensylvanica Lam.	Pensylvania sedge
Carya cordiformis (Wangenh.) K.Koch	bitternut hickory
Centaurea jacea L.	brown knapweed
Cerastium arvense L.	field chickweed
Cerastium vulgatum L.	mouse-eared chickweed
Cirsium arvense (L.) Scop.	Canada thistle
Cornus sericea L.	red-osier dogwood
Crataegus L.	hawthorn
Dactylis glomerata L.	orchard grass
Danthonia spicata L.	poverty oat grass
Daucus carota L.	queen anne’s lace
Dianthus armeria L.	deptford pink

Erigeron strigosus Muhl. Ex Wild.	daisy fleabane
Festuca rubra L.	red fescue
Fragaria virginiana L.	wild strawberry
Fraxinus Americana L.	white ash
Gallium mollugo L.	wild madder
Hieracium piloselliodes Vill.	king devil's hawkweed
Hypericum perforatum L.	common St. john's wort
Inula helenium L.	elecampane
Linaria vulgaris Miller.	butter and eggs
Oxalis corniculata L.	creeping wood sorrel
Phleum pratense L.	timothy grass
Plantago lanceolata L.	english plantain
Poa compressa L.	Canada bluegrass
Poa pratensis L.	Kentucky bluegrass
Potentilla argentea L.	silver cinquefoil
Potentilla recta L.	sulfur cinquefoil
Ranunculus acris L.	tall buttercup
Ranunculus pensylvanicus L.f.	bristly crow's foot
Rhamnus cathartica L.	common buckthorn
Rubus L.	raspberry
Rudbekia hirta L.	black-eyed susan
Rumex acetosella L.	sheep sorrel
Satureja vulgaris L.	wild basil
Sisyrinchium montanum Greene.	common blue-eyed grass
Solidago Canadensis L.	Canada goldenrod

Solidago nemoralis Aiton.	gray goldenrod
Solidago rugosa Miller.	rough-stemmed goldenrod
Taraxacum officinale Weber.	common dandelion
Tragopogon pratensis L.	meadow goat's beard
Trifolium pratense L.	red clover
Trifolium repens L.	white clover
Vicia cracca L.	cow vetch

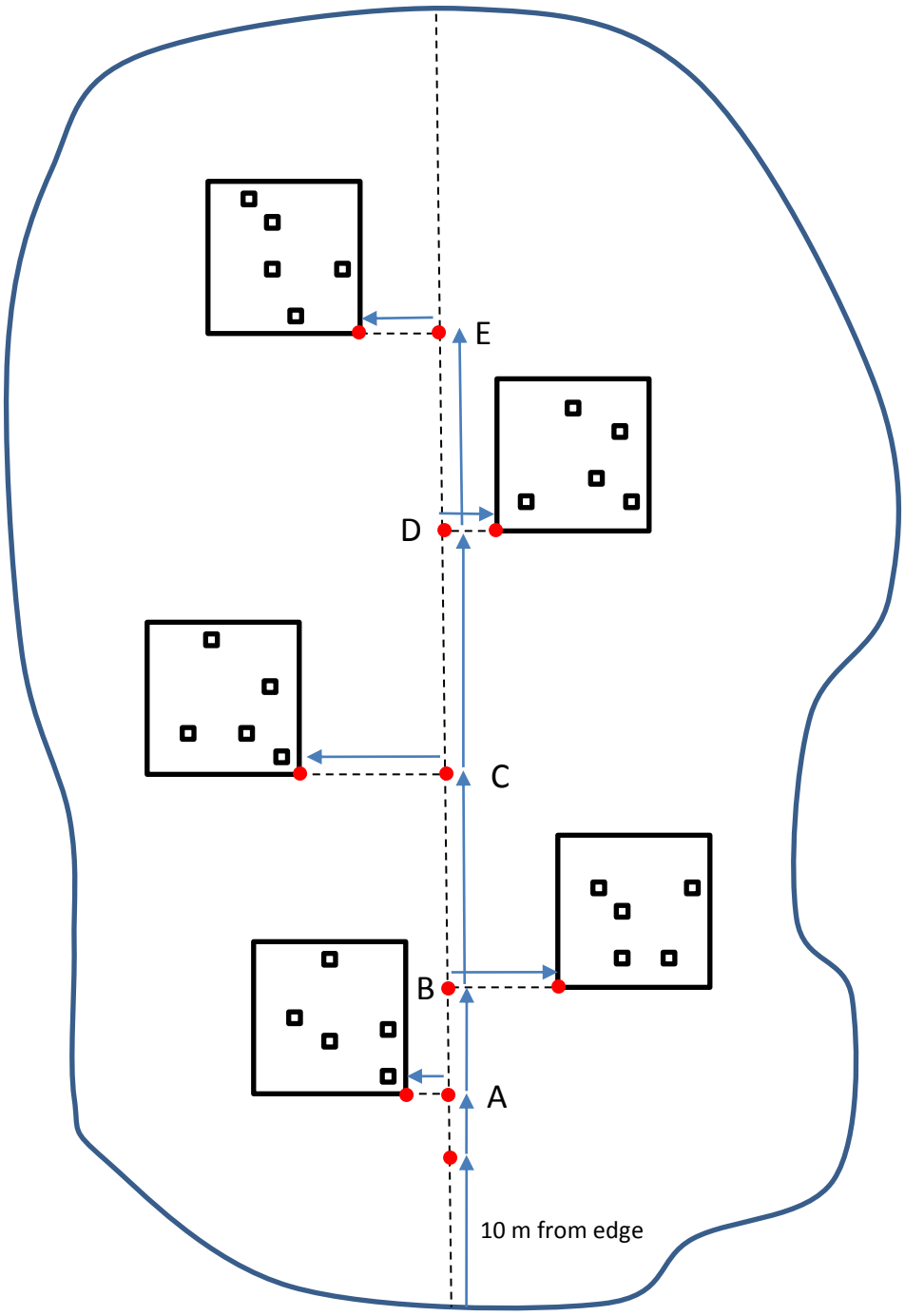
Appendix 3: List of the 69 species recorded at the Bracken shrub-land study site. Nomenclature follows Gleason and Cronquist (1991). Common names follow Newcomb (1977).

