Oecologia (2010) 162:995–1004
DOI 10.1007/s00442-009-1499-2

COMMUNITY ECOLOGY - ORIGINAL PAPER

The role of plant species size in invasibility: a field experiment

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Received: 17 November 2008 / Accepted: 26 October 2009 / Published online: 16 November 2009

Abstract Large plant species self-thin to disproportionately lower densities than smaller plant species, and therefore may leave more patches of unused space suitable for invasion. Using experimental monocultures of 11 old-field perennial plant species differing in maximum size, as well as mixtures composed of all monoculture species, we tested our primary hypothesis that monocultures of larger species will be more susceptible to natural invasion. After 3 years, monocultures of larger species were invaded by a significantly greater number of species, and more ramets, from the surrounding vegetation. Invading plant species were significantly smaller than the monoculture species being invaded, suggesting that smaller plant species may be better invaders. Thus, we quantified a trade-off between species size, which is frequently associated with increased competitive ability for light, and invasibility, suggesting one reason why large and small species coexist in virtually all plant communities. Although we expected that invasion would enhance biomass production by more fully capturing available resources, we found that the most highly invaded plots of each species produced significantly less biomass. This suggests that increased diversity resulting from invasion did not result in complementary resource use. Mixture plots containing all experimental species did not admit a significantly different number of invading ramets or species than most monocultures, indicating no obvious role for diversity in resistance to invasion, or complementary resource use. Our results suggest that relatively large species may be limited in their capacity to competitively exclude other, smaller species from communities because pure stands of the former are more susceptible to invasion by the latter.

Keywords Competitive ability · Complementarity · Physical space niche · Post-thinning invasion · Self-thinning

Communicated by John Silander.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1499-2) contains supplementary material, which is available to authorized users.

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Introduction

Why has evolution produced no single species capable of completely dominating vegetation? This basic question serves as the foundation for investigations of diversity patterns by both evolutionary and community ecologists (Tilman 1982). Even species that are considered to be highly invasive, such as *Agropyron cristatum* in grasslands (Heidinga and Wilson 2002), or *Acer platanoides* in forests (Reinhart et al. 2005), reduce species richness in plant communities but do not produce monocultures. Similarly, the highly invasive vine *Pueraria montana*, which is known to grow over the top of forests in the south-eastern United States, still allows the growth of some early flowering species in the understory (Forseth and Innis 2004). Stands of such invasive species usually represent limited monocultures with several additional species also in residence, but less conspicuous because they are relatively rare, and often much smaller (Aarssen et al. 2006). The question of why no species can completely eliminate competitors from a community remains critical to our understanding of biodiversity.

Understanding why species richness is always >1 is particularly important in diverse communities where many coexisting species overlap considerably in resource requirements (e.g., plant and phytoplankton communities; Hutchinson 1961; Aarssen 1983; Goldberg and Barton 1992; Hubbell 2001; Huisman et al. 2001). Theoretically, species with overlapping resource requirements should compete intensely, yet examination of such communities reveals considerable interspecific variation in traits that are believed to play an important role in defining species competitive ability such as species size (Weiher et al. 1998; Aarssen and Schamp 2002; Aarssen et al. 2006; Schamp et al. 2008) and seed size (Leishman 2001; Turnbull et al. 1999; Moles and Westoby 2004). Species size in particular (i.e., height or biomass), appears to play a role in driving hierarchical competitive relationships (Goldberg 1987; Gaudet and Keddy 1988; Keddy and Shipley 1989; Goldberg and Landa 1991; Shipley 1993; Rosch et al. 1997; Howard and Goldberg 2001; Keddy et al. 2002; Warren et al. 2002; Fraser and Keddy 2005, but see Gerry and Wilson 1995 for a belowground competition counter-example) that should theoretically result in the exclusion of all but the best competitor (Laird and Schamp 2006). Evidence that plant species compete hierarchically and large species possess a competitive advantage (in above-ground competition) further the conundrum of why large species never appear to form monocultures (Aarssen and Schamp 2002).

