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Impacts of invasive plant species on riparian plant assemblages: interactions with elevated atmospheric carbon dioxide and nitrogen deposition

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Abstract Resource competition is commonly invoked to explain negative effects of invasive plants on native plant abundance. If invasives out-compete natives, global changes that elevate resource availability may interact with invasives to exacerbate impacts on native communities. Indeed, evidence is accumulating that elevated CO_2 and N deposition decrease native biomass and simultaneously increase invasive biomass. However, superior competitive ability, and a relative increase in the magnitude of invasive impacts under elevated resource availability, remain to be definitively proven. Using model, multi-species, multi-individual riparian plant communities, where planting density was maintained by replacement of native with exotic individuals, we conducted a greenhouse, competition experiment using native (to the UK) and invaded communities exposed to ambient and elevated CO_2 (CO_2 experiment) or N availability (N experiment). We tested two hypotheses: (1) invasives are superior competitors to natives at ambient atmospheric CO_2 and N deposition; (2) negative effects of invasives on natives are exacerbated under elevated CO_2 or N availability. Our results provide some support for the first hypothesis: in the CO_2 experiment native biomass was significantly lower in invaded communities. In the N experiment, native biomass was unaffected by the presence of exotics but other characteristics (e.g. root:shoot ratios) were altered. Differences in light availability between the experiments may have modified the effects of the invasives on the native assemblages but our design did not permit us to determine this definitively. The hypothesis that elevated CO_2 and N availability benefit invasives at the expense of natives was not supported by our results. This may be explained either because the invasives showed minor responses to the resource manipulations or because native and exotic species were differentially limited by CO_2 and N. Our results confirm the expectation that invasives alter the characteristics of native assemblages but lead us to question whether elevated resource availability will magnify these effects.

Keywords Exotic species · Global change · *Fallopia japonica* · *Impatiens glandulifera* · Competition

Introduction

Superior competitive ability is one of the most common mechanisms invoked to explain why exotic plant species

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‘‘outbreak’’ (i.e. undergo a population explosion) at the expense of native plant assemblages (Levine et al. 2003; Vilà and Weiner 2004). However, despite the potential importance of competitive ability in determining invasive plant spread, empirical support for the importance of this mechanism remains equivocal (Levine et al. 2003). One of the main reasons for this lack of support is that few studies have compared the effects of an exotic invader on a target native species with the effects of co-existing natives on the same target native (Vilà and Weiner 2004; but see also Gaudet and Keddy 1988). Using this approach, superior competitive ability of an exotic invader is demonstrated when the reduction in growth of the target native is greater than when the target is grown with co-existing natives (Goldberg et al. 1999; Grace 1995).

The magnitude of invasive species’ impacts on native plant assemblages may be modified by global changes that increase the availability of plant resources and hence potentially alter the competitive dynamics between invasive and native species (Dukes and Mooney 1999). Indeed, there is a growing body of evidence that global changes such as elevated atmospheric CO_2 and N deposition lead to a relative decline in native species biomass and a simultaneous increase in the biomass of exotic invaders (e.g. as observed by Burke and Grime 1996; Davis and Pelsor 2001; Huenneke et al. 1990; Smith et al. 2000; Warwick et al. 1998; Wedin and Tilman 1996). Notably, current evidence suggests that elevated CO_2 may favour the better competitors in a stand, and not the individuals or species which respond most positively to elevated CO_2 in the absence of competition (Catovsky and Bazzaz 2002). To determine how global change factors such as elevated CO_2 and N interact with invasive species to affect native assemblages requires that: (1) the impact of invasive species on natives at ambient and elevated resource levels is quantified, and (2) the native response to the increase in resource availability is quantified in the absence of invasive species.

We tested two overarching hypotheses: (1) in multi-species plant assemblages, exotic plant invaders are superior competitors to native species at ambient levels of atmospheric CO_2 and N deposition; and (2) the negative effects of exotic plant invaders on native species in these assemblages are exacerbated when either atmospheric CO_2 or N availability is elevated. To test these hypotheses, we constructed model riparian communities containing native plant species only, or native plant species plus invaders. We used riparian communities because they are some of the most invaded plant communities (Planty-Tabacchi et al. 1996; Pyšek and Prach 1993; Tickner et al. 2001) and they also support high abundances of three of the most prevalent invasive plant species in Europe and North America: *Fallopia japonica* Ronse Decraene (also known as *Polygonum cuspidatum* Sieb. & Zucc., Japanese knotweed), *Impatiens glandulifera* Royle (Himalayan balsam) and, *Mimulus guttatus* D.C. (monkeyflower, invasive in Europe, native to North America) (Beerling et al. 1994; Beerling and Perrins 1993; Crawley 1987).

We examined the biomass response and N capture of the native species when grown in competition with each other, and when grown in competition with the three invasive species, under both ambient and global change conditions. The response of the native assemblage (not specific native species) was our focus and, as such, we primarily present data expressed on a mean individual native basis. For example, the mean individual native biomass (M_B) for each replicate community was calculated by considering the biomass of all the component native individuals as follows:

$$M_B = \sum_{i=1}^{S} \frac{B_i}{N_i} \div S$$

where: B_i = total biomass of all individuals of native species i; N_i = total number of all individuals of native species i; S = total number of native species in the community.

Our approach of growing abundant species in multi-species, multi-individual (24 per community) plant assemblages, while not that of a classic competition experiment, allowed us to overcome the limitations of many exotic–native pair-wise competition studies by: (1) incorporating indirect or higher-order plant–plant interactions that if omitted may preclude predictions of competitive outcomes in natural plant assemblages (Wootton 1994); (2) competing abundant exotic species against abundant native species—often available data are biased towards interactions between highly competitive, abundant exotics and uncommon/rare natives, which potentially confounds competitive ability and origin (Levine et al. 2003; Vilà and Weiner 2004); and (3) assessing the impacts on native plant assemblages as opposed to specific native species.

As far as we aware, this is the first empirical study to use a design that quantifies how exotic plant invaders and global changes (specifically elevated atmospheric CO_2 and N deposition) interact to influence the growth and N capture of abundant native plant species. We found support for the hypothesis that exotic invaders are superior competitors to abundant native species but not that this competitive dominance is exacerbated by increased CO_2 or N availability. Despite the fact the native species we used comprise many different growth forms and allocation patterns, in general they responded in a similar manner to the presence of invasive species. In addition, as a fortuitous outcome of the experimental design, we found evidence that the impacts of the exotic invaders on native plant assemblages may be dependent on light availability. This insight may facilitate the prediction of where impacts of *F. japonica*, *I. glandulifera*, and *M. guttatus* will be greatest in natural systems.