Scientific Name	Common Name
***Acer saccharum* Marshall.**	sugar maple
***Achillea millefolium* L.**	common yarrow
***Agrimonia gryposepala* Wallr.**	agrimony
***Agrostis stolonifera* L.**	creeping bent grass
***Asclepias syriaca* L.**	common milkweed
***Aster novae-angliae* L.**	New England aster
***Aster umbellatus* Miller.**	flat-topped aster
***Bromus inermus* L.**	smooth brome
***Carex cryptolepis* Mackenzie.**	cone sedge
***Carex gracillima* Shwein.**	graceful sedge
***Carex otrube* L.**	false fox sedge
***Carex pallescens* L.**	pale sedge
***Carex pensylvanica* Lam.**	Pensylvania sedge
***Carex vulpinoidea* Michx.**	fox sedge
***Centaurea jacea* L.**	brown knapweed
***Cerastium arvense* L.**	field chickweed
***Cerastium vulgatum* L.**	mouse-eared chickweed
***Chrysanthemum leucanthemum* L.**	oxeye daisy
***Cirsium arvense* L.**	Canada thistle
***Convolvulus arvensis* L.**	bindweed
***Cornus racemosa* Lam.**	gray dogwood
***Cornus sericea* L.**	red osier dogwood
***Dactylis glomerata* L.**	orchard grass
***Danthonia spicata* L.**	poverty oat grass
***Daucus carota* L.**	queen Anne's lace
***Dianthus armeria* L.**	deptford pink
***Equisetum arvense* L.**	common horsetail
***Erigeron strigosus* Muhl. Ex Wild.**	daisy fleabane
***Festuca rubra* L.**	red fescue
***Fragaria virginiana* L.**	wild strawberry
***Fraxinus Americana* L.**	white ash
***Gallium mollugo* L.**	wild madder
***Hieracium pilloselloides* Vill.**	hawkweed
***Hypericum perforatum* L.**	common St. John's wort
***Inula helenium* L.**	elecampane
***Juniperus communis* L.**	common juniper
***Juniperus virginiana* L.**	red cedar
***Linaria vulgaris* Miller.**	butter and eggs
***Lotus corniculata* L.**	bird's foot trefoil
***Malus pumila* L.**	wild apple
***Mentha arvensis* L.**	field mint
***Parthenocissus quinquefolia* (L.) Planchon.**	Virginia creeper
***Phleum pratense* L.**	timothy

