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Competition between young exotic invasive and native dominant plant species: implications for invasions within riparian areas

Marion Bottollier-Curtet, Anne-Marie Planty-Tabacchi & Eric Tabacchi

Keywords
biological invasion; biomass production; competition; introduced plant; physical disturbance; river banks

Nomenclature
Tela Botanica

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Abstract

Questions: The high competitiveness of exotic invasive species has often been demonstrated, but usually with respect to native species known to have low competitive ability. Considering five exotic and five native riparian species with close characteristics regarding competitive ability, habitat and growth form, we addressed the following questions: (i) do the selected invasive plants produce more biomass than the selected native dominants under competitive pressure; and (ii) are the selected invasive species better competitors than the selected native dominants?

Location: Common garden experiment at the Henri Gaussen Botanical Garden, Toulouse, France.

Methods: We selected five native dominant species and five exotic invasive species co-occurring along a riparian successional gradient of the middle Garonne River (SW France). Young plants of each species were planted in pots in ten intra- and 17 inter-specific combinations in conditions of high water and nutrient availability. To simulate the effects of hydrological disturbance during earlier growth stages, a partial cutting of plants was applied 6 weeks after planting. We measured above-ground and below-ground biomass of individuals of each species after 6 mo of growth.

Results: There were large disparities among species performances, regardless of whether the species were exotic or native. The exotic species produced more above-ground and below-ground biomass than the natives species for 73% of the selected species pairs. The exotic species had higher competitive ability than the native species, mainly related to the high competitive effect of *I. glandulifera*. The two species with the highest biomass production and competitive ability were invasive exotics, whereas the two species with the lowest were dominant natives.

Conclusions: Our results predict that competition among young individuals could play a major role for the invasion success of the studied exotic species in European riparian areas.

Introduction

Plants represent the majority of known introduced organisms (Pimentel et al. 2007; DAISIE 2010). More than 30 000 plant species have been introduced worldwide (Pimentel et al. 2007), and regional data show that they can represent up to 50% of the flora in islands and 30% in continental areas (Myers & Bazely 2003). More than 6000 terrestrial plants have been introduced into Europe, with at least several tens becoming invasive (DAISIE 2010) and about 16 new species introduced every year (Pyšek et al. 2009). The invasive success of some introduced plants and their ecological impacts on both native communities and ecosystem functioning depend on plant biological traits, environmental characteristics of the receptive area and biological interactions with native organisms (see Catford et al. 2008; Ehrenfeld 2010 for a review). Moreover, a synthesis of pair-wise competition experiments showed that

exotic invasive species have generally stronger competition effects on native species than *vice versa* (Vilà & Weiner 2004).

Surprisingly, studies comparing competitive abilities of exotic and native plants have mainly focused on native species that are intrinsically sensitive to competition (e.g. Gerry & Wilson 1995; Callaway & Aschehoug 2000), or rare or endemic species potentially threatened by the invasion (Aplet & Laven 1993; Huenneke & Thompson 1994). In contrast, exotic species in such studies were selected as invasive from biological traits that promote potential competitive success and invasiveness, e.g. high vegetative multiplication, high nutrient use efficiency and high growth rate (Pyšek & Richardson 2007). Thus, most previous studies compared the competitive abilities of dominant vs non-dominant species instead of native vs introduced species, and evidence that introduced invasive species are better competitors than dominant natives remains scarce (but see Hovick et al. 2011). Houlahan & Findlay (2004) showed that wetland exotic species were no more likely to dominate than wetland native species. Besides, comparisons of biological traits between dominant natives and invasive exotics show that they both share similar biological traits (Thompson et al. 1995; Smith & Knapp 2001). Recently a meta-analysis (Van Kleunen et al. 2010) highlighted that exotic invasive species do not have distinguishable fitness, size, growth rate, shoot allocation, leaf area allocation or physiology to native species that are known to be invasive elsewhere. Thus, native dominant species could have as high competitive ability as introduced invasives and therefore might resist invasion pressure.

Table 1. Mortality recorded in the experiment. The number of deaths is accumulated across all replicates. Only species that have a total number of deaths above zero are represented for the intra-specific combinations. Grey shading indicates the highest number of deaths. Plant shoot axes were cut 3 weeks before mortality monitoring in June. Note that in intra-specific combinations there were four individuals from the same species in a pot, whereas in inter-specific combinations there were two.

