Exotic tree seedlings are much more competitive than natives but show underyielding when growing together

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Abstract

Aims

Invasive species continue to be a worldwide threat to ecosystems mainly as a cause for biodiversity loss. Forest ecosystems, for example, are subject to a change in species composition due to the invasion of exotic species. Specifying the attributes that cause the strong competitiveness of several exotic species may improve the ability to understand and effectively manage plant invasions in the future. In this study the following hypotheses were tested: (1) biomass production of below- and aboveground plant components of the exotic tree species is higher than that of the natives, resulting in a higher competitiveness of the exotics; (2) the exclusion of root competition has a positive effect on the biomass production of the inferior native species; and (3) mixtures of native and exotic species yield a higher biomass production than the respective monocultures.

Methods

A pot experiment, containing about 2000 tree seedlings, was established. We investigated the biomass productivity and growth reactions of two native (*Quercus robur* L., *Carpinus betulus* L.) and two exotic tree species (*Prunus serotina* Ehrh., *Robinia pseudoacacia* L.) in different intra- and interspecific, competitive situations with and without the influence of root competition.

Important Findings

The biomass production of both exotic species was significantly higher and led to a strong competitive advantage, resulting in a biomass decrease of the less competitive native species. The high belowground biomass of both exotic species had a negative effect on the biomass production. The competitive pressure of exotic tree seedlings on the native ones was largely driven by root competition. Furthermore, mixtures of native and exotic tree species had a higher productivity than their growth in monocultures would have predicted. Competition was lower for exotic species in mixtures with the less productive native species compared to the competition in monocultures or in mixture with the other highly productive exotic species. Accordingly, both highly competitive exotic species produced less biomass in mixture with each other compared to monocultures. Despite the significantly higher biomass of *P. serotina* in all mixtures and in monoculture, *R. pseudoacacia* seemed to be the dominating species. Due to its strong root competition, *R. pseudoacacia* significantly reduced the biomass production of *P. serotina*.

Keywords: competition • biomass production • pot experiment • invasive species • *Prunus serotina* • *Robinia pseudoacacia*

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INTRODUCTION

The invasion of exotic species is regarded as one of the main reasons for changing natural plant communities and biodiversity loss worldwide. By means of human influence, a lot of invasive exotic species have successfully established in several regions across Europe in the last century (Kowarik 2010). The highly competitive invaders are not necessarily

also the dominant species in their native range (Callaway and Ascehoug 2000). Once established, however, invasive species can cause silvicultural management problems by displacing native species and possibly altering ecosystem functions (Ammer *et al*. 2011). Distinguishing the specific traits causing their high competitiveness compared to native species could improve the ability to effectively manage plant invasions in the future. But the traits causing the observed predominance of invasive species on co-occurring native species are often still unknown. There are a lot of studies trying to identify the attributes that enable a species to invade a new habitat (e.g. Alpert *et al*. 2000; Bray *et al*. 2003; Callaway and Aschehoug 2000; Closset-Kopp *et al*. 2007; Williamson and Fitter 1996). In addition to various dispersal-based characteristics (Rejmanek and Richardson 1996), other morphological attributes like biomass production, growth rate and leaf area may also play an important role for tree invasions (Lamarque *et al*. 2011; Pyšek and Richardson 2008; Williamson and Fitter 1996). One advantage for the success of invasive exotic species in new ecosystems may be a better response to unused resources (e.g. light, nutrients) followed by a higher biomass productivity compared to native species. Gurevitch *et al*. (2008) supported this assumption by studying relative growth rates of different exotic woody species, which showed highest relative growth rates in gaps with good light conditions and on fertile soils. Accordingly, Morrison and Mauck (2007) found for *Acer platanoides* L., an important invasive tree species in North America, that its seedlings produce more leaves and have a higher root biomass compared to the native maple *Acer saccharum* Marsh., and assumed this to be an explanation for the success of *A. platanoides*.