***Plantago lanceolata* L.**	English plantain
***Poa compressa* L.**	Canada bluegrass
***Poa pratensis* L.**	Kentucky bluegrass
***Potentilla argentea* L.**	silver cinquefoil
***Potentilla recta* L.**	sulfur cinquefoil
***Prunella vulgaris* L.**	common self-heal
***Prunus serotina* Ehrh.**	black cherry
***Prunus virginiana* L.**	choke cherry
***Ranunculus acris* L.**	tall buttercup
***Ranunculus pensylvanicus* L.f.**	bristly crow's foot
***Rhamnus cathartica* L.**	common buckthorn
***Rubus occidentallis* L.**	common blackberry
***Rubus* L.**	raspberry
***Sisyrinchium montanum* Greene.**	blue-eyed grass
***Solidago Canadensis* L.**	Canada goldenrod
***Solidago juncea* Aiton.**	early goldenrod
***Solidago nemoralis* Aiton.**	gray goldenrod
***Solidago rugosa* Miller.**	rough-stemmed goldenrod
***Spiraea alba* Duroi.**	broad-leaf meadowsweet
***Taraxacum officinale* Weber.**	common dandelion
***Tragopogon pratensis* L.**	meadow goat's beard
***Trifolium dubium* Sibth.**	hop clover
***Trifolium pretense* L.**	red clover
***Trifolium repens* L.**	white clover
***Ulmus Americana* L.**	American elm
***Viccia cracca* L.**	cow vetch
***Waldensteina fragarioides* Michx.**	barren strawberry

Appendix 4: List of the 27 species recorded at the Bracken wood-land site. Nomenclature and common names follows Gleason and Cronquist (1991).

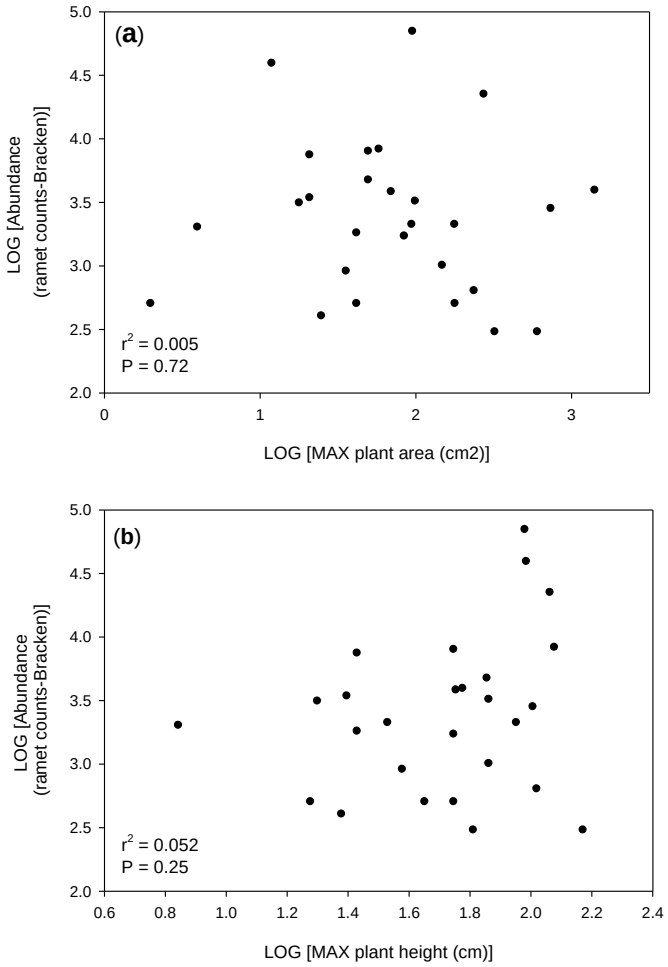
Scientific Name	Common Name
***Acer saccharum* Marshall.**	sugar maple
***Aster pilosus* Willd**	frost aster
***Aster simplex* Willd.**	panicled aster
***Betula papyrifera* Marshall.**	white birch
***Carex albursina* Sheldon.**	white bear sedge
***Carex hirtifolia* Mackenzie.**	hairy wood sedge
***Carya cordiformis* (Wangenh.) K.Koch.**	bitternut hickory
***Dryopteris intermedia* Muhl.**	wood fern
***Epigaea repens* L.**	mayflower
***Fagus grandifolia* Ehrh.**	American beech
***Fragaria vesca* L.**	wood strawberry
***Fraxinus Americana* L.**	white ash
***Gallium asprellum* Michx.**	rough bedstraw
***Gentiana linearis* Froelich.**	narrow-leaved gentian
***Geranium robertianum* L.**	herb Robert
***Hepatica Americana* (DC.) KerGawler.**	round-lobed hepatica
***Lysimachia nummularia* L.**	moneywort
***Monotropa hypopithys* L.**	pinesap
***Osmunda regalis* L.**	royal fern
***Ostrya virginiana* (Miller.) K.Koch.**	hop hornbeam
***Ranunculus pensylvanicus* L.f.**	bristly crow's foot
***Ribes cynobasti* L.**	dogberry
***Sanguinaria Canadensis* L.**	bloodroot
***Solidago caesia* L.**	bluestem goldenrod
***Tilia Americana* L.**	basswood
***Ulmus Americana* L.**	American elm
***Viola septentrionalis* Willd.**	northern blue violet



