

# Exotic grasses and feces deposition by an exotic herbivore combine to reduce the relative abundance of native forbs

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Received: 19 March 2008 / Accepted: 13 August 2008 / Published online: 10 September 2008  
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**Abstract** Increased resource availability can facilitate establishment of exotic plant species, especially when coincident with propagule supply. Following establishment, increased resource availability may also facilitate the spread of exotic plant species if it enhances their competitive abilities relative to native species. Exotic Canada geese (*Branta canadensis*) introduce both exotic grass seed and nutrients to an endangered plant community on the Gulf Islands of southwestern British Columbia, Canada. I used greenhouse experiments to assess the competitive advantage of the exotic grasses relative to native and exotic forbs in this community and to test the impacts of nutrient addition from goose feces on competitive outcomes. I grew experimental communities varying in their proportion of forbs versus exotic grasses, and added goose feces as a nutrient source. I found that both native and exotic forbs produced significantly more biomass in competition with conspecifics than in competition with the grasses, and that the proportional abundance of two out of three native forbs was lowest in the combined presence of exotic grasses and nutrient addition. In a second experiment, I found that in monoculture all species of forbs and grasses showed equal growth responses to nutrients. The exotic species did not convert additional nutrients into additional biomass at a higher rate, but did germinate earlier and grow larger than the native species regardless of nutrient availability. This suggests that the exotic species may have achieved their competitive advantage partly by pre-empting resources in

community mixtures. Small and late-germinating native forbs may be particularly vulnerable to competitive suppression from exotic grasses and forbs and may be at an even greater disadvantage if their competitors are benefiting from early access to additional nutrients. In combination, the input of exotic propagules and additional nutrients by nesting geese may compromise efforts to maintain native community composition in this system.

**Keywords** Canada goose · Competition · Oak woodland · Plant invasion

## Introduction

Exotic plant species may successfully establish in new environments when their propagules encounter unexploited light, moisture, or nutrients (Davis et al. 2000). These resources may be available when disturbance decreases uptake by native vegetation, or when a system receives elevated resource inputs (D'Antonio 1993; Davis et al. 2000; Gross et al. 2005; Hobbs and Huenneke 1992). As many authors have noted, however, it is important to distinguish between the mechanisms underlying the establishment phase of plant invasions and those controlling their subsequent spread (Dietz and Edwards 2006; Hobbs and Humphries 1995; Levine et al. 2004). While the coincidence of propagule supply and nutrient availability is important for establishment, spread should depend on the relative abilities of established native and exotic plants to compete for nutrients.

Much research has focused on the potential for high competitive abilities in exotic plant species. For example, the evolution of increased competitive ability (EICA) hypothesis (Blossey and Notzold 1995) states that exotic

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Communicated by Miguel Franco.

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plants, having escaped their co-evolved enemies, will experience selection for lower allocation of resources to defense and higher allocation of resources to growth and reproduction. This can produce exotic plants that are better competitors in their introduced range than in their native range. In a review of 79 comparisons of native and exotic growth rates, competitive abilities, and fecundity, however, Daehler (2003) found that competitive superiority was dependent on growing conditions. Exotic species out-performed native species under high resource conditions, but the reverse was often true when resource availability was reduced (Daehler 2003). For soil nutrients, observational studies have shown correlations between abundance of exotic species and soil fertility (Kolb et al. 2002; Lake and Leishman 2004; Maron and Jeffries 2001), and field and greenhouse experiments have shown increased success of exotic species under nutrient addition treatments (Groves et al. 2003; Huenneke et al. 1990; Leishman and Thomson 2005; Ostertag and Verville 2002; Perry et al. 2004). It is therefore possible that exotic plant species gain a competitive advantage over native species only when the native system experiences increased resource availability, i.e., exotic species may be “passengers” of system change rather than “drivers” (MacDougall and Turkington 2005).

One important mechanism for increased nutrient input to plant communities is nutrient addition by novel herbivores (Huntly 1991). Feces deposition by exotic herbivores may be a particularly strong facilitator of exotic plant establishment when feces contain both viable seeds of exotic species and a pulse of nutrients. Field studies in the Gulf Islands, located in the southwest corner of Canada, have shown that exotic Canada geese (*Branta canadensis*) carry viable seeds of exotic annual grasses in their guts, enabling dispersal of these grasses from cultivated feeding grounds to small, relatively un-invaded islands where they nest (R. J. Best and P. Arcese, unpublished data). Because the geese fly between feeding sites and nesting sites, their feces deposition on the latter islands represents not only a change to rates of nutrient cycling, but an overall increase in nutrient inputs. Exotic species that increase nutrient pools can have a larger impact on future vegetation dynamics than those that only alter rates of nutrient cycling (Corbin and D’Antonio 2004).