One reason why no species, large or small, can dominate a given community is that, through mortality, all plants relinquish their hold on resources, and thus even monocultures of the most competitive species are susceptible to invasion. We use the term "invasion" here to describe all colonization by non-resident species (sensu Davis 2005). For example, in a planted monoculture, weeding is necessary to prevent successful invasion by non-resident species from surrounding plant communities. Evidence of this mechanism is readily available from monoculture treatments in any diversity-productivity experiment or from the necessity of herbicide application in agricultural fields. Simply put, no monoculture or community is perfectly resistant to invasion (Crawley 1987). This is not to say that diverse communities are therefore better at resisting invasion. In fact, available data suggest that increased diversity appears to enhance invasion as often as it repels it (Levine and D'Antonio 1999; Alpert et al. 2000; Stohlgren 2003). We propose that general principles concerning invasion, and subsequently diversity, may best be obtained by first considering whether monocultures of different species are more or less likely to be successfully invaded (Milbau et al. 2003).

Plant communities vary considerably in the degree to which they are invasible (Crawley 1987; Levine and D'Antonio 1999; Alpert et al. 2000; Fridley et al. 2007) and species size may be an important source of this variation. For example, studies of self-thinning demonstrate that larger species self-thin to disproportionately lower resident densities compared with smaller species (White 1980; Enquist et al. 1998). Therefore, larger species, through mortality resulting from strong intraspecific competition, may leave more unused resources available, especially space, to smaller species that have a lower minimum resource requirement (i.e., smaller physical-space niche: Aarssen et al. 2006).

Additionally, it has been proposed that larger, competitively dominant species are less efficient in capturing resources because of more course-grained foraging, and that the persistence of competitively inferior species in relatively undisturbed, productive communities may rest in their ability to successfully capture leftover resources (Grime 1987, 1994). Thus, large species may be more susceptible to invasion because of increased density-dependent mortality (i.e., self-thinning), and because larger species forage more coarsely for resources, leaving small parcels of resources available to smaller, invading species. Moreover, if larger species are less efficient in their use of space, and thus leave resources available to potential invaders, biomass production in experimental monocultures should be enhanced by invasion. Invasion, particularly by relatively small plant species that are capable of capturing unused resources, may result in a form of post-thinning complementarity through increased resource use efficiency (Aarssen et al. 2006).

In this field experiment, we planted monocultures of 11 old-field plant species, as well as mixtures of all monoculture species. We maintained these plots for 1 year to allow intraspecific competition-induced mortality to occur, and then allowed invasion to occur over two seasons to address the following questions:

1. Are monocultures of larger plant species, after undergoing self-thinning, more susceptible to invasion?
2. Does the increased invasion of experimental monocultures contribute to increased productivity?
3. Are experimental mixtures less susceptible to invasion than monocultures of constituent species?

Materials and methods

Experimental design

The study was conducted at the Queen's University Biology Station, Canada (44°34′N, 76°20′W), in a 30 × 30-m section of an old-field. In April 2004, prior to the start of the experiment, the field was tilled to 30 cm, and again several times to 10 cm to disrupt the growth of rooted plants and to homogenize the soil.

A total of 226 treatment plots (40 × 40 cm) were set up in a grid (15 rows × 16 columns of plots) with 1-m separation between plots. Edge plots were 2 m from the surrounding fence. Each plot was delineated by a wooden frame 10 cm high and buried to a depth of 5 cm.

Plots were seeded as either monocultures or mixtures. Monocultures of 17 species of herbaceous perennial plant species were seeded into 166 plots, with ten replicates for all but one species, which had only six replicates (this species was later eliminated from analysis—see below). Target species were chosen to span the existing species size distribution in a nearby old-field plant community (Fig. S1a), although this correspondence was slightly reduced with the loss of some monoculture species (Fig. S1b; see below for explanation). Treatments were assigned to plots according to a stratified random design, so that species were evenly represented among rows and randomly placed within columns. The number of invading ramets and species, and plot biomass did not vary significantly by row; although there was a column effect on invasion (see Results). The remaining 60 plots were seeded as mixtures of the 17 species such that total plot density was expected to equal that of monocultures, with equal numbers of each species (i.e., each species making up 1/17th of the community). Grazing by deer killed most individuals in monocultures of six species at the end of the first growing season. These plots were excluded from the analysis; the remaining 11 monoculture species still spanned a wide range of maximum aboveground biomass (Table 1).

During the winter prior to preparing and seeding our plots, we performed germination trials in a growth chamber to assess species-specific germination rates. We used these germination rates to adjust the number of seeds of each species planted in the field to yield an equal density of 1,200 seedlings per 40 × 40-cm plot in both experimental monocultures and mixtures (Table 1; this density exceeded maximum densities in a nearby field). Germination trials were performed using the same soil used in our experimental plots, and were subjected to the same watering regime as the field plots. Germination rates in our experiment, measured weekly during the first growing season, varied within and among species (Table 1); however, all plots experienced mortality and final density was not related to germination rate, suggesting that this had little influence on our results.