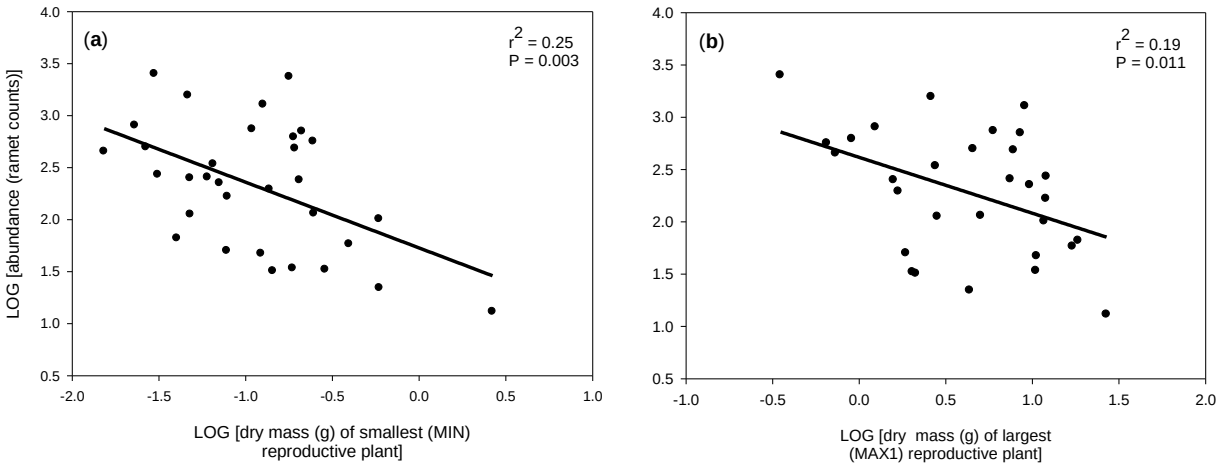
Appendix 5: Abundance sampling set-up for old-field, shrub-land and wood-land sites at Bracken. The larger square plots are 10 x 10 m, and the smaller plots within are 1 x 1 m.

Appendix 6: Data collection sheet for plant body size metrics and abundance in all habitats at Bracken.

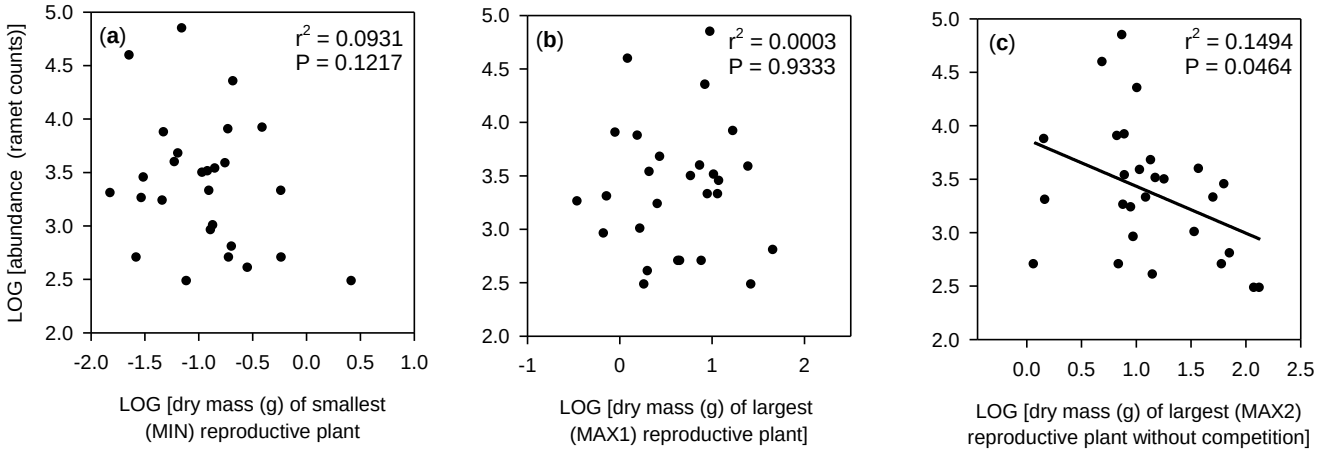
10 x 10 m Plot #	1 x 1 m Plot #	Species	# of individuals	MAX height (cm)	MAX lateral (cm)	MAX perp. (cm)