Even when goose herbivory only alters local nutrient cycling there have been substantial effects on vegetation. Available nitrogen in Canada goose feces has increased the biomass of cultivated barley crops (Cochran et al. 2000) and nitrogen in the feces of lesser snow geese (*Anser caerulescens caerulescens*) has increased biomass of wetland grasses and sedges (Bazely and Jeffries 1985). If established exotic plants are better able to compete for nutrients, feces deposition by these exotic herbivores should then facilitate the spread phase of plant invasions. This is of

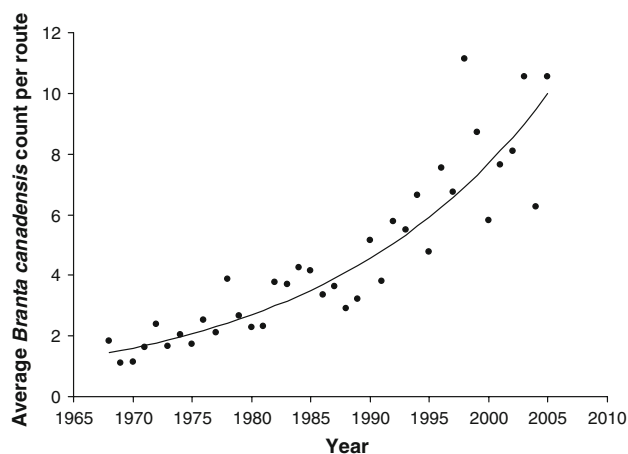
particular concern on the smallest of the Gulf Islands (0.04–600 ha), as they are some of the last remnants of endangered Garry oak ecosystems (Fuchs 2001) and because Canada goose populations are increasing exponentially in western Canada (Fig. 1). Since first nesting in the Gulf Islands in the 1980s, more pairs of geese have used the islands each spring, with two to seven nesting pairs per hectare in 2005.

In this paper, I present the results of two greenhouse experiments designed to determine the impact of nutrient addition by geese on competitive interactions between native and exotic plant species in the Gulf Islands. I first used a community experiment with four species of exotic annual grasses and four species of the most common forbs in this system. Using a  $3 \times 2$  factorial design, I grew community mixes varying in their composition (0, 35, and 70% exotic grasses), and the presence or absence of goose feces as a nutrient source. Hypothesizing that nutrient addition should provide a competitive advantage to the exotic annual grasses, I predicted a significant interactive effect of community composition and nutrient addition on the per-seed biomass and survival of the focal forbs in this experiment. To identify mechanisms underlying the competitive effects of the grasses I then grew each species in monoculture, with or without nutrient addition, and predicted that the exotic grasses would convert additional nutrients into additional biomass at a higher rate than the native forbs.

## Materials and methods

### Study system and seed source

I collected seeds and goose feces for this study from six small islands (0.4–4 ha) in the southern Gulf Islands of



**Fig. 1** Population trend for *Branta canadensis* in British Columbia. Data are from the Breeding Bird Survey (Sauer et al. 2005). An exponential function provided the best fit ( $r^2 = 0.87$ )

**Table 1** Number of seeds of each species in each level of the species composition factor (C) for the community experiment

Species	Functional group	Number of seeds		
		C 0	C 35	C 70
<i>Bromus diandrus</i> Roth	Exotic annual grass	0	44	88
<i>Aira praecox</i> L.	Exotic annual grass	0	44	88
<i>Vulpia bromoides</i> (L.) K.C. Gmel.	Exotic annual grass	0	44	88
<i>Poa annua</i> L.	Exotic annual grass	0	44	88
<i>Plectritis congesta</i> (Lindl.) DC.	Native annual forb	72	47	22
<i>Claytonia perfoliata</i> Donn ex Willd.	Native annual forb	72	47	22
<i>Collinsia parviflora</i> Lindl. <sup>a</sup>	Native annual forb	72	47	22
<i>Senecio vulgaris</i> L.	Exotic annual forb	72	47	22
<i>Grindelia integrifolia</i> DC.	Native perennial forb	72	47	22
<i>Camassia leichtlinii</i> (Baker) S. Wats. <sup>b</sup>	Native perennial forb	72	47	22
<i>Festuca idahoensis</i> Elmer <sup>c</sup>	Native perennial grass	72	47	22

<sup>a</sup> Did not mature past cotyledon stage

<sup>b</sup> Did not germinate

<sup>c</sup> Could not be distinguished from *Vulpia* and *Aira*

British Columbia, between the south-west corner of mainland Canada and the southern end of Vancouver Island (approximately 48°41'N, 123°23'W). The endangered Garry oak meadow ecosystem, also classified as Oregon white oak woodland or savannah, stretches north along the Pacific coast from southern California and covers the margins or the entirety of these islands (Fuchs 2001; Griffin 1977). Located in the rain-shadow of the Coastal Mountain Range, the ecosystem has a sub-Mediterranean climate, with mild wet winters and dry summers (di Castri 1973; MacDougall et al. 2006; Roemer 1972). On the shallow mineral soils characteristic of the islands in this system (Van Vliet et al. 1991; Ward et al. 1998), the native plant community is dominated by bryophytes and forbs, with a single native perennial grass species and no commonly found native annual grasses. Exotic annual grasses occur at high densities in areas disturbed by geese (R. J. Best and P. Arcese, unpublished data). Germination in this system begins in the fall and continues until April or May. After flowering in March–June, drought stress leads to death of the annual species and dieback of the perennials in July and August. I collected both seeds and goose feces in the spring of 2005, cold-dry stratified seeds for 2 months at 4°C, and stored the feces dry at room temperature.