Combinations	Species	No. of deaths in June	No. of deaths after June	Total no. of deaths
Intra-specific				
Agrostis stolonifera	AGR	0	0	4
Paspalum distichum	PAS	4	0	4
Rubus caesius	RUB	0	0	0
Fallopia japonica	FAL	0	0	0
Populus nigra	POP	4	3	7
Buddleja davidii	BUD	2	0	2
Urtica dioica	URT	0	0	0
Impatiens glandulifera	IMP	12	2	14
Salix alba	SAL	4	6	10
Acer negundo	ACE	2	4	6
Inter-specific				
FAL-IMP	IMP	9	1	10
URT-IMP	IMP	6	0	6
SAL-IMP	SAL	3	2	5
IMP-ACE	IMP	3	1	4
SAL-IMP	IMP	3	1	4
URT-ACE	ACE	2	0	2
POP-SAL	POP	1	0	1
POP-ACE	POP	3	3	6
SAL-ACE	SAL	2	2	4
URT-SAL	SAL	3	4	7
POP-BUD	POP	1	3	4
POP-FAL	POP	1	3	4
POP-URT	POP	1	2	3
POP-SAL	SAL	1	2	3
IMP-ACE	ACE	1	1	2
AGR-PAS	PAS	0	2	2
SAL-FAL	SAL	0	1	1

Riparian areas are intensively colonized by exotic species, some of them becoming invasive (Hood & Naiman 2000). In riparian areas plant competitive interactions are constrained by hydrological disturbances and stress (floods and drought), the intensity and frequency of which decrease along the river–floodplain gradient (Malanson 1993; Biswas & Mallik 2010). Thus plant development and competition pressure remain limited in highly disturbed habitats. Such hydrological constraints usually induce the selection of stress-tolerant or ruderal species characterizing an early successional stage (Naiman & Décamps 1997). Conversely, competition leads to more constraints to plant development in later successional stages (Naiman & Décamps 1997). Besides, young plants of any successional stage usually form dense stands in riparian areas (e.g. Barsoum 2002; Taylor 2009) and are likely to be exposed to disturbance events having strong physical effects. A higher productivity, a competitive advantage and a higher resilience toward disturbance at these early development stages can thus be decisive properties for further invasion success.

The main objective of this paper is to determine the biomass production and competitive ability of young riparian plants that are either dominant natives or invasive exotics. We compared five exotic invasive and five native dominant plant species selected along disturbance and successional gradients in riparian areas of the middle Garonne River (SW France). A pot experiment was conducted, testing inter-specific competitive abilities of 27 pairs of the selected species, based on biomass measurement (Keddy et al. 2002). In order to simulate the effects of hydrological disturbance on young riparian plants, we applied a physical disturbance. We addressed the following questions: (i) do the selected invasive plants produce more biomass than the selected native dominants under competitive pressure; and (ii) are the selected invasive species better competitors than the selected native dominants?

Methods

Selected species

Among *ca.* 700 plant species present in riparian areas of the middle Garonne River (SW France), we selected five exotic invasive and five native dominant plant species of different growth forms (herbaceous vs woody) along the successional gradient (Fig. 1). We chose the exotic and native species according to their high co-occurrence frequency at both regional (river stretch) and local (plot) scales (database from Tabacchi & Planty-Tabacchi 2005). Each selected native species is dominant at and characteristic of a given successional stage. Species origin was designated as exotic or native in the context of their status in Europe.

Studied species are presented below, dominant natives first, and from early to more mature successional stages. *Agrostis stolonifera* L. (creeping bentgrass, herbaceous) is a perennial grass that colonizes highly disturbed river gravel –sand bars but can also be found in the understorey of damp pioneer riparian forests. *Rubus caesius* L. (European dewberry, woody) is a deciduous bramble of disturbed riparian habitats and riparian forest margins. *Populus nigra* L. (black poplar, woody) is a deciduous riparian tree forming pioneer riparian forests. *Urtica dioica* L. (stinging nettle, herbaceous) is a perennial herbaceous species usually found in the understorey of white willow stands (*Salix alba* L., woody), a deciduous tree forming damp and nutrient-rich pioneer and post-pioneer riparian forests. Invasive dynamics of populations have been reported in other continents for *A. stolonifera* (Gremmen et al. 1998), *P. nigra* (USDA 2010), *U. dioica* (USDA 2010) and *S. alba* (Mills et al. 1996).