Plots were seeded in May 2004 and watered using fine-misting watering cans to minimize seed movement. Watering was continued daily as necessary through the first season until vegetation was well established. Prior to seeding, a top-layer of approximately 3.5 cm of sterilized topsoil, cow manure and leaf mold, course sand, and peat moss was added to each plot (~5 l) to suppress the germination of seed from non-experimental species in the soil below. For the first growing season, all plots were hand-weeded weekly to remove all species that were not experimentally seeded. Weed sprouting in the first season was rare and weeding did not significantly disturb plots. Beginning in the subsequent growing season (2005), all plots were

Table 1 Characteristics of the 11 study species used in field experiments

Species	Life form	Max. dry mass[a] (g)	Max. height[a] (m)	No. of seeds sown[b]	Mean no. germinating[c]
Agrostis gigantea Roth.	Forb	0.6	1.16	1,333	576.5
Aster lateriflorus (L.) Britt.	Forb	4.33	1.66	2,000	148.9
Aster novae-angliae L.	Forb	16.80	1.35	2,000	263.5
Carex vulpinoidea Michx.	Sedge	1.01	0.97	2,182	145.2
Chrysanthemum leucanthemum L.	Forb	2.21	0.8	1,333	651.6
Dactylis glomerata L.	Grass	1.40	1.21	1,200	637.6
Phleum pretense L.	Grass	2.40	1.36	1,286	689.4
Poa compresssa L.	Grass	0.41	0.79	6,000	576.5
Rudbeckia hirta L.	Forb	8.16	0.96	1,644	760.7
Solidago nemoralis Ait.	Forb	9.32	1.02	2,105	150.3
Solidago rugosa P. Mill.	Forb	11.55	1.26	6,000	103.6

All plants were sampled at the Queen's University Biology Station, Chaffey's Locks, Ontario, Canada (44°34′N, 76°20′W)

[a] Maximum (*Max.*) dry mass and max. height of experimental species were measured as the mean mass of the ten largest specimens harvested from the field at flowering

[b] Number of seeds sown indicates the sowing density for experimental plots, adjusted for germination rate to achieve a density of 1,200 seedlings per plot

[c] Mean number of germinating plants is the average per monoculture species across ten replicates

allowed to be colonized naturally by species from the surrounding field, as well as from surrounding plots. This continued until the end of the third growing season (September 2006) at which time, plots were censused and harvested for overall plot biomass. The number of ramets belonging to each species was recorded for both monoculture and mixture plots. Each stem emerging from the soil surface was counted as an individual ramet. All results were recorded from just the center 25 × 25 cm of each plot to exclude edge effects.

Analyses

To test whether larger plant species self-thinned to a lower density, the relationship between maximum species size and density at the end of the experiment was examined across monoculture treatments. Spearman-rank correlation was used because the data could not be transformed to meet normality and variance requirements of regression. We calculated maximum species size as the maximum above-ground biomass observed among the ten largest individuals of each species sampled from the experimental plots, to ensure that we identified local maximums. These maximum biomass values are also strongly positively correlated to maximum biomass data collected from a nearby old-field (Schamp et al. 2008), where 25 individuals were sampled per species ($n = 11$, $R^2 = 0.75$, $P = 0.008$). All individuals were sampled in late season at reproductive stage.

To test whether larger species would self-thin in such a way as to allow greater invasion, we regressed the number of invading species, and the number of invading ramets, against maximum species size. Dependent variables were transformed as necessary to improve normality and variance requirements for regression.

We also used a paired *t*-test to examine our prediction that invading species were significantly smaller than monoculture species. For this analysis, we used maximum potential height as a proxy measure of species size, as mature samples within the field were not available for many invading species. Maximum species height data were taken from published flora data (Gleason and Cronquist 1991).

To determine whether post-thinning invasion lead to greater overall biomass production in plots, we used multiple regression analysis with plot biomass as the dependent variable. We examined the effects of maximum species size (above-ground dry biomass in grams), and the number of ramets belonging to invaders, on the overall plot biomass.