#### Community effects of competition and nutrient addition

To test the combined effects of nutrient addition and invasion by exotic grasses on island plant communities, I used a 3 × 2 factorial cross of species composition and nutrient addition. For each experimental unit, I scattered 500 seeds over the surface of 4 cm of a low-nutrient sterile potting soil in a 25 × 25 × 6-cm plastic tray. Seed density was an approximation of early-season average plant densities observed in field plots, and soil depth was based on average depth in field sites where geese deposit feces and where

exotic grasses are beginning to dominate. Although the texture of potting soil is different from that found in the field, we were unable to remove soil from the islands due to their protected status, and required the soil to be free of seeds. The soil depth, however, was realistic. In the field, severe disturbance can result in entire patches of the shallow soil and plant matter lifting off the substrate, demonstrating that plant roots are not able to penetrate the bedrock below.

For the three levels of the composition factor (C) either 0, 35, or 70% of the seeds comprised equal numbers of each of the four most common exotic annual grass species found in the field (Table 1). The remainder of each seed mix was made up of equal numbers of each of seven common species from other functional groups (Table 1). I included the five native forbs most frequently found at high abundance at the island sites where seeds and feces were collected, along with the only native grass species present at these sites, so that the native community was accurately represented as forb dominated. I also included the exotic forb most frequently observed in areas disturbed by geese to determine if its positive association with such disturbances might be due to different responses to nutrient addition and competition from exotic grasses.

For the nutrient addition factor (N) I added either 0 or 13 g of dry goose feces, with the latter simulating the highest fecal densities observed in field plots. I added dry feces to the surface of the soil at the same time as the seed mixture to simulate nutrient release from feces that accumulate in the field over the spring and summer, dry out, and decompose in the wet fall season at the time plants begin to germinate. Importantly, goose feces from this system have been shown to contain viable seeds as well as nutrients, with 80% of those seeds being exotic annual grasses (72% *Poa annua* and 8% *Aira praecox*) (R. J. Best and P. Arcese, unpublished data). However, the average density of germinable *Poa* seeds was found to be approximately one per

18.7 g of dry feces. Although this seed density could result in substantial seed input at a field site with resident geese, it results in an average of less than one seed per replicate for this experiment. I did observe up to two *Poa* individuals emerging directly from the feces in some replicates, but these were not included in the final number or biomass.

Using nine replicates of the six treatment combinations, I arranged all 54 trays randomly in a single stretch of bench in the Horticulture Greenhouse at the University of British Columbia from 14 December 2005 to 10 February 2006. I used 10-cm buffer strips to avoid light competition from neighboring trays. Zone temperature was 20–24°C and the average photoperiod was 9 h. Trays were watered every 3–5 days as needed. I ran the experiment until the first species (*Claytonia*) was flowering in 90% of trays, then harvested all above-ground biomass, counting and separating individuals by species. I dried all plant material at 70°C for 48 h to obtain dry weight. At the end of the experiment, all species had germinated except for *Camassia*, but *Colinsia* was still at the cotyledon stage. Because they had zero or negligible biomass, these two forbs were excluded from the analysis. In addition, because they did not flower within the time frame of the experiment, *Festuca*, *Aira*, and *Vulpia* were sufficiently difficult to distinguish from one another that they were analyzed as a group.

For each species, I tested the effect of *C*, *N*, and their interaction ( $N \times C$ ) on the biomass per original seed, the species' proportion of the total biomass, and the proportion of individuals germinating and surviving. I included relative date of harvest (1–13) as a covariate and ran each analysis as an analysis of covariance using the GLM procedure in SAS version 9.1 (SAS Institute 2003). To account for testing multiple species (four forbs, two grasses, and one group of the remaining grasses), I used  $\alpha = 0.05/7 = 0.007$ . To test for equality of covariate slope across levels of the *C*, *N*, and  $N \times C$  factors, I ran the models with all  $2 \times$  and  $3 \times$  interaction terms involving the date of harvest, and removed them if not significant. To meet assumptions of normality and equal variance, I used a logarithmic transformation of *Senecio* biomass per seed, a square root transformation of biomass per seed for all other species, and an arcsine square root transformation of all proportions.

#### Individual effects of nutrient addition

To test the response of individual species to nutrient addition, I used an  $8 \times 2$  factorial cross of species (*S*) and *N*. Using the same seed density as in the community experiment, I scattered 75 seeds of a single species (the four exotic annual grasses and the four forb species from the community experiment) over the surface of 4 cm of a low nutrient sterile potting soil in  $7.5 \times 12.5 \times 6$ -cm plastic

inserts. The equivalent amount of dry feces per surface area was 1.95 g per replicate. I used ten replicates of each treatment combination, for a total of 160 inserts, and randomly arranged these on the same greenhouse bench, from 30 March to 5 May 2006. Zone temperature was 20–24°C and average photoperiod was 13.5 h. Trays were watered every 3–5 days as needed. Early germinants were counted on the fifth day, and again the experiment was harvested when 90% of *Claytonia* replicates had flowers. All individuals were counted, and above-ground biomass was dried at 70°C for 48 h.