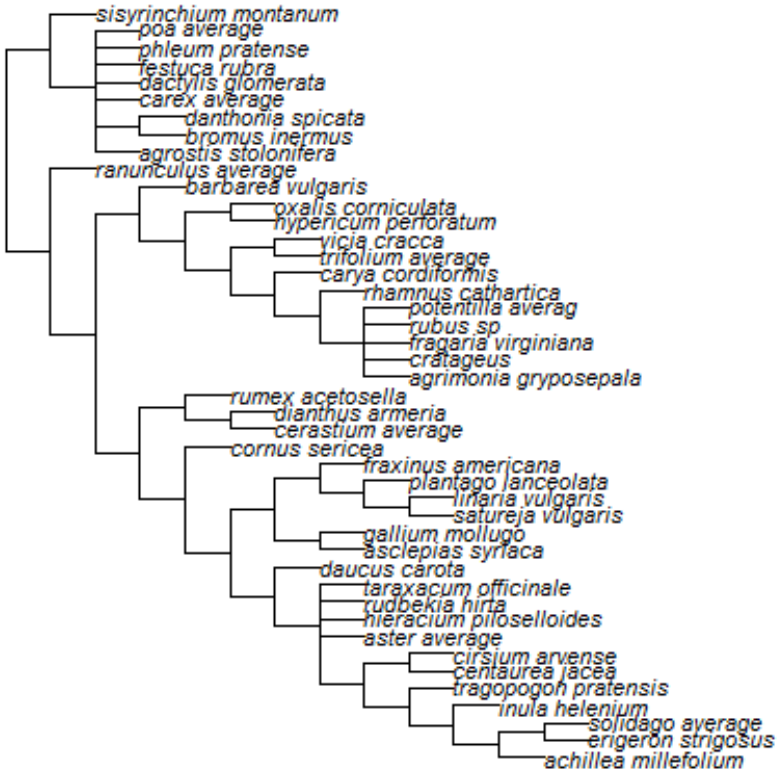
Appendix 7: between-species relationship (for log-transformed data) for species abundance (ramet counts at Bracken old-field site) versus: (**a**) MAX plant height (cm) for each species collected; (**b**) MAX plant area or canopy spread (cm^2) for each species collected. r^2 and associated P values are from Type I regression analyses. (This is to aid with interpretation of the multiple regression results in Table 2).



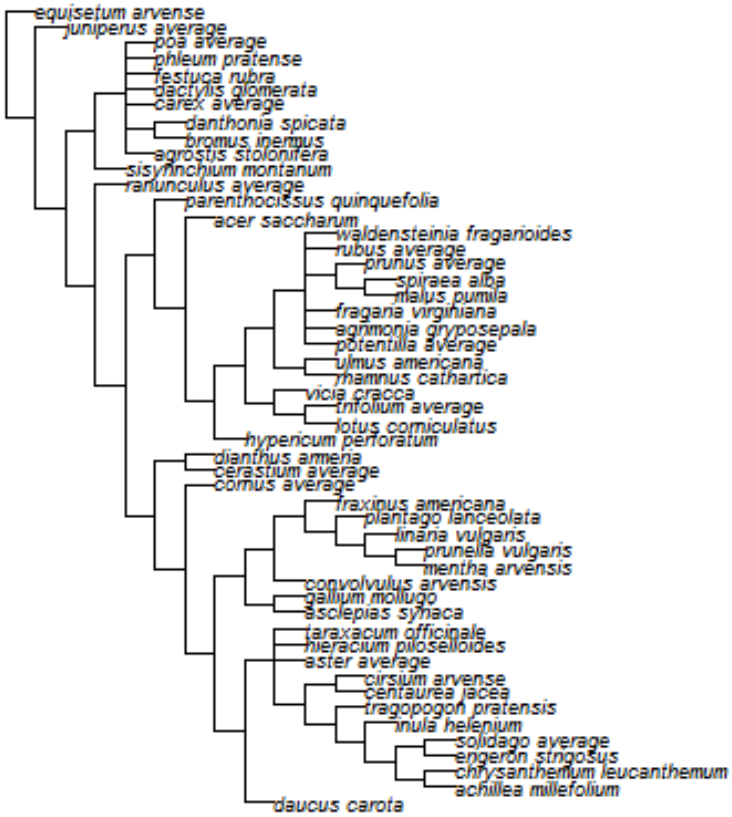
Appendix 8: From Fig. 5(b): Between-species relationships (for log transformed data) for species abundance at the Wire Fence old-field study site versus (a) dry mass (g) of the smallest (MIN) reproductive plant, with outlier removed. (b) dry mass (g) of the largest (MAX1) reproductive plant with three obvious outliers removed (Fig. 5(d)).. r^2 and associated P values are from Type I linear regression analyses.