We investigated whether species mixtures were more or less susceptible to invasion by comparing invasion between mixtures and each monoculture treatment using a fixed-effects, single-factor ANOVA. We treated monocultures as discrete categories for this analysis to observe how mixtures compare to monocultures of different sized species. This allowed us to consider the relative importance of species size and species richness on invasion. We used the Tukey–Kramer test to distinguish between significantly different treatments. Additionally, we used a fixed-effects, single factor ANOVA to investigate whether mixture treatments, on average, had greater biomass production than monoculture treatments.

Results

Final density in monocultures was negatively correlated with species size ($n = 110$, $r = -0.24$, $P = 0.012$; Fig. 1), confirming that large species self-thinned to lower densities. Variation in germination rate among species was unrelated to final density ($n = 110$, $r = 0.11$, $P = 0.27$).

Larger species' monocultures were invaded by a greater number of ramets ($n = 110$, $R^2 = 0.07$, $P = 0.006$; Fig. 2a) as well as by a significantly greater number of species ($n = 110$, $R^2 = 0.10$, $P = 0.0009$; Fig. 2b). Invasion was also significantly influenced by plot location, and the effect of monoculture species size on invasion (Fig. 2) was assessed on residual variation in invasion (species and ramet level) after variation due to plot location was accounted for. The inclusion of plot location (experimental grid column 1–17) as an additional independent variable in multiple regression analyses increased the variance explained in the number of species invading monocultures, but did not explain substantial additional variation in the number of ramets invading plots (multiple regression models including plot location: ramets—$n = 110$, $R^2 = 0.08$, $P = 0.006$; species—$n = 110$, $R^2 = 0.28$; $P < 0.001$). Including germination in a multiple regression model did not yield a significant effect or increase the explanatory power of our model, suggesting

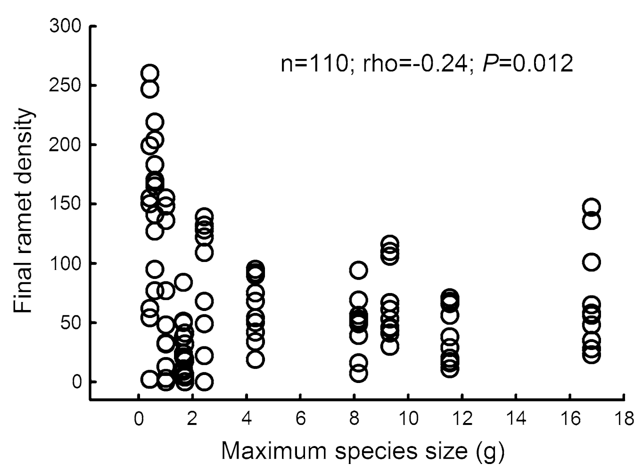

Fig. 1 Relationship between maximum species size (above-ground biomass) and ramet density ($n = 110$). Ramet density is calculated as the number of stems of the monoculture species remaining 3 years after planting

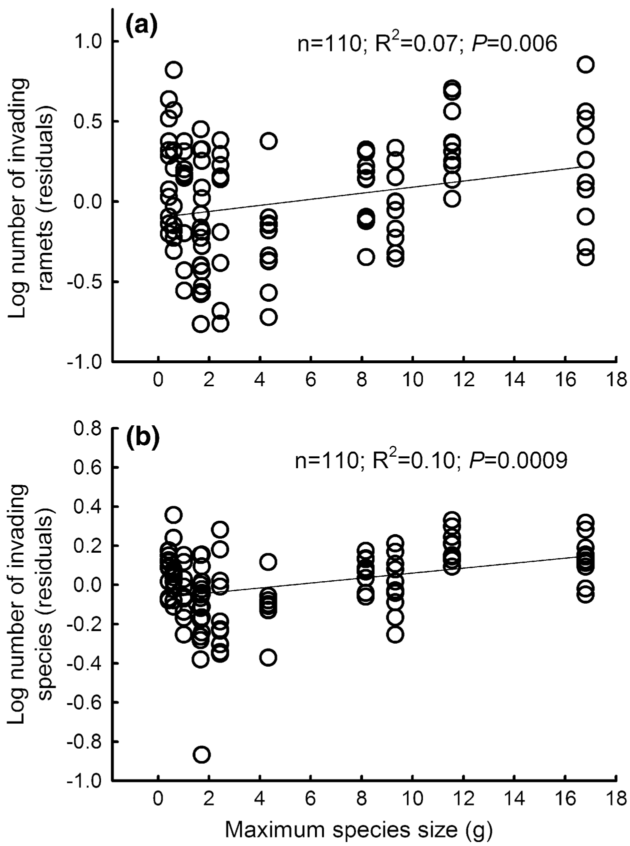

Fig. 2 Relationships between **a** number of invading species, and **b** number of invading ramets, and species size, measured as maximum per plant above-ground biomass (g), in experimental monoculture plots. *y*-axes represent residual variation in invasion after variation explained by plot location (experimental column) has been removed. Regression analyses include 11 monoculture species with ten replicates per species for a total of $n = 110$