Materials and methods

Model communities

We established model riparian communities in 0.5-m-diameter pots, with a total soil volume of 0.036 m^3. Two different community types were assembled and designated ‘‘native’’ or ‘‘invaded’’. The ‘‘native’’ communities were based on a plant assemblage composition typical of riparian communities in the United Kingdom, and the experimental composition was based both on field and literature observations (H. B. Schumacher, S. Catovsky and G. M. Tordoff, unpublished data; Beerling et al. 1994; Beerling and Perrins 1993; Merry et al. 1981). Native assemblages comprised the following six abundant, native C_3 herbaceous species: *Calystegia sepium* (L.) Junger (hedge bindweed), *Epilobium hirsutum* L. (great willowherb), *Poa trivialis* L. (rough meadow-grass), *Ranunculus repens* L. (creeping buttercup), *Rumex obtusifolius* L. (broad-leaved dock) and *Urtica dioica* L. (stinging nettle). Four individuals of each species were included in each model native assemblage. Invaded plant assemblages comprised the same six native species, in addition to the following three abundant, C_3 herbaceous exotics: *F. japonica*, *I. glandulifera* and *M. guttatus*. Two individuals of each native species and four individuals of each exotic species were included in each model invaded assemblage. Native and invaded assemblages both contained 24 individuals for an initial density of 120 plants m^{-2}, which is within the seedling density range for these communities (Beerling and Perrins 1993; Prowse 1998).

Two-week-old seedlings were transplanted into randomly chosen, evenly spaced positions, creating a unique species arrangement in each model community replicate. All species were grown from seed (Herbiseed Nursery, Wokingham, UK; Chiltern Seeds, Ulverston, UK), except *F. japonica* (an exotic) and *U. dioica* (a native), which were established from 5-cm-long rhizomes collected from streamsides in Silwood Park, UK (51°22′N, 00°37′W). There was no evidence that establishment from rhizome, as opposed to seed, provided a competitive advantage. Seeds of *I. glandulifera* were cold stratified at 4°C in wet sand for 21 days to break dormancy (Mumford 1988).

Soils were a typical (loamy) alluvial brown soil (Avery 1990), had a pH of 6.5, and were collected from an alluvial floodplain quarry (Rigby Taylor, Guildford, UK). A 2-cm-deep, surface organic horizon (Irish moss peat) was included in each community. The soils were mostly free draining, with 2 cm standing water at the base. Once added to the microcosm pots, they were gently leached across 2 weeks to reduce the nutrient pulse associated with soil disturbance (Bradford et al. 2002).

Climate

Communities were grown under controlled, greenhouse conditions for two, 70-day growing periods (16 h light at 22°C, 8 h dark at 14°C). Between the growing periods, we simulated a ‘‘winter’’ of 56 days’ duration to senesce the annual *I. glandulifera* (all other species are perennials). During this time communities received only natural UK winter month sunlight and were maintained at 6°C. Transition periods (12 h light at 14°C, 12 h dark at 6°C) of 14 days’ duration were included between the growing periods and the ‘‘winter’’ to prevent potential plant shock responses to changes in the climatic regime.

To maintain observed field values of approximately 20% volumetric soil water content for riparian communities (H. B. Schumacher, S. Catovsky and G. M. Tordoff, unpublished data), communities received 1 l H_2O daily during growing and transition periods, and 1 l every 2 days during the simulated winter. To mimic yearly recruitment of the annual *I. glandulifera*, standing *I. glandulifera* stems were cut at the base and returned to the communities as litter 2 weeks prior to the second growing period. These stems were replaced by new, 2-week-old, *I. glandulifera* seedlings in the same positions.

CO_2 and N treatments

Model communities were assembled and then maintained in one of two experimental greenhouses: the CO_2 greenhouse or the N greenhouse. The former is a purpose-built facility in which atmospheric CO_2 concentrations can be tightly controlled in ten clear-perspex growth chambers. A native and an invaded community were maintained in each chamber, with five chambers assigned to an elevated atmospheric CO_2 treatment (750 μmol mol^{-1}) and five to an ambient atmospheric CO_2 treatment (375 μmol mol^{-1}). We maintained CO_2 treatments for the duration of the experiment. CO_2 concentrations were maintained within ±14 μmol mol^{-1} of the target.

Ten native and ten invaded communities were placed into the N greenhouse and five of each community type were assigned to either an elevated N treatment (5 g N m^{-2} growing $period^{-1}$) or an ambient N treatment (0 g N m^{-2} growing $period^{-1}$). N was added to each community every 7 days during the growing periods as NH_4NO_3 (Fisher Scientific UK, Loughborough, UK) dissolved in 1 l H_2O. In both greenhouses, model communities were arranged in spatially defined blocks, with each block containing one replicate of each treatment; the location of a community within a block was changed every 14 days.

Abiotic conditions (diurnal air temperature and humidity, soil water) were maintained at equivalent values in the CO_2 and in the N greenhouses throughout the study. However, we knew before we initiated the study that light levels differed between the greenhouses (approximately 520 and 1,250 μmol m^{-2} s^{-1} in the CO_2 and N greenhouses, respectively, during the growing periods at full light). Given that we recognised a priori that this difference in light availability might influence both growth of individual plants and interactions between species, we effectively established two independent experiments. In the CO_2 greenhouse we investigated the interactive effects of elevated atmospheric CO_2 and exotic species on native plants and in the N greenhouse the interactive effects of elevated N deposition and exotic species on native plants. Each experiment had its own set of control communities (i.e. native communities exposed to ambient CO_2 or ambient N)—henceforth we refer to the two studies as the ‘‘CO_2 experiment’’ or the ‘‘N experiment’’.