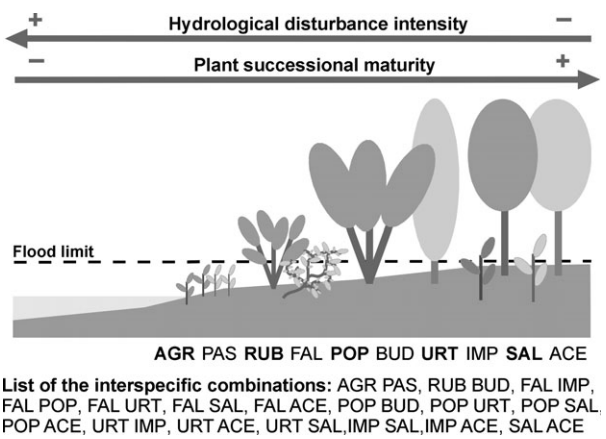

Fig. 1. Distribution of exotic (normal) and native (bold) species along the gradients of hydrological disturbance and successional stage of maturity in the riparian area. Full species names correspond to coded species name given Table 1. Flood limit corresponds to 1- to 3-yr frequency of flooding.

All exotics used in the experiment are neophytes and are recognized as highly invasive in Europe (DAISIE 2010). *Paspalum distichum* L. (water couch grass, herbaceous) is a perennial grass that colonizes highly disturbed and winter-flooded areas on river gravel–sand bars. *Fallopia japonica* (Houtt.) Ronse Decr. (giant knotweed, herbaceous) is a giant herbaceous perennial of disturbed riparian or wasteland habitats. *Buddleja davidii* Franch. (butterfly bush, woody) is a semi-deciduous shrub occupying disturbed riparian habitats and the margins of pioneer riparian forests. *Impatiens glandulifera* Royle (Himalayan balsam, herbaceous) is a tall annual species found in the understorye of damp riparian forests. *Acer negundo* L. (boxelder, woody) is a deciduous tree forming damp post-pioneer riparian forests.

Experimental design and measures

We estimated biomass production of exotic and native plant species in intra- and inter- specific interaction, during an outdoor experiment conducted in the Henri Gaussen Botanical Garden in Toulouse (SW France), starting in the middle of April 2008. We studied ten intra-specific (i.e. monocultures) and 17 inter-specific (i.e. mixtures of two species) combinations. We considered all the possible intra-specific combinations, but took into account only the most probable inters-pecific ones, based on field co-occurrence data (cf. selected species, Tabacchi & Planty-Tabacchi 2005). We planted four individuals in 10-L pots whatever the combination: four individuals from the same species for intra-specific combinations and two individuals from each of the two species for inter-specific combination (15 replicate blocks for a total of 405 pots; Fig. 1). We filled pots with a mix of 1:1 compost (Proven substrate NF U44-551, BAS Van Buuren; NO_3-N: 42 mg·kg^{-1}; NH_4-N: 9 mg·kg^{-1}; PO_4-P: 750 mg·kg^{-1}) and river sand (0–2 mm). Each pot received 2 L of water per day from a drip system as soon as individuals were planted and 20 g of slow-release fertilizer (Osmocote exact high K 5-6M, Scotts; 11% N, 11% P_2O_5, 18% K_2O, 1.5% MgO) at the beginning of June to ensure nutrient supply until the end of the experiment.

One week before planting, we took individual plants from a natural riparian area of the Garonne River (stream order six) located downstream from the confluence with the Ariège River and upstream from the city of Toulouse (43°31′36.96″N, 1°25′38.24″E, 147 m a.s.l.). Individuals consisted of: (i) seedlings from the previous year (spring or autumn 2007) for *A. negundo*, *B. davidii*, *P. nigra* and *S. alba*; (ii) rhizomes with three nodes (6–7 cm) for *A. stolonifera*, *F. japonica*, *P. distichum*, *R. caesius* and *U. dioica*; and (iii) seedlings from the current year for *I. glandulifera*. We replaced each dead individual during

the first week following the planting to ensure that mortality observed during the experiment was not due to transplantation stress.