that variable germination did not drive our results. Further, as predicted, the mean size (maximum potential height) of invaders was significantly smaller than that of monoculture species ($t = 2.50$, $df = 10$, $P = 0.031$).

Monocultures of larger species yielded significantly greater overall plot biomass ($P < 0.001$); however, contrary to our predictions, more invaded monocultures of each species produced less biomass (marginally significant: $P = 0.054$).

Species monocultures, as well as mixtures, differed significantly in the degree to which they were invaded by non-treatment ramets (ANOVA, $F = 9.57$, $P < 0.0001$). Mixtures had the lowest mean number of invading ramets, across both monocultures and mixtures, although a Tukey–Kramer multiple comparisons test revealed that invasion into mixtures was not significantly less than invasion into five of 11 monoculture treatments (Fig. S2).

Given the fact that many of our experimental species did not grow in the hay field immediately surrounding our fenced-in experimental plots, there was a strong bias in favor of experimental species invading monoculture plots, especially given proximity (i.e., as many as 16 extra potentially invading species for monocultures). Likewise, it was impossible to determine whether mixtures lost experimental species, but were re-invaded by these from surrounding plots, thus increasing the likelihood that estimates of invasion including experimental species are biased toward low invasion for mixtures. We re-analyzed these data, excluding experimental species as invaders to avoid the bias of monocultures having a larger pool of potentially colonizing species. Treatments still differed significantly with respect to the number of non-experimental ramets invading ($F = 2.34$, $P = 0.011$); however, there were far fewer treatment pairs that were significantly different (Fig. 3a). Mixtures were not invaded by a significantly greater number of ramets than any monoculture treatment and were only significantly less invaded by monocultures of two species (Fig. 3a). A similar set of analyses revealed significant differences in the number of invading species overall ($F = 9.08$, $P < 0.0001$; Fig. S2), and the number of non-experimental species invading among mixtures and all monoculture treatments ($F = 2.59$, $P = 0.0048$), but a multiple comparisons test did not reveal significant differences between treatment pairs (Fig. 3b). The conflict between a significant ANOVA result and no significant findings using Tukey–Kramer tests is likely due to reduced power in these tests.

Above-ground plot biomass production in mixtures was significantly greater than that of only one monoculture (*Chrysanthemum leucanthemum*; $F = 8.56$; $P < 0.0001$; Fig. 4), was significantly less productive than one monoculture (*Solidago rugosa*; Fig. 4), and not significantly different than the remaining nine monocultures (i.e., no evidence for overyielding).

Discussion

Monocultures of relatively large species were invaded by significantly more ramets and species (Fig. 2)—providing support for our primary prediction that monocultures of large species are more inefficient in spatial resource use, and consequently leave more space, and related resources, available to smaller, invading plants. While it appears that self-thinning played a role in determining final resident plant density (Fig. 1), variation will certainly have resulted from several other factors over the experimental period, including interspecific competition with invaders, differences in species-specific senescence schedules, disturbance-mediated mortality, size asymmetries that develop during monoculture thinning (Weiner and Thomas 1986) as well as mortality resulting from grazing and pathogens. Plot location also played a role in affecting variation in