Response variables

At the end of the second growing period the 40 model communities were destructively harvested. Plants were harvested individually, and shoots and roots were separated. After washing to remove soil, plant material was dried at 80°C for 4 days prior to determination of shoot and root dry weight biomass. Root material that could not be sorted to species was only used when calculating the total biomass of the communities (see Discussion). Total N contents per mass of shoots and roots were determined, after pooling individuals of the same species from a model community replicate, using coupled combustion chromatography (Natural Resource Management, Bracknell, UK). This allowed us to calculate total N contents by mass and shoot N concentrations, both of which are variables that can be related mechanistically to the performance of the native plant assemblage. The total N content by mass is indicative of how much N individuals are able to acquire from the soil (Chapin et al. 1987) and can therefore be used as an estimator of relative soil N competition. Shoot N concentrations are indicative of the photosynthetic enzyme capacity of a plant (Hirose and Werger 1987).

Statistical analysis

Linear mixed effects models were used to investigate how interactions between exotic species presence and resource availability (ambient or elevated) affected the native plant assemblages. For each experiment (CO_2 or N), the model structure was the same. Models included two fixed, discrete factors (resource level and community type), with block as a random, discrete factor. All statistical analyses were performed in S-PLUS 7.0 for Windows. Significance for a test is reported when the critical α-level is <0.05; when the P-value is >0.001 we report the actual P-value, whether the test is significant or non-significant.

We investigated the impacts of the treatments on the following native species properties: total biomass, root and shoot biomass, root:shoot ratios, total plant N content by mass, shoot N concentrations. We expressed biomass values as mean individual native biomass. To calculate these expressions we calculated the mean, individual biomass for each native species within a community replicate, then summed these values and divided by six (the number of native species) to give the mean native value. The mean, individual biomass for each native species was the mean of four individuals in the native community replicates, and two individuals in the invaded community replicates. This method of calculating mean individual native values ensured that the different numbers of native individuals in the different community types did not bias our analyses. The same method (i.e. determination of mean individual native values) was employed for analysis of the shoot biomass, root biomass, root:shoot ratio and N data.

To help explain observed impacts of exotic species presence on mean native individual responses, we analysed the responses of the exotic species to the resource level manipulations. In contrast to the natives, exotic plant responses were assessed on a species basis. Linear mixed effects models were used with ‘‘species’’ and ‘‘resource level’’ as fixed, discrete factors and block as a random, discrete factor. Significant interactions between the species and resource level factors were further investigated, for each species, using models where only resource level was included as a fixed effect. Exotic plant data were $\log_e$ transformed to homogenize variance.

Results

Native response: CO_2 experiment

In the CO_2 experiment, the mean individual native biomass was significantly lower in invaded communities but responded positively to elevated CO_2 availability (main effects: community type $F_{1,12} = 49.2$, $P < 0.001$; resource level $F_{1,12} = 12.7$, $P = 0.0039$; Fig. 1). There was no significant interaction between community type and resource level ($P = 0.64$). This indicates that CO_2 availability did

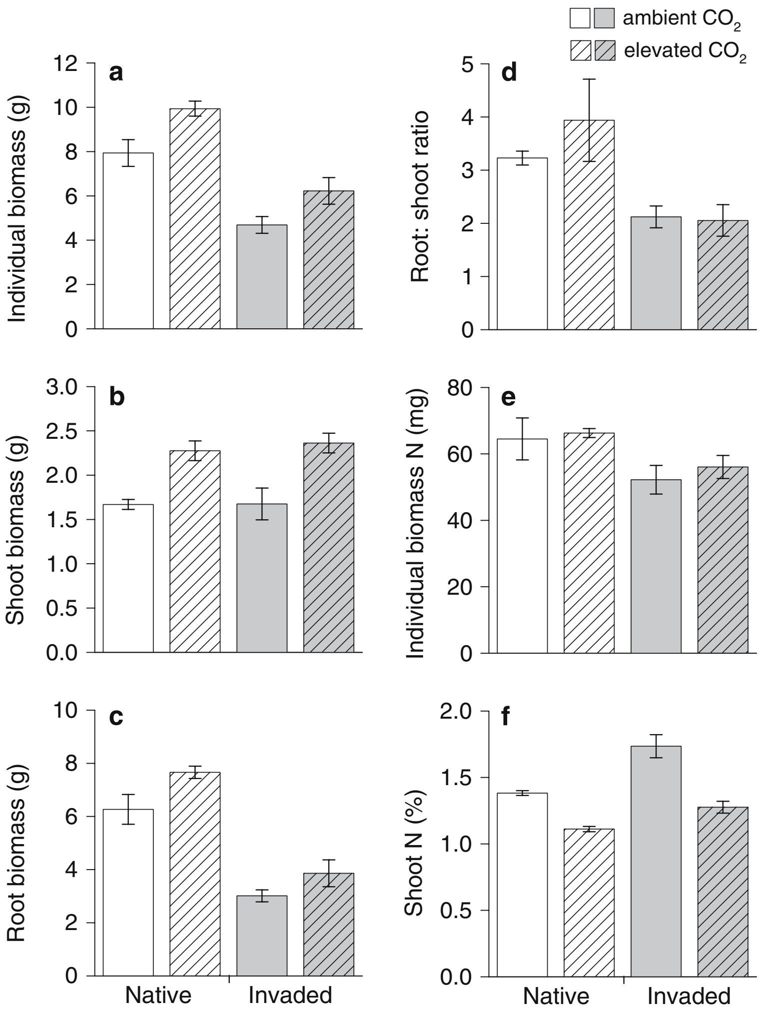

Fig. 1a–f Mean individual native responses to the presence of exotic species and elevated CO_2 availability. Shown are the individual (**a**), shoot (**b**) and root (**c**) biomass responses. Also shown are the mean native root:shoot ratio (**d**), mass of N captured (**e**) and shoot N concentration (**f**) responses. *Open bars* represent native (*white*) and invaded (*grey*) communities at ambient CO_2. *Hatched bars* represent native (*white*) and invaded (*grey*) communities under elevated CO_2. Note the different scales on the *y*-axes. Values are mean ± 1 SE ($n = 5$)

not modify the effects of the exotic species or vice versa on mean individual native biomass.