Six weeks after the beginning of planting (mid-May), we cut each shoot axis of each individual just above the third node to simulate biomass destruction of young plants by hydrological disturbance. We recorded mortality of individuals at the beginning of each month during the experiment (May, June July, August, September and October). As the competitive pressure was modified, we excluded the related pots from biomass measurements (Resource S1). We stopped the experiment during the second week of October, before the beginning of leaf senescence. We collected the above-ground and below-ground parts of all of the four individuals in each pot. We treated together individuals of the same species because of the difficulty in disentangling their respective below-ground parts. We gently rinsed the below-ground parts to remove substrate particles. Above-ground and below-ground parts were weighed to the nearest 0.01 g after drying at 105°C until constant weight.

Data analysis

We systematically used individual mean biomass per pot and per species for the statistical analyses. We assessed the effect of species identity and species growth form on above-ground and below-ground biomasses among monocultures with analyses of variance (ANOVA). We used replicate blocks as random factors to take variability in outdoor environmental conditions into account. We species identity and species growth form were fixed factors. We considered species identity as a fixed factor because the studied species were selected on precise ecological criteria and in a determined geographic area and were not used as a random sample of a larger population (Doncaster & Davey 2007). We nested species effect in species growth form. When ANOVA indicated a significant general effect, we performed *post-hoc* Tukey's pair-wise comparisons. A similar analysis was made on data from mixture combinations.

For each replicate block, we expressed above-ground and below-ground biomass of species in mixtures as proportions of the above-ground and below-ground biomass of each species in monocultures. This competition index, called relative yield (RY), gives a simple evaluation of the competitive effect of one species on another (Weigelt & Jolliffe 2003):

$$\mathrm{RY} = (\text{biomass in mixture})/(\text{biomass in monoculture})$$

An RY of 1 indicates similar competitive effects in monoculture and mixture, an RY below 1 indicates a higher competitive effect in the monoculture than in the mixture and an RY above 1 indicates a higher competitive effect in the mixture than in the monoculture. To test whether mean RY differed significantly from 1, we assessed whether the 95% bootstrap confidence interval of mean RY did not overlap 1 based on 1000 iterations (Diciccio & Efron 1996). For the bootstrap confidence intervals of exotic, native, herbaceous and woody species groups, bootstrap resampling was done among both species and blocks and within each group.

We log-transformed above-ground biomass and below-ground biomass to approach the normality and homogeneity of variance assumptions. Because the sample sizes were unequal we used the type II sum of squares in the ANOVAS (Doncaster & Davey 2007). All the analyses were performed with Statistica (v. 6.0; Statsoft, Tulsa, OK, US).

Results

Mortality

No mortality in any of the clonal species, *A. stolonifera*, *F. japonica*, *R. caesius* and *U. dioica*, occurred, except *P. distichum* (Table 1). The highest mortality was recorded for the annual *I. glandulifera*, with more deaths recorded in June. The highest mortalities recorded after June were for *S. alba* and *P. nigra.*

Biomass production performances

Overall, herbaceous species produced at least 1.4-fold more above-ground and below-ground biomass than woody species (Resource S3 and 4; $P < 0.001$) in monocultures and in mixtures. The biomass differences between herbaceous and woody species was three-fold larger in mixture than in monoculture.

There were strong above-ground and below-ground biomass production differences among species in monocultures (Fig. 2a, Resource S3). *I. glandulifera* and *B davidii* produced up to 42- and to 24.5-fold, respectively, higher above-ground biomass than all the other species (*post-hoc* Tukey tests, $P < 0.05$). Conversely, *P. nigra* and *S. alba* produced lower above-ground biomass than all the other species ($P < 0.05$). The highest below-ground biomass was produced in *F. japonica* and *U. dioica* because of rhizome production, whereas *P. nigra* and *S. alba* had, respectively, 31- and 17-fold lower below-ground biomass than the other species ($P < 0.05$). These species-specific differences lead to a higher mean above-ground and below-ground biomass production for exotic species (exotics: 37.0 ± 4.2, 18.9 ± 1.7; natives: 16.8 ± 1.6, 12.0 ± 1.7 for above-ground and below-ground biomass, respectively). In mixtures, inter-specific variation in above-ground and below-ground biomass production was also high (Fig. 2b,