To describe the effects of competition between native and exotic species more precisely, interactions between plants should be studied by distinguishing between belowground and aboveground competition. Root competition is an important and sometimes dominant factor in plant communities (Casper and Jackson 1997; Schenk 2006; Wilson 1988) and involves more neighbors and resources (water, several essential mineral nutrients) than does aboveground competition, which is mainly based on light availability (Casper and Jackson 1997). The intensity of root competition imposed by the dominant species is one factor determining the growth and survival of adjacent trees (Coomes and Grubb 1998). However, only few studies investigated the importance and intensity of root competition between different tree species in forests stands (Bi *et al*. 1992; Casper and Jackson 1997; Fredericksen and Zedaker 1995; Leuschner *et al*. 2001; Meinen *et al*. 2009). For instance, Leuschner *et al*. (2001) found that the highly competitive beech (*Fagus sylvatica* L.) suppresses the growth and vitality of admixed oaks (*Quercus robur* L.) belowground. The strong competitiveness of beech trees in mixtures resulted in a remarkable decrease of the oak's fine-root biomass. In the study presented here, we hypothesized that the exotic species have similar negative effects on the growth of the native species.

Apart from individual plant growth, interactions in species mixtures, based on competition and facilitation, have an important influence on the individual plant survival and growth. Niche partitioning allows species to share the same resources and to coexist. Positive interactions between species can result in an increasing biomass production of one of the species or of the species collective as a whole. Possible explanations for this higher biomass production are a reduction of competition in species mixtures compared to monocultures due to complementarity effects, on the one hand, and facilitation, i.e. one species has a beneficial effect on the growth of another species, on the other (Kelty 1992; Pretzsch and Schütze 2009). While aboveground productivity of grasslands usually increases with increasing species diversity (e.g. Dybzinski *et al*. 2008; Hector *et al*. 1999; Tilman *et al*. 1996), studies regarding the influence of tree species diversity on the productivity of forests show inconsistent results. Some tree species mixtures yielded a higher biomass production than did monocultures (Bauhus *et al*. 2000; Brown 1992; Erskine *et al*. 2006; Pretzsch *et al*. 2010; Vilà *et al*. 2007), whereas others result in similar (Vilà *et al*. 2003) or even lower biomass production (Jacob *et al*. 2010; Szwagrzyk and Gazda 2007). As Pretzsch *et al*. (2010) showed, site productivity does strongly influence the diversity–productivity relationship. So far, the question whether mixing tree species increases productivity (Cardinale *et al*. 2007; Hector 2006; Pretzsch and Schütze 2009) in managed forests or in biodiversity experiments has not been conclusively answered. However, focusing on mixtures between native and exotic species may help to disentangle the complex interactions between tree species. Thus, the traits leading to over- or underyielding might be more striking in such mixtures than in mixtures having a long history of coevolution.

The aim of our study was to evaluate the predominance of the two North American species, black cherry (*Prunus serotina* Ehrh.) and black locust (*Robinia pseudoacacia* L.), which have effectively invaded many European forest ecosystems (e.g. Annighöfer *et al*. 2012; Closset-Kopp *et al*. 2011; Kleinbauer *et al*. 2010; Motta *et al*. 2009; Starfinger *et al*. 2003). The study site of our research group, the biosphere reserve 'Valle del Ticino' in Northwestern Italy, represents such an area that is affected by these species. Since the two exotic tree species were introduced to the area during the end of the 19th century, their abundance has strongly increased, so that the integrity of the forest ecosystem is endangered at present (Annighöfer *et al*. 2012). In Europe, *P. serotina* and *R. pseudoacacia* are invasive exotic species (Kowarik 2010) that have established and are regarded as strong competitors of native tree species (e.g. Closset-Kopp *et al*. 2011; González-Muñoz *et al*. 2011; Kleinbauer *et al*. 2010; Vanhellemont *et al*. 2010). Both species were introduced to Europe for various reasons, e.g. timber production, soil improvement and fire prevention (Godefroid *et al*. 2005; Knight *et al*. 2008; Motta *et al*. 2009). Due to its great competitiveness, *P. serotina* displaces local species and thus is considered to be invasive (Closset-Kopp *et al*. 2007);

it is even referred to as an 'aggressively spreading species' (Knight *et al.* 2008; Starfinger *et al.* 2003). As a nitrogen-fixing species, *R. pseudoacacia* changes soil conditions and species compositions on many sites (Motta *et al.* 2009; Rice *et al.* 2004).

In our study, the growth reactions of two native (*Quercus robur* L. and *Carpinus betulus* L.) and two exotic (*P. serotina* and *R. pseudoacacia*) tree species in different inter- and intraspecific competitive situations were investigated under the controlled conditions of a pot experiment. The different tree species were arranged in monocultures and two-species mixtures. The following hypotheses were tested: (1) biomass production of below- and aboveground plant components of the exotic tree species is higher than that of the natives, resulting in a higher competitiveness of the exotics; (2) the exclusion of root competition has a positive effect on the biomass production of the inferior species; and (3) mixtures of native and exotic species yield a higher biomass production than the respective monocultures.