Similarly, there were no interactive effects of CO_2 and exotics on mean native shoot or root biomass ($P = 0.74$ and 0.52, respectively). Shoot and root biomass responded positively to elevated CO_2 availability irrespective of community type (resource level main effects of $F_{1,12} = 27.9$, $P < 0.001$ for shoot biomass and $F_{1,12} = 7.46$, $P = 0.018$ for root biomass; Fig. 1) but only root biomass was significantly affected by the presence of exotic species (community type main effect of $F_{1,12} = 73.9$, $P < 0.001$ for root biomass). The positive responses of both shoot and root biomass under elevated CO_2 meant that no significant differences ($P = 0.42$) in root:shoot ratios were observed between communities maintained in ambient and elevated CO_2 (Fig. 1). However, the decrease in native root allocation but no change in native shoot allocation in the presence of exotics meant that root:shoot ratios were lower in invaded than in native communities (community type main effect of $F_{1,12} = 14.8$, $P = 0.0023$; Fig. 1).

Total native N content by mass was not significantly affected by elevated CO_2 availability ($P = 0.46$). Total native N content was, however, significantly affected by the presence of exotics, being greater in native communities (community type main effect of $F_{1,12} = 7.95$, $P = 0.016$; Fig. 1). Mean native shoot N concentrations were lower in native communities, and under elevated CO_2 (main effects: community type $F_{1,12} = 27.8$, $P < 0.001$; resource level $F_{1,12} = 56.1$, $P < 0.001$; Fig. 1). There was no interactive effect of CO_2 and exotics on total native N content ($P = 0.80$) and while the interaction effect on shoot N concentrations was marginally significant ($P = 0.075$) it was not apparent from these data that the main effects of community type and resource level were dependent on one another (see Fig. 1).

Native response: N experiment

In the N experiment, mean native individual biomass was not significantly affected by N availability ($P = 0.27$) or by exotic species presence ($P = 0.20$; Fig. 2). In contrast,

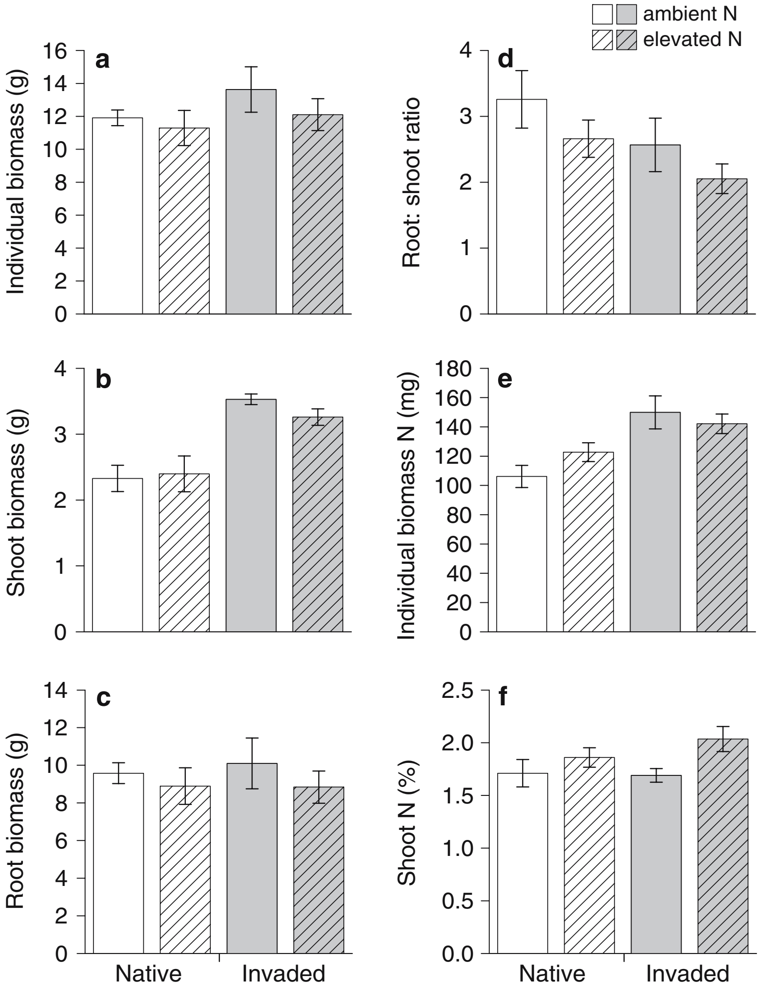

Fig. 2a–f Mean individual native responses to the presence of exotic species and elevated N availability. Shown are the individual (**a**), shoot (**b**) and root (**c**) biomass responses. Also shown are the mean native root:shoot ratio (**d**), mass of N captured (**e**) and shoot N concentration (**f**) responses. *Open bars* represent native (*white*) and invaded (*grey*) communities at ambient N. *Hatched bars* represent native (*white*) and invaded (*grey*) communities under elevated N. Note the different scales on the *y*-axes. Values are mean ± 1 SE ($n = 5$)

mean native shoot biomass was lower in native than in invaded communities (community type main effect: $F_{1,12} = 33.5$, $P < 0.001$; Fig. 2). This variable was not significantly affected ($P = 0.58$) by elevated N availability. Root biomass was not significantly affected by N availability ($P = 0.30$) or by exotic species presence ($P = 0.80$; Fig. 2). There were no interactive effects of N and exotics on mean native individual, shoot or root biomass ($P = 0.64$, 0.36 and 0.76, respectively).

Root:shoot ratios were, on average, lower in invaded than in native communities but this effect was only marginally significant (community type main effect: $F_{1,12} = 3.48$, $P = 0.087$; Fig. 2). The lower ratio was a function of the reduced shoot biomass in native compared to exotic communities, while root biomass did not differ between the community types. There were no interactive effects ($P = 0.92$) of N and exotics on root:shoot ratios, and no affect ($P = 0.14$) of N availability.

Community type significantly affected total native N content by mass (community type main effect: $F_{1,12} = 15.6$, $P = 0.0019$)—mass of N was greater in invaded than in native communities (Fig. 2). There were no interactive effects ($P = 0.19$) of N and exotics on total native N content by mass, and no effect ($P = 0.30$) of N availability. Mean native shoot N concentrations were not significantly affected by community type ($P = 0.45$), nor the community type × resource level interaction ($P = 0.35$). Shoot N concentrations were, however, significantly greater under elevated N availability (resource level main effect: $F_{1,12} = 6.11$, $P = 0.0294$; Fig. 2).