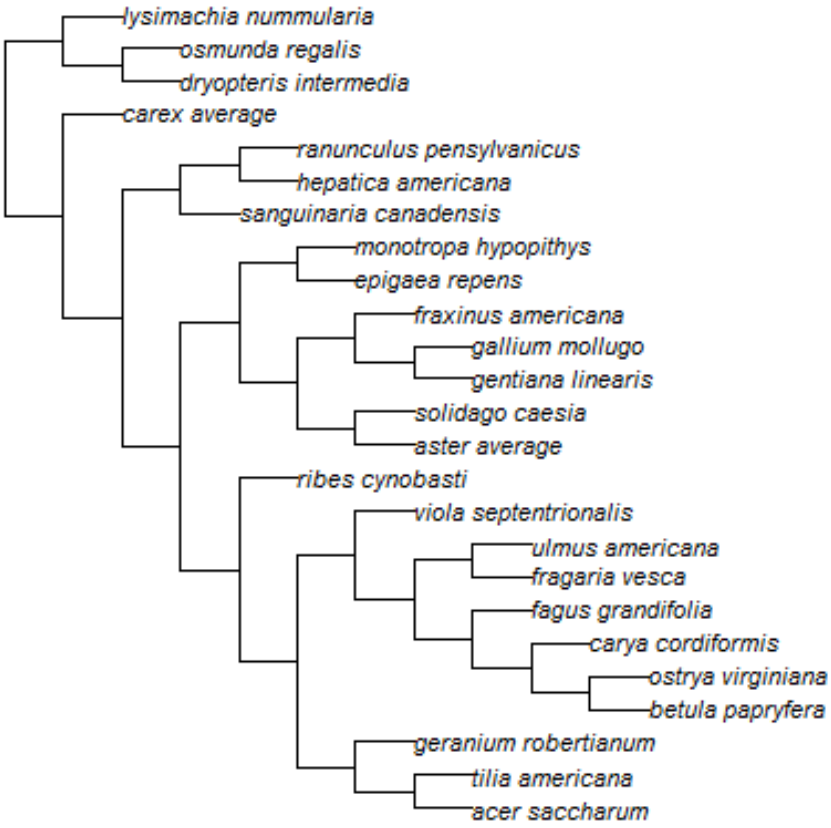
Appendix 9: Between-species relationships (for log-transformed data, n=27 species) for species abundance (measured in ramet counts per 500 m^2) within surveyed plots at the Bracken old-field study site versus MIN (**a**), MAX1 (**b**), and MAX2 (**c**) recorded for the same species also resident at the Wire Fence old-field study site. [See Figure 4 legend for definition of MIN, MAX1 and MAX2]. r^2 and associated P values, and regression line in (c), are from Type I linear regression.



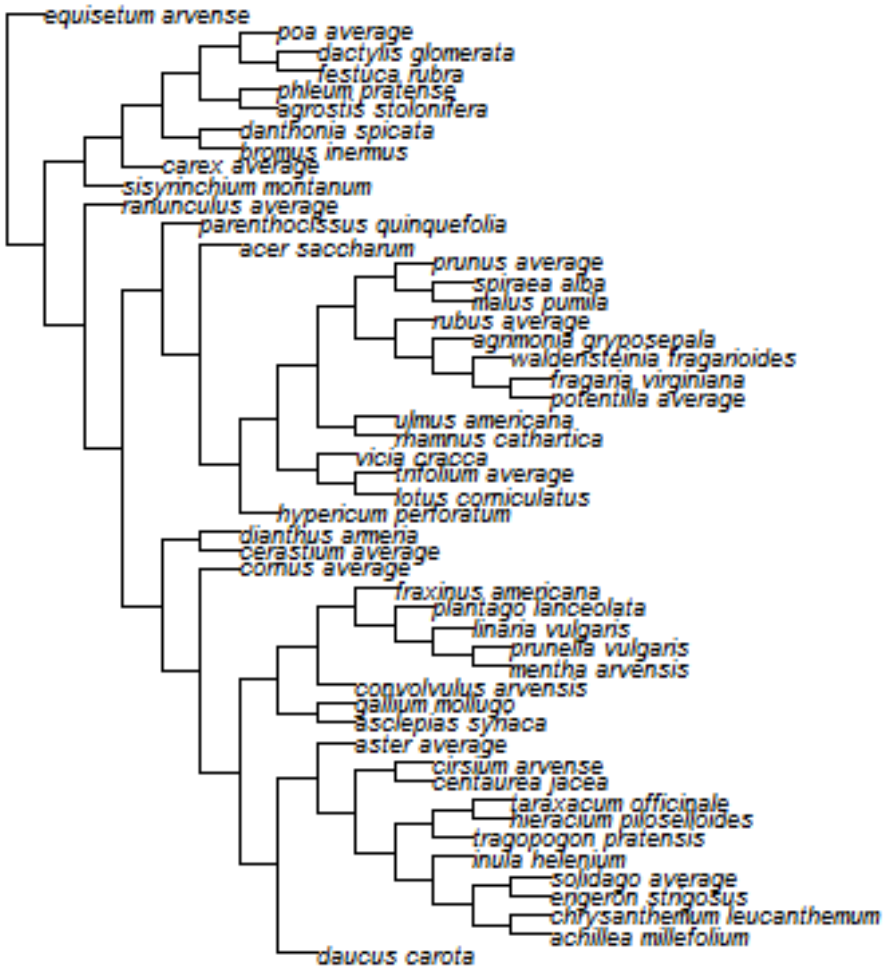
Appendix 10: Phylogenetic tree for Bracken old-field species (n = 54). Tree was made using Phylomatic and all branch lengths are equal to 1.0. Tree was plotted using R version 2.14.2.