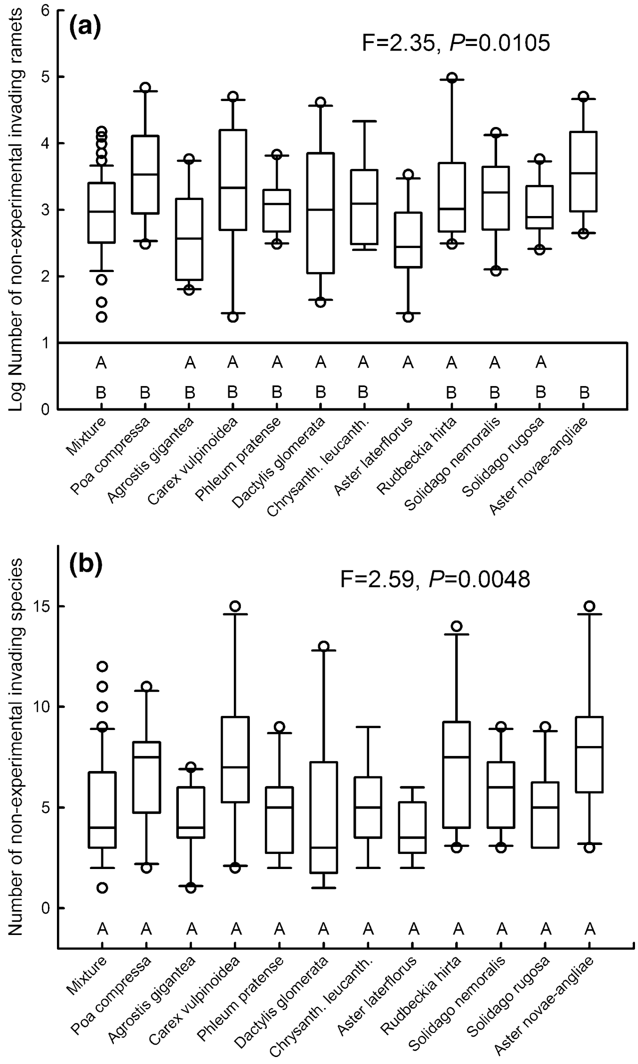

Fig. 3 Box plots depicting **a** number of non-experimental ramets invading monoculture and mixture treatment plots from the surrounding grassland community, and **b** number of non-experimental species invading all treatments. Monoculture treatments are presented in order of increasing maximum species size (biomass) from *left* to *right*. Non-experimental plants are species that were not planted in the experiment. Results of ANOVA testing for differences in invasion by **a** ramets, and **b** species across treatments are indicated. **a, b** *Letters* distinguish treatments that were significantly different according to a Tukey–Kramer multiple comparisons test (α = 0.05)

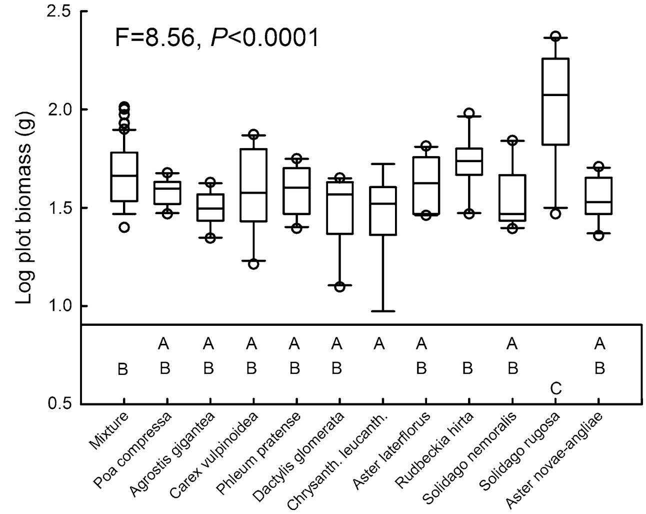

Fig. 4 Box plots depicting plot biomass for mixture and monoculture treatments. Monoculture treatments are presented in order of increasing maximum species size (*left* to *right*). Results of ANOVA testing for differences in biomass per treatment are indicated. *Letters* distinguish treatments that were significantly different according to a Tukey–Kramer multiple comparisons test (α = 0.05). Treatments that share the *same letter* are not statistically different

invasion (28% of variance in species invasion explained by plot location and monoculture species size). Factors such as prevailing winds, orientation with respect to nearby forests, and landscape management, are likely to play important roles in affecting variation in the invasion process. Nevertheless, our results show that as much as 10% of variation in species invasion across three seasons could be accounted for by variation in species size. Because germination rate varied among species, we could only indirectly explore our hypothesis that increased invasion results from greater intraspecific density-dependent mortality.