Invasive species response: CO_2 experiment

In the CO_2 experiment, the only exotic plant variable to respond to elevated CO_2 availability was shoot N concentration. All three species responded similarly (species × resource level interaction: $P = 0.145$), there being significantly lower shoot N concentrations under elevated CO_2 availability (resource level main effect: $F_{1,20} = 17.6$, $P < 0.001$). Across all species, the mean ± 1 SE shoot N concentrations under ambient and elevated CO_2 were 1.39 ± 0.060 and 1.07 ± 0.053, respectively. For all other variables *P*-values for species, resource level and the interaction between these factors were greater than 0.28.

Invasive species response: N experiment

In the N experiment, for all exotic plant variables except shoot biomass and shoot N concentration, there were significant, or marginally significant, resource level × species interactions. The significance levels for each of these interactions were: mean individual biomass ($F_{2,20} = 3.11$, $P = 0.067$), mean root biomass ($F_{2,20} = 3.73$, $P = 0.0420$), root:shoot ratio ($F_{2,20} = 2.83$, $P = 0.083$), total N content ($F_{2,20} = 3.94$, $P = 0.0362$). The interactions for mean individual biomass, root biomass and total N content arose because *I. glandulifera* showed significant ($P = 0.0070$, 0.0312 and 0.005, respectively), positive responses for these variables to elevated N availability whereas the other two exotic species were unresponsive (for each variable *P* was >0.57 for *F. japonica* and >0.13 for *M. guttatus*; Fig. 3). The interaction for root:shoot ratios appeared to be driven by the fact *I. glandulifera* and *F. japonica* ratios were unaffected ($P = 0.75$ and 0.26, respectively) by N availability, while the root:shoot ratio of *M. guttatus* was lower under elevated than under ambient N availability ($F_{1,4} = 7.38$, $P = 0.053$).

As for mean individual and root biomass, shoot biomass was significantly different between species (species main effect: $F_{2,20} = 8.02$, $P = 0.0028$; Fig. 3). Shoot biomass was significantly greater, for all species, under elevated as opposed to ambient N availability (resource level main effect: $F_{1,20} = 14.6$, $P = 0.0011$; Fig. 3). Similarly, shoot N concentrations were significantly different between species (species main effect: $F_{2,20} = 28.6$, $P < 0.001$; Fig. 3) and greater under elevated than under ambient N availability (resource level main effect: $F_{1,20} = 3.07$, $P = 0.095$; Fig. 3).

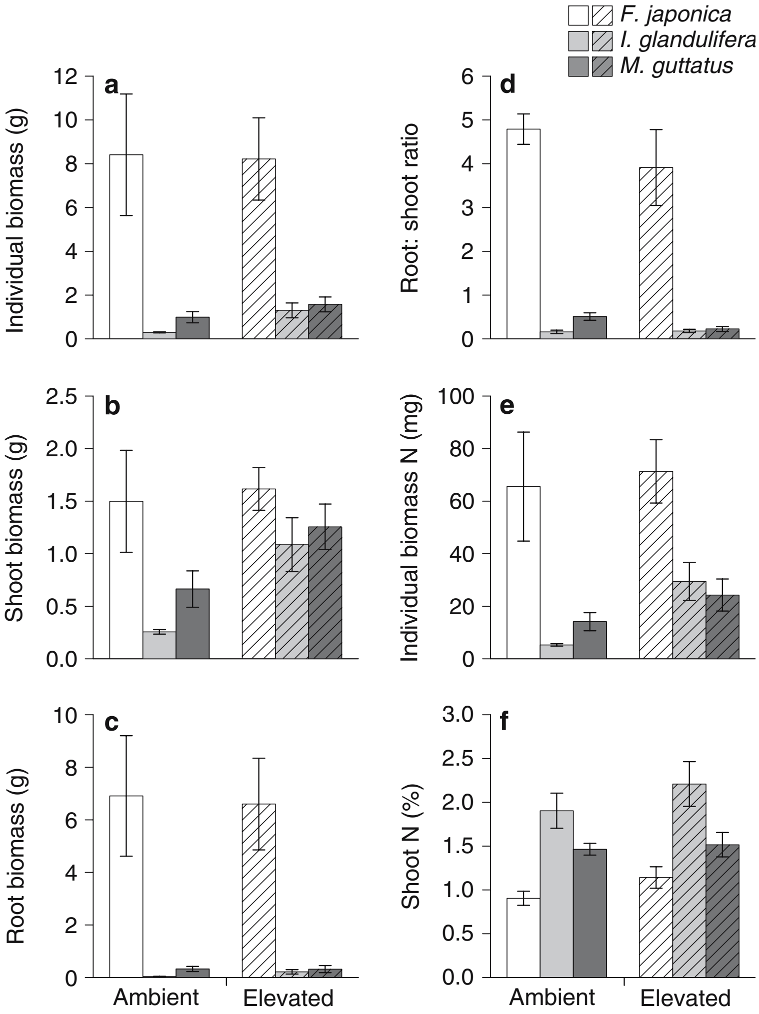

Fig. 3a–f Mean individual exotic species responses to elevated N availability. Shown are the individual (**a**), shoot (**b**) and root (**c**) biomass responses for each of the three exotic species (*white bars F. japonica*, *light grey bars I. glandulifera*, *dark grey bars M. guttatus*). Also shown for each species are the mean individual root:shoot ratio (**d**), mass of N captured (**e**) and shoot N concentration (**f**) responses. *Open bars* represent ambient N and *hatched bars* represent elevated N. Note the different scales on the *y*-axes. Values are mean ± 1 SE ($n = 5$)

Discussion

Are invasive species better competitors?

In the CO_2 experiment we found strong support for our first hypothesis that invasive plant species are better competitors than natives: mean individual biomass and total N contents of native species were significantly lower in invaded than in native communities (Fig. 1). These lower biomass values were the result of lower native root biomass in invaded communities; there was no significant effect of exotic species presence on mean native shoot biomass. In contrast, in the N experiment there was no support for our hypothesis that invasive plant species are better competitors. Indeed, while mean native individual and root biomass were unaffected by the presence of exotics in the N experiment, mean native shoot biomass and total N were actually greater in invaded than in native communities (Fig. 2). The reason for the differences in native suppression by the invasive species between the CO_2 and N experiments may be due to differences in the light regime of our two experimental greenhouses.