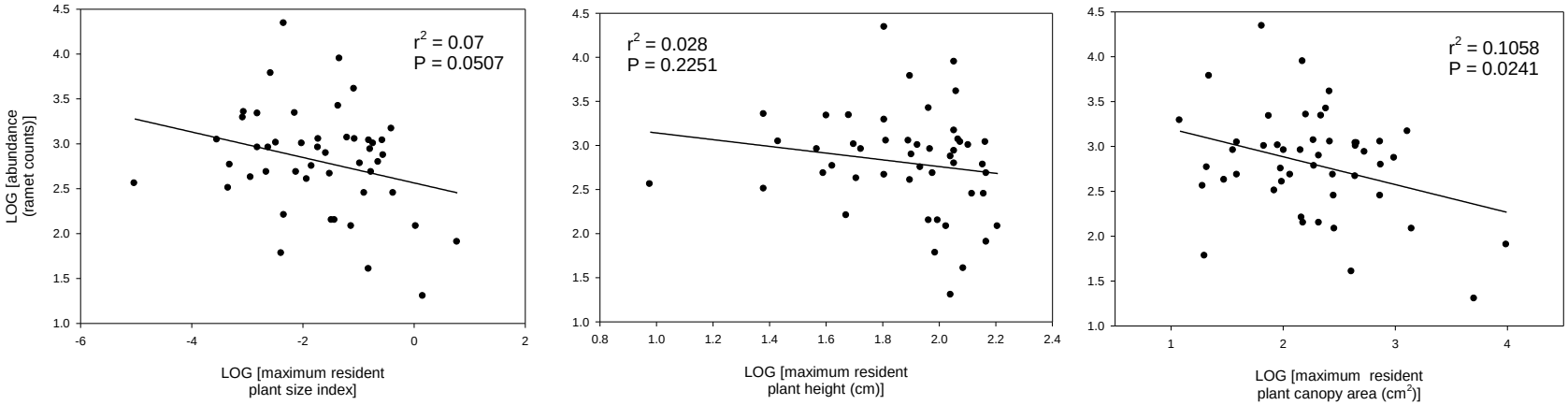
Appendix 11: Phylogenetic tree for Bracken shrub-land species (n = 69). Tree file was made using Phylomatic and all branch lengths are equal to 1.0. Tree was plotted using R version 2.14.2.



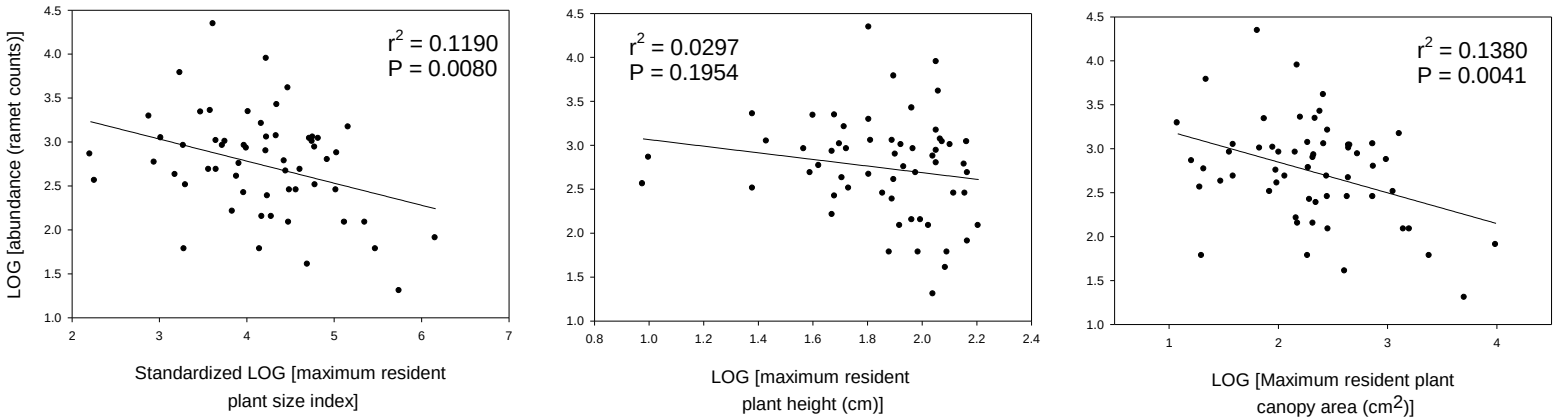
Appendix 12: Phylogenetic tree for Bracken wood-land species (n = 27). Tree was made using Phylomatic and all branch lengths are equal to 1.0. Tree was plotted using R version 2.14.2.