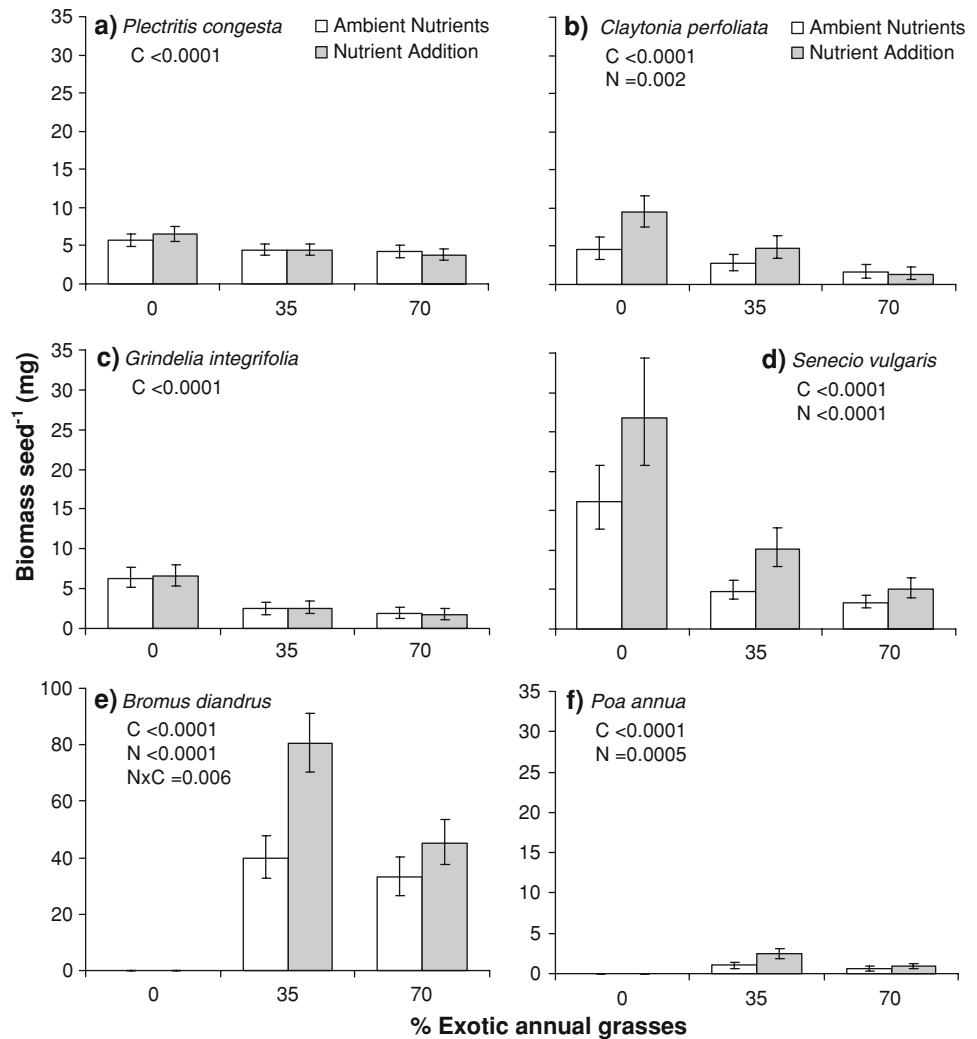
To determine the impacts of *S*, *N*, and the interaction between these factors ( $N \times S$ ) on biomass, the number of individuals germinating and surviving, and proportion of individuals germinating early (by day 5), I used three ANOVA analyses with  $\alpha = 0.05/3 = 0.017$  for each. It was not necessary to include date of harvest as a covariate because replicates did not need to be sorted by species and could therefore be harvested in only 2 days. To meet assumptions of ANOVA, I used a logarithmic transformation of biomass and a square root transformation of the proportion of final individuals that had germinated by day 5. To test for differences in each response variable between grasses and forbs, and between native and exotic species, I used two planned contrasts of least squares means with  $\alpha = 0.017/2 = 0.008$  for each contrast.