Our experimental design does not enable us to disentangle why we observed contrasting effects of exotic species presence on mean native performance in the CO_2 and N experiments. The only pronounced difference that we measured between the two greenhouses where these experiments were conducted was in the light availability: communities in the N greenhouse experienced higher light availabilities over the duration of our study than communities maintained in the CO_2 greenhouse (see Materials and methods). Comparisons between the two greenhouse experiments are pseudo-replicated (we only have one greenhouse per light availability). However, it is worth considering whether the light differences contributed to the differing effects of exotic species presence in the two experiments because the communities we worked with occur both in open and shaded areas. For this comparison we restrict our discussion to those native and invaded communities exposed to ambient CO_2 and ambient N only (i.e. the CO_2 and N ‘‘control’’ communities). By doing so, we ensure that our comparison of the community treatments under differing light levels is not confounded by effects resulting from the elevated CO_2 and N treatments.

In both experiments the native assemblages (under ambient CO_2 and N conditions) exhibited shifts in biomass allocation patterns when grown with the invasive species. In the CO_2 experiment, these shifts are indicative of a relative increase in light competition in the presence of invasive species; native species root:shoot ratios were lower and foliar N concentrations were higher in invaded communities (Fig. 1). Indeed, we tested this assumption using vector analysis (Haase and Rose 1995; Imo and Timmer 1998) and our interpretation of competition for light was supported (Table 1). In the N experiment, there were also lower root:shoot ratios in the presence of exotics, an effect which resulted from the greater mean native shoot biomass in invaded communities (Fig. 2). The interpretation of vector analysis, however, was that the native community in the N experiment was not, predominantly, light limited (Table 1). In the CO_2 experiment light-limitation of the native assemblage in the invaded communities perhaps arose because of the combination of the lower light levels in the CO_2 greenhouse and the fact the exotic species we used were generally taller than our native species. For example, *I. glandulifera* is ≤2.5 m tall (Beerling and Perrins 1993), *F. japonica* ≤3 m tall (Beerling et al. 1994), while the tallest natives, *E. hirsutum* and *U. dioica*, reach heights of ca. 1.5 m (Clapham et al. 1987). Although we did not measure plant height at the end of the second growing period, we did observe that both *I. glandulifera* and *F. japonica* had the tallest individuals in the invaded

Table 1 Relative change (%) in mean individual native biomass, N concentration and N content from control conditions (i.e. native community, ambient resource availability) in the CO_2 and N experiments determined using vector analysis[a] (Haase and Rose 1995; Imo and Timmer 1998). Shown is the interpretation of the most likely, dominant ecological effect of the community and/or resource manipulations relative to the control conditions

Experiment	Community	Resource level	Biomass	[N]	N content	Interpretation
CO_2 experiment	Native	High	125	91	103	Growth dilution: improved moisture and light availability
	Invaded	Ambient	59	117	81	Excess uptake: light and/or moisture competition
	Invaded	High	78	98	87	Antagonistic dilution: nutrient competition
N experiment	Native	High	95	108	116	Excess uptake: moisture and/or light competition
	Invaded	Ambient	114	100	141	Sufficiency: improved nutrient, moisture and light availability
	Invaded	High	102	125	134	Deficiency: improved nutrient uptake

[a] In vector analysis relative response is normalized by dividing each value of biomass, N concentration and N content for each treatment by the corresponding value for the control conditions and then multiplying by 100. In this way, a value of 100 shows no change relative to the control, values <100 a negative response relative to the control, and values >100 a positive response relative to the control. Biomass, N concentration and N content values are shown on a whole plant (shoot and root) basis

communities at this time and, also, these species were recorded as the tallest when a subset of the communities were measured at the end of growing period 1 (data not shown).

We chose our native and invasive species based solely on their abundance in local riparian communities, not on the possession of unique traits or life forms. Therefore, life form differences in species traits (possibly maximum height in this study) between native and invasive species may be an important means by which invasive species alter competitive dynamics and thereby suppress native species. Certainly, this seems to be a possibility for the particular native community and three exotic species we studied. Given the prevalence of invasion of riparian systems in Europe and North America by *F. japonica*, *I. glandulifera* and *M. guttatus*, it seems worth investigating whether this mechanism operates in other native communities across the two continents. Notably, other studies have shown that unique traits of invasive species may facilitate the suppression of native species; including by altering fire regimes (D'Antonio et al. 2001), nutrient cycling (Mack et al. 2001) and belowground mutualisms (Stinson et al. 2006).

To conclude the first section of this discussion, our first hypothesis that exotic plant invaders are better competitors than native species at ambient levels of atmospheric CO_2 and N deposition cannot be simply supported. However, in both the CO_2 and N experiment the presence of the invasive species significantly altered at least some of the measured characteristics of the native assemblages. The impacts were most pronounced in the CO_2 greenhouse, which also had lower light availability. However, given that the greenhouse comparison is pseudo-replicated, the potential role of light competition in mediating the invasive species' impacts on the native assemblages requires further experimentation.

Interactions between invasive species and elevated CO_2 or N

Dukes and Mooney (1999) postulated that resource elevation as a consequence of global environmental change might favour invasive species in competition with native species. We hypothesized that, were this to be so, then negative effects of our exotic invaders on our native assemblages would be more pronounced under elevated than ambient atmospheric CO_2 or N deposition. There was no empirical support for this hypothesis in either the CO_2 or N experiments. Indeed, in neither experiment were there significant interactions between community type and resource level, indicating that exotic species presence did not affect the impacts of elevated resource availability on the native assemblages and vice versa.

One of the main reasons for the lack of empirical support for our second hypothesis (invasive impacts being exacerbated by global changes) in the CO_2 experiment may be that the only significant response of the three invasive species to elevated CO_2 was a reduction in shoot N concentrations. This reduction in N concentration is typical for herbaceous species exposed to elevated CO_2 availability in nutrient-limited systems (Nowak et al. 2004); the mean native response was also a decrease in shoot N concentration (Fig. 1). Interestingly, despite the suppressive effects of invasive species presence on mean native individual biomass in the CO_2 experiment, mean native shoot and root response to elevated CO_2 was positive and approximately equivalent (relatively) in both native and invaded communities (Fig. 1). Weltzin et al. (2003) have argued that science is poorly prepared to predict the combined consequences of elevated CO_2 and biological invasions for native communities and ecosystems. We concur with their point: future research would be required to understand the mechanisms facilitating a positive response of our native assemblage to elevated CO_2 when apparently suppressed by the presence of exotic species.