We also found support for our prediction that invading species would be significantly smaller than monoculture species, adding evidence that smaller species may invade larger species' monocultures by capturing small patches of space left available by larger species. Smaller plant species, if they possess lower minimum light requirements, may be generally capable of invading a monoculture of a larger species (Perry et al. 2003). Although species maximum biomass explains only a small portion of the variation in invasion, it is likely that other architectural variation related to size, such as height, canopy spread, and rooting depth, will also contribute to species-level variation in intraspecific density dependence, and relative efficiency of resource, or space use. Furthermore, it was not the intention of this study to explain all existing variation in invasion, which will inevitably be influenced by multiple factors.

Our findings provide support for the prediction that larger species may not only leave more unused resources available to other, smaller species, but that these unused resources may vary in quantity and quality such that they support the invasion of a greater richness of species (Fig. 2b; Aarssen et al. 2006). The fact that monoculture species size accounted for different proportions of variance in ramet and species invasion may be due to the fact that space left available by a large species' monoculture, may be captured by a single individual of one species, or by several individuals of a smaller species. Other studies have also reported that resident plant density plays a role in driving invasibility insofar as density is related to mean plant size (e.g., Von Holle and Simberloff 2005). Invasion by a larger number of species, however, may simply be a product of invasion by more individuals. Indeed, a post hoc regression analysis shows that the number of individuals invading monoculture plots is a significant predictor of the number of species invading ($n = 109$, $b = 0.415$; $R^2 = 0.25$, $P < 0.001$), although invading species accumulated at a significantly slower pace than did individuals (i.e., slope significantly <1; $t = 4.07$, $df = 107$, $P < 0.0001$). The fact that invading species accumulate significantly more slowly suggests that the number of species invading is not a simple function of the number of ramets invading. Consequently, these results suggest support for our hypothesis that large species leave resources available in patches that are suitable for a larger *variety* of species (Aarssen et al. 2006).

Our results are inconsistent with findings that more diverse assemblages of species are less susceptible to invasion (Levine et al. 2004; Fargione and Tilman 2005). Once the bias of mixtures having fewer potential colonists available was removed, mixtures were not significantly less invaded, by either ramets, or species, than most monoculture treatments (Fig. 3; although our results do not address the potential for the evenness component of diversity to significantly influence invasion). Results from previous studies examining the effect of diversity on invasibility have been mixed, varying with scale, methodology, and habitat (Levine and D'Antonio 1999; Alpert et al. 2000; Fridley et al. 2007). A general theory for the impact of diversity on invasibility therefore has remained elusive. One possible explanation is that diversity itself necessarily results from the very process of invasion (Davis 2005).

Our data offer no support for the prediction that more diverse assemblages will more completely capture available resources (i.e., niche complementarity; evidence reviewed in Cardinale et al. 2006; and see Grace et al. 2007). Species mixtures did not produce significantly higher biomass than most monoculture treatments (Fig. 4). Furthermore, experimental monocultures of larger species produced more biomass per plot, and more invaded monocultures tended to have lower biomass production per plot when we controlled for monoculture species size, suggesting that increased diversity can lead to lower resource use efficiency for some of the monoculture species. Our results therefore offer support for the sampling effect hypothesis, whereby mixture biomass production is driven by the inclusion of more productive species (Aarssen 1997; Huston 1997; Cardinale et al. 2006).

While our results do not support the predicted benefit of diversity in reducing invasibility through niche complementarity, diversity may yet play a role. For example, the monoculture of a large species can consist of a population of mature plants and several small individuals that are in the process of being competitively excluded (i.e., size asymmetry sensu Weiner and Thomas 1986; Fig. S3a). Importantly, these small individuals contribute to overall plot productivity in biomass, but not to population growth through seed production, or to community-level seed production. The invasion of smaller plant species with lower resource requirements (i.e., smaller physical space niches) and/or greater reproductive economy (Aarssen 2008), that take the place of competitively suppressed "host" species plants, may not increase plot biomass (Fig. S3c), but will inevitably improve seed output per unit area given their increased ability to reach reproduction (Fig. S3b, d). This is particularly important given that propagule pressure has consistently been a strong predictor of invasion success (Everett 2000; Turnbull et al. 2000; Zobel et al. 2000; Brown and Fridley 2003; Lockwood et al. 2005; Von Holle and Simberloff 2005). We hypothesize that community-level seed production, which determines the probability that a gap will be captured by a resident species, will play a large role in determining the degree to which a community is susceptible to invasion (Fig. S3f). When constituent species are perennial, such a community, with more individuals reaching reproductive maturity, will also have a lower mortality rate. In densely growing herbaceous plant communities, colonization primarily occurs in gaps created through disturbance or mortality (van der Maarel and Sykes 1993; Brokaw and Busing 2000). Given that disturbance-generated gaps are relatively uncommon in herbaceous vegetation (Goldberg and Gross 1988), it follows that resources will be made available for seedling establishment primarily through the death of resident plants (Sarukhan and Harper 1973). We hypothesize that communities with a lower mortality rate will reduce invasibility by slowing the rate at which resources (i.e., gaps) become available (Fig. S3e, f; Davis et al. 2000).