## Results

### Community effects of competition and nutrient addition

All four forb species decreased in biomass per seed when conspecific competitors were replaced with exotic annual grasses (Fig. 2; *Plectritis*  $F_{2,47} = 13.95$ , *Claytonia*  $F_{2,47} = 33.54$ , *Grindelia*  $F_{2,47} = 49.19$ , *Senecio*  $F_{2,47} = 85.58$ , in all cases  $P < 0.0001$ ). In contrast, the exotic grasses *Bromus* and *Poa* showed increased biomass per seed as their conspecifics were replaced with native forbs ( $F_{1,31} = 22.37$  and  $F_{1,31} = 20.04$ , respectively, in both cases  $P < 0.0001$ ). Both of these results suggest that the exotic grasses were stronger competitors than the forbs, both with and without nutrient addition. The effects of nutrient addition varied between species; biomass per seed increased in the native forb *Claytonia* ( $F_{1,47} = 10.76$ ,  $P = 0.002$ ), the exotic forb *Senecio* ( $F_{1,47} = 30.63$ ,  $P < 0.0001$ ), and the exotic grasses *Bromus* and *Poa* ( $F_{1,31} = 40.01$ ,  $P < 0.0001$ , and  $F_{1,31} = 14.97$ ,  $P = 0.0005$ , respectively), but did not change in the native forbs *Plectritis* and *Grindelia* ( $F_{1,47} = 0.09$ ,  $P = 0.8$ , and  $F_{1,47} = 0.01$ ,  $P = 0.9$ , respectively). *Plectritis* also showed a lower germination and survival rate under nutrient addition (56% survival without goose feces compared to 45% survival with goose feces,  $F_{1,47} = 9.04$ ,  $P = 0.004$ ).

**Fig. 2** Average biomass per seed for species in the community experiment, in response to exotic grass abundance. Data are least squares means back-transformed to original units. Error bars are 95% confidence intervals. **a–f** *P*-values are given for significant effects of composition (*C*), nutrients (*N*), and their interaction (*N* × *C*)



Germination and survival in the other forb and grass species were not affected by community composition or nutrient addition (all *P*-values > 0.04, compared to  $\alpha = 0.007$ , adjusted for multiple species). For all three response variables, there was no interaction between composition and nutrient addition.

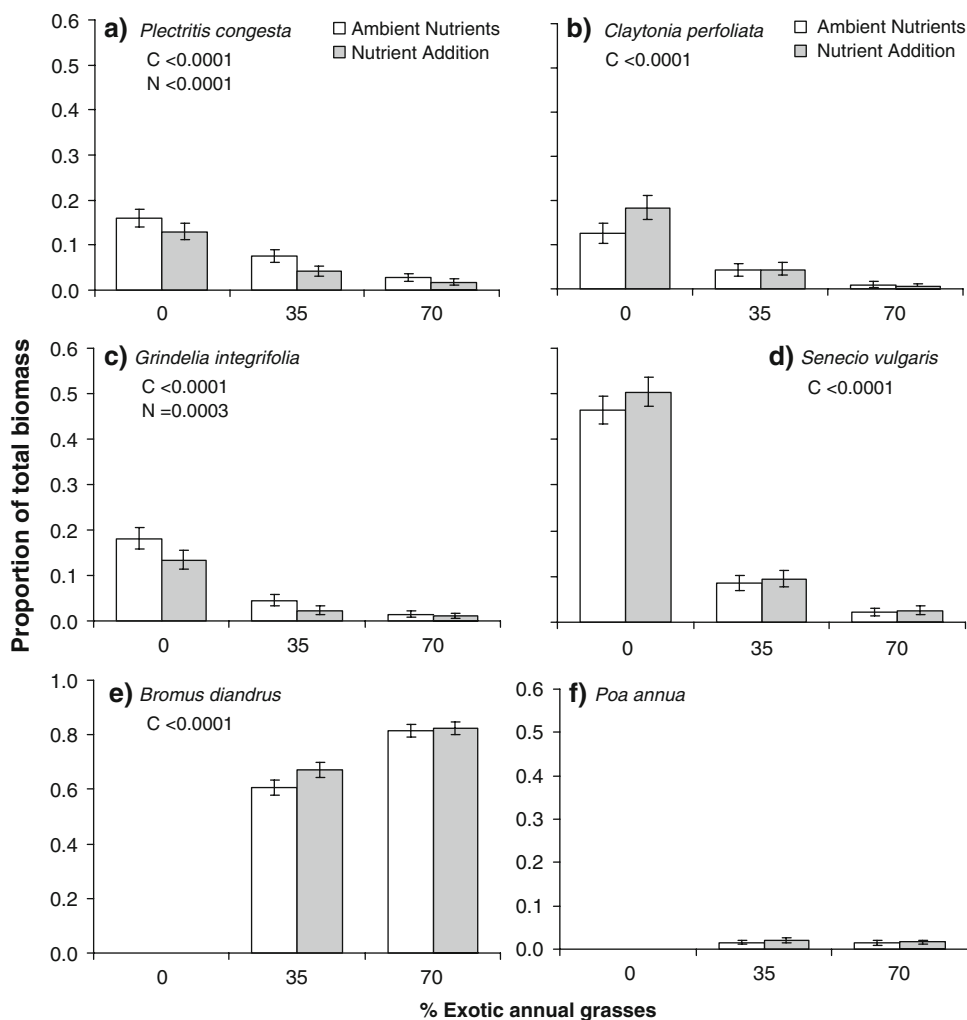
While per-seed biomass of the forbs declined with the addition of exotic annual grasses, the grasses caused the total community biomass to increase (95% confidence intervals for 0, 35, and 70% exotic grass composition were, respectively,  $3.19 \pm 0.36$ ,  $4.07 \pm 0.36$ , and  $4.22 \pm 0.36$  g total biomass per replicate,  $P < 0.0001$ ). Most of the exotic annual grass biomass was produced by a single species, *Bromus diandrus*, which germinated early and grew rapidly. Total community biomass also increased with nutrient addition (95% confidence intervals were  $3.04 \pm 0.30$  vs.  $4.62 \pm 0.30$  g per replicate,  $P < 0.0001$ ). Nutrient addition also changed the proportion of the total biomass contributed by each of the forb species. Both *Plectritis* and *Grindelia* decreased in proportional abundance when nutrients were added ( $F_{1,47} = 20.67$ ,  $P < 0.0001$ , and  $F_{1,47} = 14.93$ ,