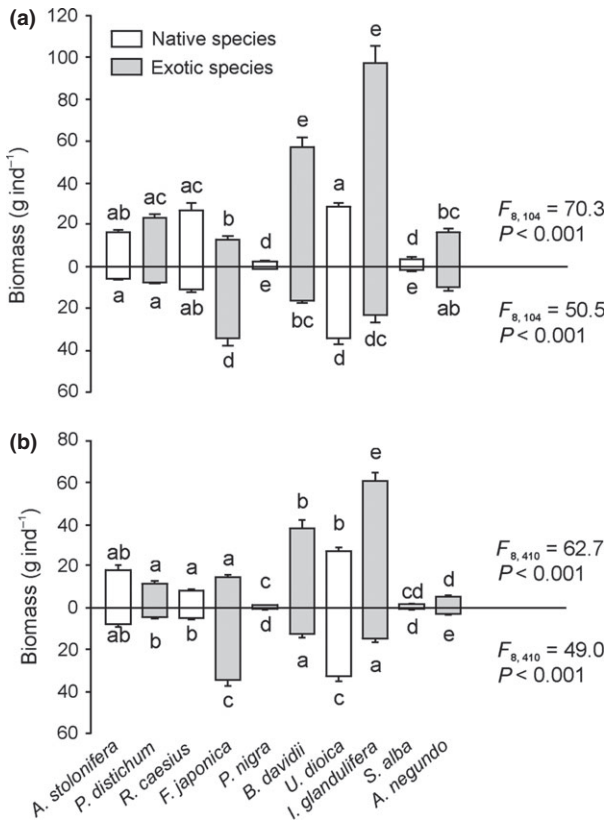

Fig. 2. Above-ground (above the *x*-axis) and below-ground (below the *y*-axis) biomass (mean + SE) of the ten selected species in monocultures (**a**) and mixtures (**b**). Identical letters denote no statistical differences (*post-hoc* Tukey tests, $P < 0.05$).

Table 2. Mean above-ground (A) and below-ground (B) biomass (±SE) produced by species in native–exotic mixtures. Grey highlighted rows: combinations where the exotic species produced more biomass than the native species.

Combination Species 1	Species 2	Biomass of species 1 (g)	Biomass of species 2 (g)
(A)			
AGR	PAS	18.1 ± 2.3	11.4 ± 1.3
RUB	BUD	7.9 ± 1.1	27.3 ± 3.4
POP	ACE	0.5 ± 0.1	11.4 ± 1.8
POP	BUD	1.0 ± 0.1	48.8 ± 6.2
POP	FAL	1.0 ± 0.2	24.9 ± 2.0
URT	ACE	34.2 ± 3.9	0.3 ± 0.0
URT	FAL	25.7 ± 2.4	4.5 ± 0.6
URT	IMP	5.3 ± 0.5	54.9 ± 5.8
SAL	ACE	2.1 ± 0.6	10.8 ± 2.1
SAL	FAL	0.6 ± 0.1	14.0 ± 2.2
SAL	IMP	0.6 ± 0.1	49.1 ± 5.5
(B)			
AGR	PAS	7.7 ± 1.3	4.5 ± 0.5
RUB	BUD	4.6 ± 0.8	12.2 ± 1.9
POP	ACE	0.3 ± 0.1	5.9 ± 1.0
POP	BUD	0.5 ± 0.1	13.1 ± 2.0
POP	FAL	0.7 ± 0.1	54.1 ± 3.5
URT	ACE	38.9 ± 4.8	0.2 ± 0.0
URT	FAL	31.4 ± 3.5	12.2 ± 2.3
URT	IMP	8.0 ± 0.8	11.7 ± 2.1
SAL	ACE	0.7 ± 0.2	7.8 ± 1.6
SAL	FAL	0.5 ± 0.1	29.9 ± 3.5
SAL	IMP	0.4 ± 0.1	9.5 ± 1.3

Resource S4). The same overall species-specific differences in biomass production were observed in both mixtures and monocultures (see above). In addition, Table 2 shows that in eight of 11 (i.e. 73%) of the native–exotic mixtures, exotic species produced more above-ground and below-ground biomass than native species.

Inter-specific competition effects

The RYs for biomass varied according to competitor origin (Fig. 3a), competitor growth form (Fig. 3b) and competitor identity (Fig. 3c). Competition between exotic and native species induced RYs below 1 (Fig. 3a). In particular, competition with exotic species significantly decreased the native above-ground and below-ground biomass by 24% on average (both RY = 0.76). Competition with herbaceous species induced RYs, below 1, and thus a decrease in the above-ground and below-ground biomass of both herbaceous and woody species (Fig. 3b). These effects were larger for the woody species. In contrast, woody competitors allowed an RY above 1, which equates to an increase in both the above-ground and below-ground biomass of herbaceous species.