Given the importance of propagule pressure in determining invasibility, it is possible that larger species' monocultures were more invaded in our experiment because larger species generally produce larger seeds, and therefore fewer seeds per unit canopy area (Moles et al. 2004). This explanation, however, cannot fully explain our results as species seed mass and maximum plant mass among our experimental species are not positively correlated (results not shown); but may still be important at the community scale.

Our results suggest an important trade-off between maximum species size, and the ability to capture, and maintain control of resources—space in particular—over potential invaders (Figs. 1, 2). In densely growing herbaceous plant communities, colonization/invasion primarily occurs in gaps created through disturbance or mortality (van der Maarel and Sykes 1993; Burke and Grime 1996; Kotanen 1997; Brokaw and Busing 2000; Marvier et al. 2004; Vandvic 2004; Gross et al. 2005; Hierro et al. 2006). Given that disturbance-generated gaps are relatively uncommon in herbaceous vegetation (Goldberg and Gross 1988), it follows that resources will be made available for seedling establishment primarily through the death of resident plants (Sarukhan and Harper 1973). Plant mortality will result in the release of different resource quantities among plant species and the death of a relatively large plant represents a larger scale disturbance, inevitably releasing a greater quantity of resources. A gap generated through the death of a relatively large plant may be successfully colonized by an equally large plant species, or by several smaller plant species that have lower minimum resource requirements (i.e., smaller physical space niches and/or greater reproductive economy; Aarssen et al. 2006; Aarssen 2008; see also smaller EED; Antonovics and Levin 1980). The rate at which resources become available, therefore, either through inefficient use of space by resident plants, or through plant mortality, may be the ultimate determinant of the invasibility of plant communities.

Given that plant communities generally consist of a much greater number of small plant species, and individuals of small species (Aarssen et al. 2006), there may simply be a higher probability that seeds of relatively small plant species will colonize gaps of any size. This may, in large part, explain our findings that monocultures of larger species are invaded by more ramets, as well as more species (Fig. 2), and that invaders were significantly smaller than monoculture species. The inevitable role of plant mortality in invasion signals the importance of community-level attributes above and beyond species richness, evenness, and functional group diversity [e.g., community birth rate sensu Bruun and Ejrnæs (2006)]. Community mortality rates, as well as community seed production, may represent important, although possibly quite variable, determinants of community invasibility (Fig. S3), and invasion resistance.

Although some studies have demonstrated that monocultures of different plant species vary in susceptibility to invasion (e.g., Dukes 2002; Fargione and Tilman 2005), our results further demonstrate that these differences are driven, in part, by differences in species size. These results may help explain why relatively large plant species, which are frequently considered competitively superior, do not eliminate smaller species completely from plant communities, and thus add to our growing understanding of how many plant species can coexist under strong, hierarchical competition. If competitive ability is related to species size, as is indicated by some experimental evidence (e.g., Gaudet and Keddy 1988; Goldberg and Landa 1991; Warren et al. 2002), these results may identify an important trade-off between species' competitive ability and monoculture invasibility in communities where above-ground competition is intense and important, as is the case in densely growing old-field communities (e.g., Goldberg 1987). Indeed, the evolution of a completely dominant species is highly improbable, and this is reflected, we suggest, in the fact that all of our experimental monocultures were highly invasible.

Acknowledgments We thank Joyce Chau, Ryan Ouckama, Michael Burtnyk, Jennifer Waugh, Andrew Stevens, Lisa Duke, Jon Aarssen, Marina Neytcheva and Corinne Daly for field help, and Scott Wilson, Andrew MacDougall, John Silander, and anonymous reviewers for valuable comments on an earlier draft of this manuscript. This research was supported by the Natural Sciences and Engineering Research Council of Canada through a research grant to L. W. A. and a postgraduate scholarship to B. S. S., and by an Ontario Graduate Scholarship to B. S. S.

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