$P = 0.0003$ , respectively), whereas *Claytonia* did not ( $F_{1,47} = 1.97$ ,  $P = 0.17$ ). Also, although not significant when  $\alpha$  was adjusted to account for multiple species, it appears that *Bromus* compensated by increasing its proportional abundance slightly (Fig. 3;  $F_{1,31} = 7.34$ ,  $P = 0.01$ ). The grouped analysis of the remaining grasses (*Festuca*, *Aira*, and *Vulpia*, indistinguishable before flowering) showed that their proportional abundance was not affected by nutrient addition ( $F_{1,47} = 2.78$ ,  $P = 0.10$ ).

#### Mechanisms for competitive effects

When grown individually, all species in this experiment increased in biomass under nutrient addition (Fig. 4a;  $F_{1,144} = 17.16$ ,  $P < 0.0001$ ). The interaction between species and nutrient addition did not affect log-transformed biomass, indicating no difference in the proportional effect of nutrient addition between species ( $F_{7,144} = 0.94$ ,  $P = 0.5$ ). Across both nutrient treatments, however, average biomass did differ between species ( $F_{7,144} = 35.75$ ,  $P < 0.0001$ ). The two planned contrasts show that biomass was not significantly different

**Fig. 3** Proportion of total biomass for each species in the community experiment. Data are least squares means back-transformed to original units. Error bars are 95% confidence intervals. **a–f** *P*-values are given for significant effects of *C*, *N*, and *N* × *C*. For abbreviations, see Fig. 2



between forbs and grasses ( $F_{1,144} = 0.16$ ,  $P = 0.7$ ), but in combination the exotic grasses and the exotic forb *Senecio* had higher biomass than the native species ( $F_{1,144} = 39.20$ ,  $P < 0.0001$ ). The number of individuals germinating and surviving to the end of the experiment also differed by species and nutrient addition (Fig. 4b;  $F_{7,144} = 61.24$ ,  $P < 0.0001$ , and  $F_{1,144} = 9.58$ ,  $P = 0.002$ , respectively), and was higher overall for grasses than for forbs ( $F_{1,144} = 51.52$ ,  $P < 0.0001$ ). Finally, early germination was also higher for the grasses than for the forbs (Fig. 4c;  $F_{1,144} = 29.63$ ,  $P < 0.0001$ ), but was not affected by nutrient addition ( $F_{1,144} = 2.12$ ,  $P = 0.1$ ). Within the forbs, *Senecio* germinated first, followed by *Grindelia*, then *Claytonia* and *Plectritis*.