In the N experiment, and in contrast to the CO_2 experiment, there were significant invasive species responses to elevated N availability (Fig. 3). In the main, however, these responses were restricted to the two subordinate invasive species, *I. glandulifera* and *M. guttatus*. *F. japonica* dominated the invasive species biomass and was largely unresponsive to N addition. While shoot biomass of all three invasive species did respond positively to N addition (the species × community type interaction was not significant), on a mean basis the *F. japonica* response appeared relatively minor compared to the other two species (Fig. 3). Had the invasive species biomass, overall, responded markedly to elevated resource availability in either the CO_2 or N experiment then we might have observed quite different native assemblage responses. As it happened, the relatively minor invasive species responses to the resource manipulations probably best explain the lack of significant invasive presence × resource availability interactive effects on the native assemblages. Dukes and Mooney's (1999) hypothesis needs to be tested in systems where the exotics are more responsive to increases in resource availability associated with global changes. Notably, however, the minor responses of the exotic species we used to elevated resource availability may not be atypical (LeJeune et al. 2006) but at least in some systems invasion or invasive species success is correlated with increased resource availability (Dukes 2002; Hättenschwiler and Körner 2003; Howard et al. 2004; Nagel et al. 2004).

Our results must be seen in the context of artificially assembled communities (Lawton 1996). It is possible that the disturbance associated with assembling our communities altered soil nutrient availability (e.g. Bradford et al. 2002) and that this might explain why the native assemblages were largely unresponsive to N addition. To test this possibility, during the second growing period we measured soil inorganic N availability and net mineralization rates for the N experiment communities. Inorganic N availability was (mean ± 1 SE, $n = 10$) 0.84 ± 0.100 and 1.40 ± 0.160 mg N kg soil^{-1} in the ambient and elevated treatment communities, respectively. Net mineralization rates were, for the same treatment communities, 0.07 ± 0.024 and 0.12 ± 0.041 mg N kg soil^{-1} day^{-1}. These availabilities and rates are within the ranges observed for undisturbed soils in natural ecosystems (Barrett and Burke 2000; Zak et al. 1994). Given the relatively low N availabilities in our microcosm soils it seems unlikely that the non-significant native assemblage biomass response to N addition was an experimental artefact. Indeed, all of the exotic species showed positive shoot biomass responses to N addition and all natives and exotics had higher shoot N concentrations in the elevated compared to the ambient N treatments. Instead, it is possible that the lack of native assemblage response to N addition resulted from the fact we added N weekly (see Materials and methods) in an attempt to mimic chronic N deposition. Often experimental N enrichment consists of one to a few large N amendments per year (e.g. Neff et al. 2002) and, when applied chronically, observed effects of N differ to results obtained with acute N addition (Bradford et al. 2001). Whether more acute N enrichment of our riparian communities would generate a native assemblage response and/or interactive effects with exotic species presence remains to be tested.

As well as a non-significant native biomass response to N addition, the total community biomass of both native and invaded community types was not significantly affected by elevated N [means ± SE (g) for the native communities at ambient and elevated N; and the invaded communities at ambient and elevated N were, respectively: 315 ± 9.2 and 316 ± 16.5; 220 ± 28.2 and 204 ± 18.1]. From these data we might infer that the communities were not N limited. Had we observed significant, total community biomass responses to N addition, indicative of community N limitation, then would our second hypothesis that the negative effects of invasive species will be exacerbated when resource availability is elevated have been supported? Our data from the CO_2 experiment do not suggest this is necessarily likely. In the CO_2 experiment community biomass was greater under elevated than under ambient CO_2 in both native and invaded community types [means ± SE (g) for the native communities at ambient and elevated CO_2; and the invaded communities at ambient and elevated CO_2 were, respectively: 203 ± 15.4 and 253 ± 9.2; 94 ± 3.3 and 115 ± 6.4], yet invasives did not have a disproportionately greater impact on the native assemblage under elevated CO_2 availability. The greater biomass in the elevated CO_2 treatments resulted from an increase in native species biomass (Fig. 1); exotic species biomass was unresponsive to CO_2 availability. In contrast, in the N experiment native biomass was unresponsive to N addition, whereas exotic biomass did respond (suggesting that exotic species were N limited; see Fig. 3). This sets up the possibility that native and exotic species in our experiment were differentially limited by CO_2 and N. Vector analysis supported this assumption. That is, in the CO_2 experiment elevated CO_2 improved the moisture availability for the invasive species (data not shown) and enhanced nutrient competition for the native assemblage, relative to the invaded, ambient CO_2 control (Table 1). In the N experiment elevated N, relative to the invaded, ambient N control, resulted in luxury N uptake for *F. japonica* (i.e. higher N concentration and content but no biomass change), improved growth of *I. glandulifera* and *M. guttatus* but no change in their N concentrations (i.e. sufficiency) and higher biomass, and N content and concentration, of the natives (Table 1). For our second hypothesis to have been supported our assumption was that native and exotic species were competing for the same limited resource. Our findings suggest that they were not and so set up the intriguing possibility that native and exotic species may be differentially limited by different resources, meaning that potential negative effects of exotics on native species may not necessarily be exacerbated under elevated availability of a single resource. Note that, in both the CO_2 and N experiments, the lower biomass in the invaded communities resulted from the replacement design used and the fact that exotic species had lower total biomass than the native species. Hence, our data do not suggest that, in field communities, invaded communities will necessarily have lower total biomass.

As well as potential nutrient pulses associated with assembly of artificial communities, a number of other factors must be considered when extrapolating results from microcosms to the field. That we used relatively large pots (0.196 m^2 surface area), a multi-species, multi-individual plant community, a multi-trophic level community (soil microbe and faunal inoculations), consecutive growing seasons and real soils all increase the likelihood that results from our experiments might be expected to be observed, qualitatively at least (i.e. ±effects) in field, riparian communities (Bradford and Reynolds 2006; Jones et al. 2000; Lawton 1996; Navas et al. 1999). Limitations to our approach include that, despite the fact we observed flowering for a number of the species, we established the second growing period from current individuals (the perennials) or, for *I. glandulifera*, seeds that had not been exposed to the experimental environment. Hence, maternal effects did not contribute to our results but may do so in field communities. Further, our community assembly probably most faithfully ‘‘recreates’’ community establishment following a major disturbance; hence early competition might be the key structuring force in the results we report. Further work would need to be conducted to establish whether our results would apply to invasions occurring in later successional communities.