METHODS

Experimental set-up

The pot experiment was conducted under outdoor conditions in Göttingen, Germany. The experimental site was located at 170 m above sea level. The climate is temperate with an average annual precipitation of 644.9 mm and most of the rain falling in June (81.3 mm). The temperature ranges from 4.8 to 13°C with a mean annual temperature of about 8.7°C. To ensure comparability with the vegetation of the biosphere reserve 'Valle del Ticino', tree species were used that are typical for the vegetation found in the reserve: pedunculate oak (*Q. robur*) and hornbeam (*C. betulus*) as native species, black cherry (*P. serotina*) and black locust (*R. pseudoacacia*) as exotic species. In order to use already established plants and to minimize transport-induced damages, all trees were about 1 year old and originated from a nursery in Germany (Münchehof, Lower Saxony), where all plants had grown under homogenous conditions. In spring 2010, the seedlings were planted into pots (volume 65 l, diameter 54 cm, height 33 cm). The pots were filled with fertilized potting soil (Einheitserde- und Humuswerke, Gebr. Patzer GmbH & Co. KG, Sinntal-Jossa/Germany, type Eurohum CRH) above a 5-cm layer of coarse gravel to improve drainage. We used potting soil to ensure homogeneous substrate and nutrient conditions in all pots. The tree seedlings were watered as needed with all pots receiving the same amount of water. Excess water was drained through holes in the bottom of the pots. During winter, the pots were arranged close to each other and embedded in foliar litter to prevent frost damage to the roots. All pots were placed randomly on the area to avoid edge effects. The plants were examined during two growing periods lasting from April 2010 to October 2011.

Four seedlings were planted per pot and arranged in 10 different species mixtures, of which 4 were monocultures and 6

were species mixtures. The species mixtures consisted of not more than two species and were: (1) *Q. robur* with *C. betulus*, (2) *R. pseudoacacia* with *P. serotina*, (3) *Q. robur* with *R. pseudoacacia*, (4) *Q. robur* with *P. serotina*, (5) *C. betulus* with *R. pseudoacacia* and (6) *C. betulus* with *P. serotina*. There were 36 replicates for the monoculture pots and 60 replicates for each of the six species mixtures. Pots with dead seedlings were excluded from further analyses, since even one dead plant per pot would have changed the competitive situation compared to those pots containing four plants. This reduced the number of pots from 504 to 201 (Table 1).

In the study area, *P. serotina* and various shrubs create quite shady conditions in the understorey. Thus, *Q. robur* and *C. betulus* seedlings can hardly be found, even under a loose canopy of mature oak trees in the overstorey. Since *Q. robur* is a shade-intolerant species and we did not want to reduce its competiveness by shade, the study was carried out under full light. Nevertheless, the growing conditions for all individuals and all species were similar.

Competition treatments

To study the competitive mechanisms in more detail, root and shoot competition were investigated using a modified 'divided pot technique' (Donald 1958; McPhee and Aarssen

Table 1: amount of pots per mixture type and treatment at the beginning (intended) and at the end (effective) of the pot experiment. The treatments were RC and nRC. Mortality reduced the amount of replicates. All pots contained four plants

Species composition	Treatments	Replicates	
		Intended	Effective
Monoculture *Q. robur*	RC	24	18
	nRC	12	6
Monoculture *C. betulus*	RC	24	15
	nRC	12	8
Monoculture *R. pseudoacacia*	RC	24	11
	nRC	12	7
Monoculture *P. serotina*	RC	24	5
	nRC	12	6
Mixture of *Q. robur* with *C. betulus*	RC	40	20
	nRC	20	16
Mixture of *R. pseudoacacia* with *P. serotina*	RC	40	8
	nRC	20	4
Mixture of *Q. robur* with *R. pseudoacacia*	RC	40	14
	nRC	20	9
Mixture of *Q. robur* with *P. serotina*	RC	40	11
	nRC	20	5
Mixture of *C. betulus* with *R. pseudoacacia*	RC	40	16
	nRC	20	7
Mixture of *C. betulus* with *P. serotina*	RC	40	12
	nRC	20	3
Amount of pots		504	201