Competition with *I. glandulifera*, *U. dioica*, *B. davidii*, *A. stolonifera*, *R. caesius* and *F. japonica* induced RYs below 1 for above-ground and below-ground biomass of species, indicating a decrease of these biomasses (Fig. 3c). Overall, the annual *I. glandulifera* had the strongest competitive effect and induced a mean decrease of at least 75% of above-ground (RY = 0.15 ± 0.02) and below-ground (RY = 0.23 ± 0.04) biomass of other species. *U. dioica* and *B. davidii* induced a mean decrease of, respectively, 50% and 30% in above-ground and below-ground biomass of other species. *A. stolonifera* and *R. caesius* induced a decrease of 50% of only above-ground biomass. Conversely, competition with *P. distichum*, *S. alba*, *A. negundo* and *P. nigra* induced RYs above 1 and thus an increase of both above-ground and below-ground biomass of species. These effects were up to 30% and significant for *P. nigra* and *A. negundo*. According to Fig. 3c, exotic species displayed higher competitive ability in four on 11 pairs of species, whereas native species displayed higher competitive ability in two on 11 pairs. For five on 11 species pairs, bootstrap confidence intervals overlap, at least partially.

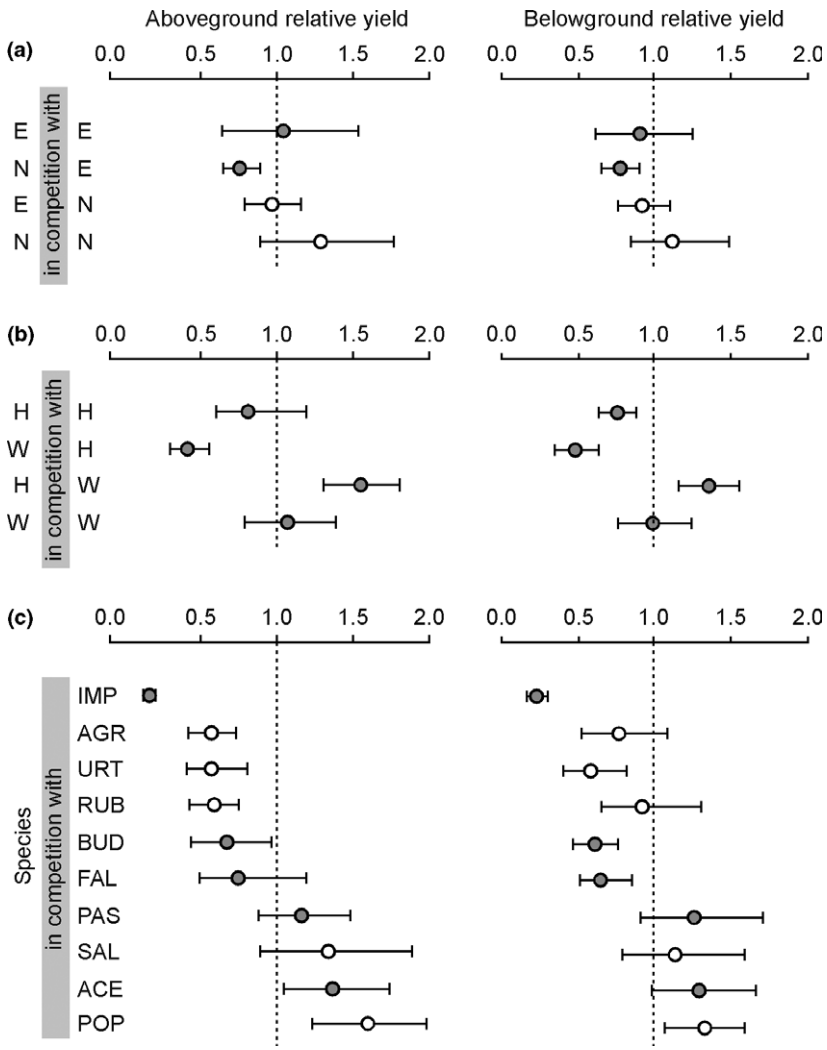

Fig. 3. Mean competition effect (± 95% bootstrap confidence interval) on individual biomass according to origin (exotic vs native; (**a**), growth form (herbaceous vs woody; (**b**) and identity of competitors (**c**). E, exotic species; N, native species; H, herbaceous species; W, woody species; grey circles, competition effect of exotic species; white circles, competition effect of native species. Competitive effect is expressed as mean relative yield (RY, see Methods for calculation details). Panel C shows mean RYs for all individuals when in competion with species (for full names of coded species, see Fig. 1). Competition effects are considered as significant when 95% confidence intervals on mean RYs do not exceed 1.