Idiosyncratic versus general species responses to exotics

Our approach of growing abundant native species in multi-species, multi-individual plant assemblages, with and without exotics, allowed us to overcome the limitations of many exotic–native pair-wise competition studies (Levine et al. 2003; Vilà and Weiner 2004). As such, our focus was on the response of the overall native assemblage, as opposed to specific native species. This approach can be criticised: it is feasible that a single native species could drive the mean native assemblage responses we observed. To explore this possibility, we compared the relative mean individual native response to that of the relative response of each native species. Given the minor effects of CO_2 and N, and the general absence of interactions between these factors and invasive species presence, we restricted this comparison to the relative response of the native assemblage/species to invasive presence alone. Our results are shown in Table 2. Across both the CO_2 and N experiments, at least four of the six native species overlapped with that of the mean individual (i.e. assemblage) response. The exception was root:shoot ratios in the CO_2 experiment, where three of the species responses differed to the mean individual native response. In general then, and despite the fact the native species we used comprise many different growth forms and allocation patterns, the native species responded in a similar manner to the presence of the invasive species.

Table 2 Relative mean individual (*ind.*) native response and the relative response[a] of each native species to the presence of exotic species for plant biomass and N response variables in the CO_2 and N experiments. *CalSep Calystegia sepium*, *EpiHir Epilobium hirsutum*, *PoaTri Poa trivialis*, *RanRep Ranunculus repens*, *RumObt Rumex obtusifolias*, *UrtDio Urtica dioica*

Experiment	Variable	Mean ind. native	CalSep	EpiHir	PoaTri	RanRep	RumObt	UrtDio
CO_2 experiment	Individual biomass	38.22 (9.50)	**–14.15 (13.30)**[b]	27.52 (32.70)	–34.94 (74.54)	29.61 (24.70)	47.72 (14.58)	47.56 (25.77)
	Shoot biomass	–2.61 (8.40)	**–105.30 (92.51)**	–31.50 (59.48)	–20.21 (56.24)	5.38 (32.62)	3.91 (26.53)	**49.34 (33.25)**
	Root biomass	49.71 (10.44)	20.97 (22.31)	68.30 (19.15)	–59.10 (98.71)	51.65 (16.32)	52.01 (13.69)	45.62 (28.30)
	Root:shoot	41.41 (7.62)	53.86 (19.28)	**74.62 (13.64)**	**–39.76 (62.94)**	49.47 (6.31)	49.19 (5.05)	**–28.23 (44.10)**
	Total plant N	16.65 (9.52)	–7.42 (32.05)	6.64 (39.55)	–62.88 (87.38)	12.86 (31.00)	28.82 (27.95)	46.54 (26.25)
	Shoot N concentration	–20.77 (7.60)	–28.94 (32.34)	–20.82 (9.16)	–33.69 (5.90)	–12.51 (8.66)	–22.14 (7.28)	–8.01 (15.68)
N experiment	Individual biomass	–11.33 (11.65)	**–184.50 (105.96)**	–38.55 (120.94)	–33.77 (58.51)	**–83.91 (38.48)**	1.15 (13.71)	–40.64 (71.95)
	Shoot biomass	–47.15 (21.57)	–97.18 (134.06)	–30.40 (98.57)	–42.36 (91.53)	–99.15 (35.13)	–34.87 (24.52)	–36.15 (49.79)
	Root biomass	–2.72 (13.32)	**–366.05 (290.18)**	–56.75 (163.75)	–37.95 (51.98)	**–66.05 (42.02)**	4.23 (13.64)	–50.91 (99.10)
	Root:shoot	18.14 (22.21)	–128.98 (145.59)	4.54 (40.48)	–1.51 (53.17)	12.35 (17.29)	27.42 (15.75)	7.04 (54.88)
	Total plant N	–27.55 (10.21)	**–226.59 (155.12)**	–8.39 (62.88)	–33.68 (50.62)	**–96.87 (35.10)**	–6.95 (14.99)	–42.34 (70.10)
	Shoot N concentration	–5.22 (12.21)	6.83 (15.86)	–23.51 (45.65)	–7.33 (14.69)	–4.02 (3.12)	–7.68 (17.62)	–6.68 (6.92)

[a] Relative response was calculated as: $\frac{X_{\text{native}}-X_{\text{invaded}}}{X_{\text{native}}}\times 100$ where, X_{native} represents the response variable in native communities and X_{invaded} represents that response variable in invaded communities

[b] Values highlighted *in bold* are those where the 95% confidence interval of species response does not overlap the mean individual native response. Positive relative responses show suppression of the native individuals in invaded communities relative to native communities and vice versa for negative relative responses. Response variables are pooled across levels of resource availability (ambient and elevated)

Conclusion

Our approach focused on the response, to the presence of invasive species and elevated CO_2 and N availability, of a multi-species assemblage of abundant native species. Our objective in using this approach was to account for indirect and higher-order interactions between multiple species and to avoid confounding species origin with species abundance (and therefore possibly with competitive ability). Under these conditions, we found support for the hypothesis that invasive species are better competitors than native species. It is possible that life form differences between the invasive and native species used accounted for this effect. Higher light availability may have ameliorated the negative effects of the invasive species by decreasing light competition but this remains to be definitively tested. Regardless of whether the invasive species used were superior competitors, their presence did alter at least some of the measured characteristics of the native assemblages. Thus, the presence of the invasive species might be expected to alter the ecology of similar riparian communities in the wild. Given that the exotic species we used are prevalent invasive species in Europe and/or North America, their potential impacts on the ecology of riparian systems merits further study. Elevated CO_2 and N availability did not modify the effects of the invasive species on our native plant assemblages. This lack of modification may be explained by the fact that the invasive species, overall, showed only minor responses to the resource manipulations and/or it may be because native and exotic species were differentially limited by CO_2 and N. Our results confirm the expectation that invasive species alter the characteristics of native assemblages but lead us to question whether elevated resource availability will magnify these effects.

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