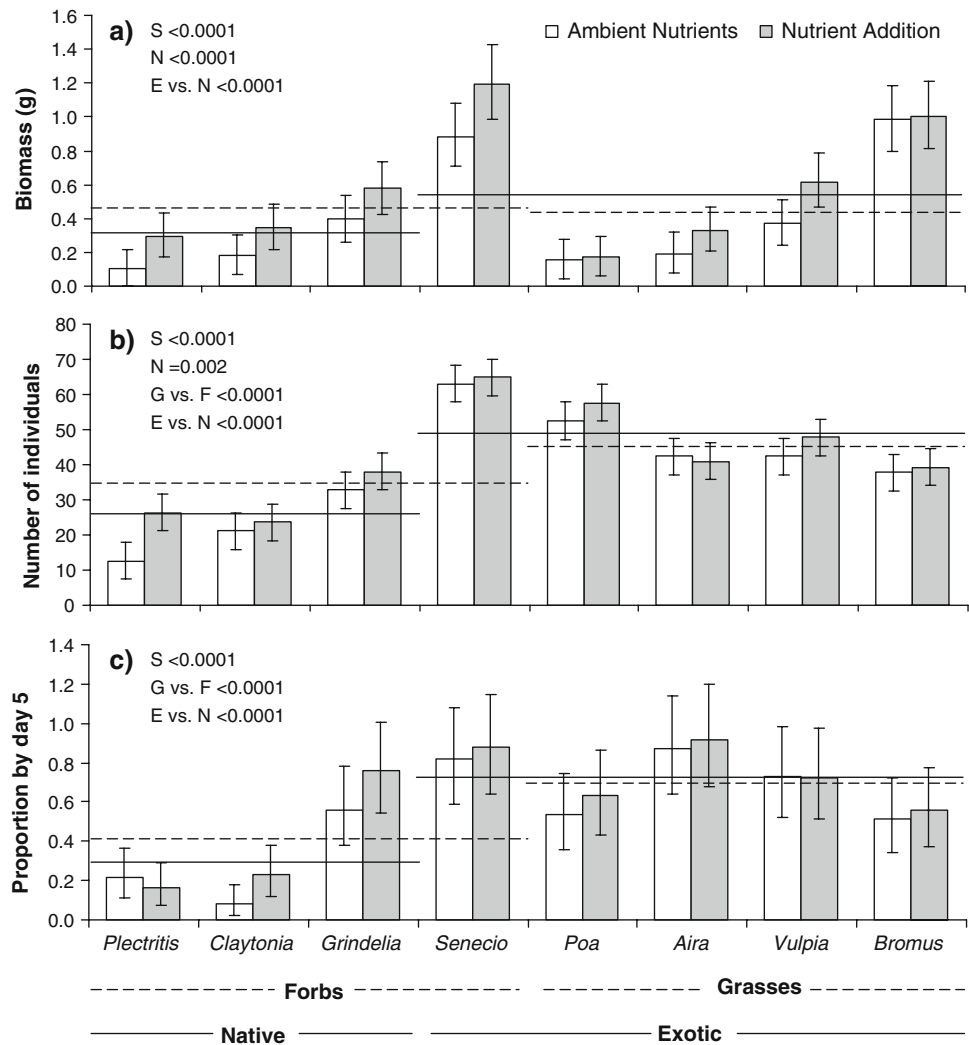
## Discussion

### Competition for nutrients

The results from the community experiment indicate that as a group the exotic grasses do have stronger competitive

suppression abilities than the forbs in this community. Whether native or exotic, annual or perennial, the forbs investigated here grew larger when competing with themselves than when competing with exotic grasses (Fig. 2). In contrast, the effects of nutrient addition on competitive interactions between grasses and forbs were species dependent. Nutrients from goose feces increased total community biomass and biomass per seed in *Claytonia*, *Senecio*, *Bromus*, and *Poa*, but not *Plectritis* or *Grindelia*. Because there was no interactive effect of community composition and nutrient addition on biomass per seed, these results suggest that nutrient addition did not enhance the competitive advantage of the exotic grasses. By analyzing the proportional contribution of each species to the total community biomass, however, I found that the proportional abundance of *Plectritis* and *Grindelia*, two of the three native forbs, was lowest in the combined presence of exotic grass competitors and additional nutrients (Fig. 3a, c). This suggests that nutrient addition did increase the competitive advantage of the exotic grasses and the exotic forb *Senecio* over these two native forbs. Because the relative abundance of

**Fig. 4** Performance of each species in the individual experiment. Data are least squares means of each species' **a** biomass, **b** number of individuals germinating and surviving until the end of the experiment, and **c** proportion germinating by day 5. All response variables were back-transformed to original units. Error bars are 95% confidence intervals. **a–c** *P*-values are given for significant effects of *S*, *N*, and *N* × *S*, and for the two planned contrasts ( $\alpha = 0.017/2 = 0.008$ ). Dashed lines indicate mean levels of the grass versus forb (*G* vs. *F*) contrast, and solid lines indicate mean levels of the exotic versus native (*E* vs. *N*) contrast. For other abbreviations, see Fig. 2



each species should determine its relative reproductive output and therefore its proportion of the community in the future, this measure should be the most appropriate assessment of competitive advantage.

To understand the mechanisms putting the native forbs *Plectritis* and *Grindelia* at a disadvantage, especially under increased nutrient availability, I tested for a species by nutrient addition interaction in the individual experiment, where all species were grown in monoculture. Results from this experiment show no difference between species in their ability to convert additional nutrients to additional biomass (Fig. 4a). This is somewhat surprising. Exotic species have generally been found to have lower tissue construction costs, enabling faster growth response to nutrient addition (Baruch and Goldstein 1999; Daehler 2003). Furthermore, previous research has shown positive correlations between nutrient availability and abundance of the *Vulpia*, *Bromus*, and *Poa* grasses studied here (Allcock 2002; Busey 2003; Rice and Nagy 2000; Schippers and Joenje 2002). In contrast, the native forbs in this study should be adapted to shallow mineral soils with low nutrient availability, there-

fore lacking mechanisms for rapid growth response to nutrient addition. Field experiments on Californian serpentine soils and Australian sandstone soils have shown nutrient addition to increase the performance of exotic grasses relative to native species adapted to low levels of nutrients (Huenneke et al. 1990; Leishman and Thomson 2005). The ability to respond to nutrient input may, however, be retained in native species that inhabit but are not limited to low-nutrient environments (Huenneke et al. 1990). The Garry oak ecosystems to which these island communities belong occur along a gradient of soil depth, ranging from <10 cm on the small islands and rocky outcrops to >35 cm in meadows on Vancouver Island (MacDougall et al. 2006). The native forbs investigated here also occur along that gradient, including deeper soil sites where nutrient limitation should be lower than it is on the small islands.