2001; Snaydon 1971). All tree seedlings were distributed to root, shoot and full competition treatments. We installed aboveground partitions allowing only root competition, and belowground partitions allowing only shoot competition. The above- and belowground partitions were made of white rigid PVC sheets. White aboveground partitions reflected the sunlight and thus leveled the light conditions on all four sections of the pot. In our experiment, shoot competition had no significant effect on tree growth (data not shown). However, if the two treatments in which the seedlings were exposed to root competition (i.e. root and full competition) were pooled and compared with the treatment excluding root competition (i.e. shoot competition), for *C. betulus* ($P = 0.03$) and *P. serotina* ($P = 0.02$) an effect of root competition was found (Table 3). In the following, we therefore contrast 'root competition' (RC) with 'no root competition' (nRC). The number of pots per mixture type and treatment is shown in Table 1.

Measurements

To assess the initial dry weight of each species, a random sample of 10 plants per species was collected at the beginning of the experiment. To assess the dry weight at the end of the experiment, all pots with four living plants were harvested resulting in a total of $n = 804$ trees, of which $n = 246$ were *Q. robur*, $n = 240$ were *C. betulus*, $n = 188$ were *R. pseudoacacia*, and $n = 130$ were *P. serotina* seedlings. The biomass of every tree seedling, both at the beginning and at the end of the study, was assigned to one of the four tree components: main shoot, branches, roots or leaves. The dry weight of all four biomass categories was determined separately by drying for 3 days at 70°C in a temperature-controlled oven until a constant weight was achieved. The tree components were then weighed with an accuracy of 0.001 g.

Data analysis

In order to facilitate the comparison of our findings with other studies on biomass productivity in monocultures and species mixtures, we were interested whether or not pattern of over- and/or underyielding might be observed when analysing the different mixtures. A mixture is showing 'overyielding' if the yield of the mixture is greater than expected based on a weighted average of the monoculture yields of the component species, i.e. $p_{1,2} > (m_1 \cdot p_1 + m_2 \cdot p_2)$ (see Pretzsch 2005). In our experiment, only balanced two-species mixtures were used, i.e. every species in a mixture had a proportion of 50%. Thus, no weighing of species share was necessary. According to the definition of overyielding, 'underyielding' indicates a negative interaction. Over- and underyielding were calculated by

$$\Delta p_{rel} = [p_{1,2} / (m_1 \cdot p_1 + m_2 \cdot p_2) - 1] \cdot 100, \qquad (1)$$

where $p_{1,2}$ is the dry mass of the mixture, p_1 and p_2 are the dry biomass productivities of species 1 and 2 in monocultures, and m_1 and m_2 are the proportions of species 1 and 2 in the mixture.

The so-called transgressive overyielding of the mixture occurs if biomass productivity of a mixture outperforms even the yield of the most productive monoculture of the species involved. Thus, transgressive overyielding is characterized by $p_{1,2} > \max(p_1, p_2)$ (see Pretzsch 2005). Accordingly, transgressive overyielding was calculated as

$$\Delta p_{abs} = [p_{1,2} / \max(p_1, p_2) - 1] \cdot 100 \qquad (2)$$

and transgressive underyielding was calculated as

$$\Delta pabs = [p_{1,2} / \min(p_1, p_2) - 1] \cdot 100. \qquad (3)$$

All statistical tests and graphs were conducted using the free software environment R (R Development Core Team 2012). The Shapiro–Wilk normality test was used to analyse data distribution. To assess homoscedasticity, we used Levene's test. If data showed a normal distribution and if the variances were homogenous, we used an analysis of variance (ANOVA) and Tukey range test to find significant differences between groups. If data could not be assumed to be normally distributed and/or did not show homoscedasticity, we used the Kruskal–Wallis test and applied pairwise comparisons with Wilcoxon rank sum test. All tests comparing groups were two-sided.

# RESULTS

Biomass and allocation

The woody biomasses per plant at the beginning of the pot experiment differed considerably between the four species (Table 2) even though the individuals of all species were of the same age (1 year old). Total biomass (i.e. root, shoot and branch biomass) of *Q. robur* was highest, followed by *R. pseudoacacia*. Both species had significantly higher initial biomasses than had *C. betulus* and *P. serotina*. Initial belowground biomass of *Q. robur* was also significantly higher (8.41 g) than that for all other species. In contrast, *C. betulus* had the lowest aboveground, belowground and total biomass.