Discussion

Disparities among species

While the selected herbaceous species overall produced higher biomass than the selected woody species, the two species with the highest above-ground biomass production in both intra- and inter-specific competition were the annual invasive *I. glandulifera* and the woody invasive *B. davidii*. The best competitor in our study was also *I. glandulifera*. This should be viewed in the context of an experimental design using young plants. It is possible that perennial herbaceous species (including *U. dioica*) will become better competitors after several growing seasons. However, this result points to a rare case of annual herbaceous species able to outcompete perennial herbaceous species, and especially *U. dioica* (Tickner et al. 2001). It is even more surprising as *I. glandulifera* was also the most sensitive to disturbance. Not surprisingly, the high competitive ability of *I. glandulifera* is related to high physiological performance compared with other exotic invasive or co-occurring native species: high specific leaf area (SLA) (Andrews et al. 2009), high leaf nutrient content (Beerling & Perrins 1993) and high growth rate (Prach 1994). Despite *I. glandulifera* having high competitive ability, modification of the recipient riparian communities seems to be negligible until *I. glandulifera* cover reaches 40% (He-

jda et al. 2009). The habitats highly invaded displayed lower species richness than the non-invaded habitats (Hulme & Bremner 2006). However, seed dispersion through ballochory induces a small displacement of *I. gandulifera* populations over the years and could allow initial community recovery from the seed bank. Finally, the sensitivity of the species to physical disturbance is indicated by its high mortality just after cutting in the experiment, and suggests that its population could be easily regulated.

The high production of *B. davidii* is also related to high physiological performance compared with other exotic invasive or co-occurring native species: high specific leaf area (SLA) (Cornelissen 1996), high photosynthetic nitrogen use efficiency (Feng et al. 2007) and high leaf nutrient content (Feng et al. 2007). In agreement with this, the competitive ability of *B. davidii* were high and its effects were particularly strong on *P. nigra* (data not shown). This confirms the results obtained by Smale (1990), who showed that *B. davidii* development on gravel bars quickly displaced pioneer herbaceous and woody species.

In contrast to *I. glandulifera* and *B. davidii*, *P. nigra* and *S. alba* had the lowest biomass produced, and yet these two keystone riparian species are known to be fast-growing woody pioneers (Brzeziecki & Kienast 1994). We hoped to provide optimal growth conditions for the species, but some abiotic factors are difficult to control, e.g. insufficient incident light, can reduce the production of *P. nigra* and *S. alba*. Moreover, while we did not note indices of herbivory on the seedlings, biotic factors, e.g. pathogens, could also have reduced *P. nigra* and *S. alba* vitality and could explain their low growth and high mortality. However, in accordance with our results and despite the growth potential of these two species, Saccone et al. (2010) showed that growth of *S. alba* and *P. nigra* cuttings was as much affected by herb layer competition as *A. negundo* seedlings. Moreover, in our study, *S. alba* and *P. nigra* suffered the highest mortality after June, probably due to competition. The combination of physical effects of disturbance and intra- and inter-specific competition seems thus having significantly reduced the performance of young *S. alba* and *P. nigra*.

The only exotic species that produced significantly lower shoot biomass than at least one native species in intra-specific competition was the perennial herbaceous *F. japonica*. This result is surprising since *F. japonica* is considered the tallest and most productive herbaceous species in Europe (Beerling et al. 1994). In addition, the effect of *F. japonica* on shoot biomass production of its competitors is not significant in our study, whereas this species has been found to outcompete herbaceous species and trees smaller than 2-m tall in the field (Bimova et al. 2004; Aguilera et al. 2010). Two main and not exclusive hypotheses can be proposed. First, *F. japonica* competition could be less effective on dominant native species than on non-dominant ones. Second, our results could also be related to the choice of young individuals for the experiment. As the modification of native communities by *Fallopia* sp. competition is mainly light-driven (Siemens & Blossey 2007), the competition effect could be effective only after several years of growth, when rhizomes are able to accumulate reserves and increase above-ground biomass production. Despite its low production, *F. japonica* appears to be insensitive to physical disturbance in this experiment.