Early growth and competition for light

Given no difference in growth response to nutrient addition, the competitive advantage of the grasses may be due to

faster or pre-emptive resource uptake (Titman 1976). The individual experiment showed that the native forbs produced fewer individuals and germinated later (Fig. 4b, c). Further, both experiments demonstrated that native forbs produced less biomass than the exotic species (Figs. 2, 4). Early germination and growth may thus be a novel resource acquisition strategy allowing the exotic species to pre-empt additional nutrients and to shade native forbs, and may explain why *Plectritis* and *Grindelia* did not increase in biomass when given additional nutrients in mixture (Fig. 2a, c), even though all of the native forbs in these experiments were capable of making use of additional nutrients in monoculture (Fig. 4a). At the plot scale, such dissimilarity in function or phylogeny between exotic and native plants has been hypothesized to facilitate invasion success by providing an “empty niche” (Daehler 2001; Fargione and Tilman 2005; Fox 1987; Mitchell et al. 2006). In this system, the exotic annual grasses constitute a functional group not well represented in the native species pool, which is dominated by annual and perennial forbs.

A conclusive test of the role of competition for light in these experiments would have required direct measurements of treatment-specific light availability and below-ground biomass. However, the large range in biomass between species does suggest that species that are smaller in stature than the average mixture component may have experienced more nutrient limitation in monoculture and more light limitation in mixture (Jackson and Caldwell 1992). Any switch from below-ground competition for nutrients to above-ground competition for light may thus be regulated not only by total nutrient availability (Tilman 1988; Wilson and Tilman 1993), but also by community composition.

Although differences between the community and individual experiments may also have been driven by differences in overall light availability, given their temporal separation, I observed nearly the same order of germination and the same order of individual size in both cases. This consistency is important given that plant communities in the field are subject to fluctuation in climatic variables that is not represented in the greenhouse environment. The only difference in germination order among forbs was that *Claytonia* germinated before *Grindelia* in the community experiment, while the reverse was true in the individual experiment. This difference is consistent with the hypothesis that light limitation due to late germination in the community experiment prevented *Grindelia* and *Plectritis* from benefiting from nutrient addition.

#### Multiple exotic species with competitive advantages

Although multi-species experiments can obscure the relative competitive effects of particular species, using multiple

representatives of the grasses and forbs in these experiments made it possible to observe general differences in competitive traits between these two groups. Including multiple exotic species also allowed a more realistic simulation of community composition in invaded Garry oak plant communities and produced information about variation between and within exotic and native species. For example, while the exotic forb *Senecio* was suppressed by the exotic grasses just as the native forbs were (Fig. 2d), in the community experiment *Senecio* may have prevented some of the native forbs from benefiting from nutrient addition even in the absence of exotic grasses.

#### Implications for native forbs

The Garry oak plant community in the Gulf Islands is considered to be endangered, and currently covers approximately 5% of its former extent in Canada (Fuchs 2001). The small islands where geese nest are particularly valuable representatives of this community as the proportion of the vegetation biomass occupied by exotic plant species is lower than on larger Gulf Islands or Vancouver Island. Forces facilitating the greater establishment of exotic species on these islands are therefore of great concern. Understanding these forces is essential for both preventing further spread and designing effective restoration initiatives.

Field studies in this system have already shown that goose feces contain exotic grass seed, possibly transported from highly invaded feeding grounds on larger, inhabited islands (R. J. Best and P. Arcese, unpublished data). The combined introduction of propagules and additional nutrients in goose feces increases the likelihood that exotic grasses will successfully colonize island sites where they are not already abundant, if dispersed there by geese (Davis et al. 2000). Following colonization, the higher competitive suppression abilities of the grasses should allow them to spread by replacing the forbs. Finally, the rate of spread may be increased if nutrient addition from goose feces increases exotic biomass while providing no benefit to native species that germinate later and grow smaller. If maintenance or restoration of the native composition of these island plant communities is to be successful, the input of exotic seed and nutrients in goose feces may need to be reduced.

**Acknowledgements** I thank P. Arcese, D. S. Srivastava, R. Turkington, A. S. MacDougall, M. Vellend, J. R. McLaren, R. L. Jefferies, R. D. Guy, and two anonymous reviewers for helpful comments on methodology and the manuscript. I thank D. Kaplan, N. Diner, M. Flint, and J. Muir for assistance in the greenhouse, and M. Flint for assistance in the field. I thank the Gulf Islands National Park Reserve for seed collection permits and, especially, A. J. Brumbaum, W. Hesse and H. Hesse for their very generous contributions to this research. I received funding support from an NSERC Research Scholarship and the UBC Faculty of Forestry. All research described here is in compliance with Canadian law.



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