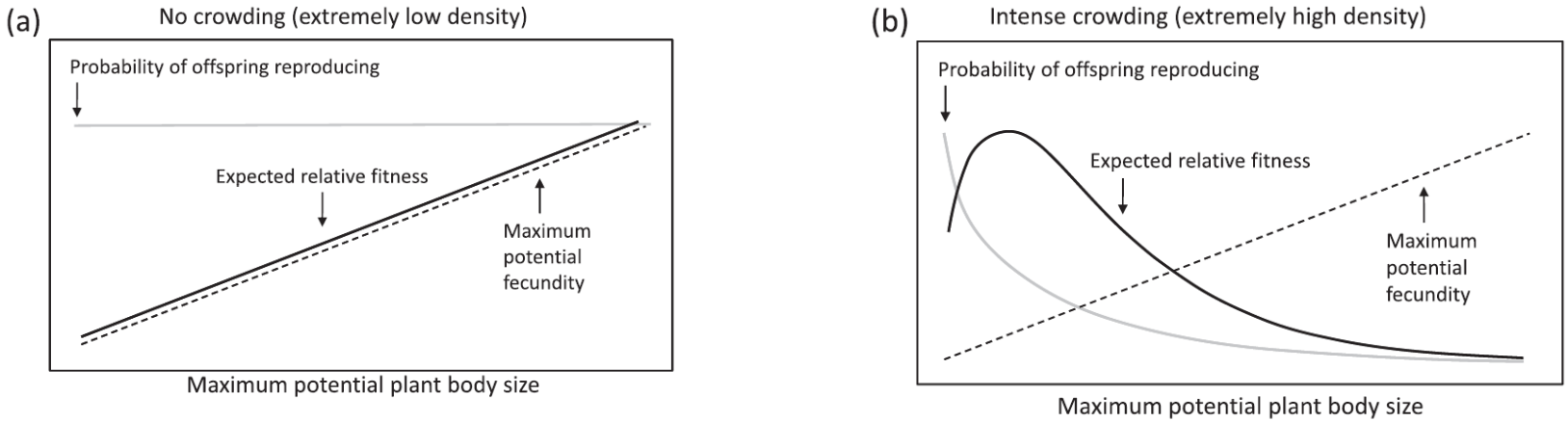
Appendix 13: Phylogenetic tree for Bracken shrub-land species (n = 69) after resolving polytomies using current literature. Tree was made using Phylomatic and all branch lengths are equal to 1.0. NEXUS file was edited manually and tree was re-plotted using R version 2.14.2



Appendix 14: Between-species relationships (for log-transformed data) for species abundance (based on ramet count estimates per 500 m^2) at the Bracken study site within shrub-land (n=47 species, only those species that were also found in the Bracken old-field site) versus: standardized maximum recorded plant size index; maximum recorded resident plant height (cm); and maximum recorded resident plant canopy area (cm^2). Standardized LOG [maximum resident plant size index] is the sum of standardized LOG [maximum resident plant height] and standardized LOG [maximum resident plant canopy area] (see text). r^2 and associated P values, and regression lines, are from Type I linear regression analyses.



Appendix 15: Between-species relationships (for log-transformed data) for species abundance (based on ramet count estimates per 500 m^2) at the Bracken study site within shrub-land (n=58 non-woody species) versus: standardized maximum recorded plant size index; (maximum recorded resident plant height (cm); and maximum recorded resident plant canopy area (cm^2). Standardized LOG [maximum resident plant size index] is the sum of standardized LOG [maximum resident plant height] and standardized LOG [maximum resident plant canopy area] (see text). r^2 and associated P values, and regression lines, are from Type I linear regression analyses.



Appendix 16: From Tracey and Aarssen (2011) fitness model predicting that when the effect of crowding intensity (competition) increases, natural selection generally favours traits associated with relatively small body size, not larger maximum potential body size, contrary to the predictions of traditional theory.