The best native competitors are *A. stolonifera*, *U. dioica* and *R. caesius*. Among them, only *U. dioica* induced significantly less biomass of both above-ground and below-ground parts for the species that competes with. This confirms its ruderal ecological status and its strong competitive strategy (Grime et al. 2007). Such results suggest that this native species could, at least, persist in invaded stands, as already observed in the field (Bimova et al. 2004).

Overall species performances

Overall species performances in production and competition according to species origin are difficult to interpret because of the large variability among these two species groups. However, exotic species had higher biomass production in 73% of the species pairs and invasive exotic species displayed higher competitive ability than dominant natives, mainly related to the high competitive effect of *I. glandulifera.* Higher biomass production and superior competitive performance for exotic invasive grasses and tree seedlings compared with natives have been reported in many species-specific studies (e.g. Nernberg & Dale 1997; Ehrenfeld et al. 2001), and confirmed in the meta-analyses of Vilà & Weiner (2004) and Vilà et al. (2011). However, such results were mainly supported by comparisons with native species known to be excluded by the invasive species in the field, and thus already identified as having lower biological performance (Huenneke & Thompson 1994; Gerry & Wilson 1995; Callaway & Aschehoug 2000). In this study, among the selected species, exotic invasives seem to have higher performance than native dominants.

According to the review of Daehler (2003), the result of competition studies comparing exotic and native species strongly depends on the environmental conditions maintained during the experiments. In many studies, exotic species appeared to be better competitors only in high-nutrient conditions (e.g. Herron et al. 2001) or with high water availability (Smith & Brock 1996). Similarly, Davidson et al. (2011) showed, in a meta-analysis, that native species recorded a smaller decline in fitness than invasive exotics when resources are limited or conditions stressful. Our experimental conditions of high nutrient and water

availability and the application of an early physical disturbance were chosen to mimic the overall riparian environmental conditions for young plants.

Implications for the invasion process and riparian ecosystems

According our results, the observed replacement of *P. nigra* by *B. davidii* (Tallent-Halsell & Watt 2009) and *U. dioica* by *I. glandulifera* (Beerling & Perrins 1993) along some European riparian areas could be explained by the early competitive superiority of the considered exotic invasive species. In addition, the selected herbaceous species are more competitive than the selected woody species, especially tree seedlings. Such competition effects have been the focus of several studies that highlighted an inhibition of exotic tree seedling development by native grasses (e.g. Facelli & Pickett 1991; Gordon & Rice 2000), or the reduction of native tree regeneration by competition with exotic grasses (e.g. Miller et al. 2010; Ortega-Pieck et al. 2011). In our study, both exotic and native grasses had a negative effect on the biomass production of exotic and native tree seedlings. While such conclusions from young individuals do not prejudge the competitive abilities of adults, the results have strong ecological implications, through the modulation of resistance to the invasion process in the context of riparian plant succession.

Dominant plant species, whether native or invasive exotic, strongly modulate species interactions and community composition (Hillebrand et al. 2008). Invasive species are considered more deleterious to communities than dominant natives, although evidence for this is rare (but see Hovick et al. 2011). In our study, the higher competitive ability of the selected invasive exotics during earlier stages of development suggest that they could increase the competitive pressure and decrease the community diversity when they replace dominant natives. In turn, the high competitive ability of some dominant native species also raises the question of the diversity of their associated community. For example, some studies mention large and almost monospecific stands of well-developed *U. dioica* along riparian corridors (e.g. Taylor 2009), comparable to monospecific stands of invasive exotic species. Even if better competitors, the selected invasive exotics could thus have low effects on species diversity of communities previously dominated by highly-competitive natives (e.g. Houlahan & Findlay 2004; Hejda et al. 2009).

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Supporting Information

Additional supporting information may be found in the online version of this article:

Resource S1. Number of replicates considered in the experiment.

Resource S2. Mortality monitoring.

Resource S3. Summary of the ANOVA on intra-specific combination data.

Resource S4. Summary of the ANOVA on inter-specific combination data.