Woody biomass per plant in monocultures at the end of the pot experiment was significantly lower for both native species, *Q. robur* and *C. betulus*, compared to the exotic species,

Table 2: mean total, aboveground (shoot and branches) and belowground (root) biomass at the beginning of the pot experiment (spring 2010). Different characters indicate significant differences between the species ($P < 0.05$, Wilcoxon rank sum test, two-sided)

Species	n	Total biomass (g)	Aboveg round biomass (g)	Below ground biomass (g)
Q. robur	10	14.17[a]	5.76[a]	8.41[a]
C. betulus	10	6.82[b]	2.47[b]	4.36[bc]
R. pseudoacacia	10	11.63[a]	6.67[a]	4.96[b]
P. serotina	10	7.70[b]	3.55[c]	4.14[c]
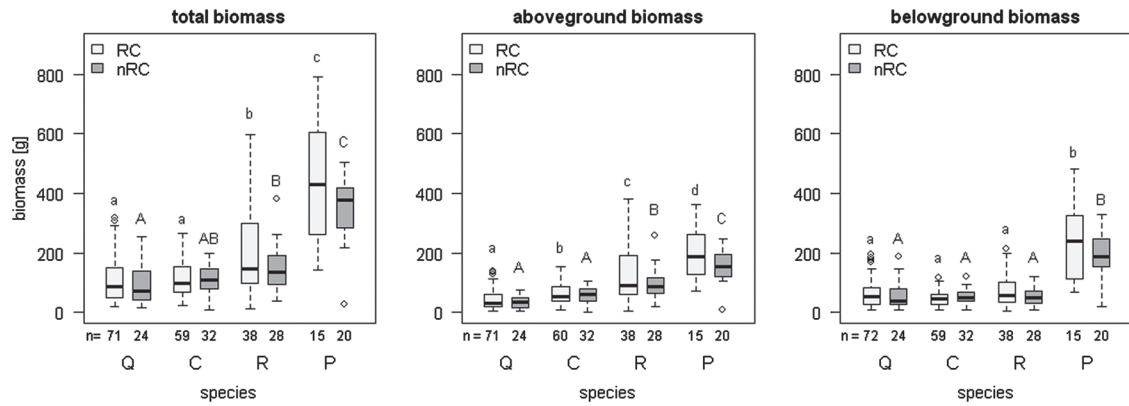
Figure 1: boxplots of total, aboveground (shoot and branches) and belowground (roots) biomass per single plant. Biomasses are given for the end of the pot experiment (autumn 2011) in RC and nRC monocultures. Horizontal lines in each box represent medians. Different characters above each box indicate significant differences between the species in RC (small characters) and nRC (capital characters) ($P < 0.05$, ANOVA and Tukey test). Q = *Q. robur*, C = *C. betulus*, R = *R. pseudoacacia*, P = *P. serotina*.

P. serotina and *R. pseudoacacia* (Fig. 1). The initial biomass of *P. serotina* was very low (Table 2). Nevertheless, this species produced a total biomass that was 3.5 times higher than that of *Q. robur* and *C. betulus*. Even compared to *R. pseudoacacia*, the total biomass of *P. serotina* was more than twice as high. In comparison with all other species, *P. serotina* showed a significantly higher belowground biomass (213.03 g). The belowground biomasses of *Q. robur*, *C. betulus* and *R. pseudoacacia* (62.64, 49.70 and 67.46 g, respectively) did not differ significantly (Fig. 1). In contrast, significant differences between all species growing in monoculture were found for their aboveground biomasses (Fig. 1). Overall, the biomasses of the exotic species were much higher than those of the native species. No significant differences between RC and nRC were found in the monocultures.

Biomass production per plant was different for all species depending on whether they grew in monocultures or in different species mixtures (Table 3, Fig. 2). While *Q. robur* yielded the same plant biomass regardless of growing in monoculture or in mixture with *C. betulus*, biomass production of *C. betulus* increased in mixture with *Q. robur* in both competition treatments (Fig. 2). The exotic species had a strongly negative effect on the mean plant biomass production of both native species (Table 3, Fig. 2). The biomass of the two native species was up to 4.5 times lower in mixtures with *P. serotina* or *R. pseudoacacia* than in monocultures (Table 3, Fig. 2). In mixture with *R. pseudoacacia*, *Q. robur* showed a slightly higher total biomass in the nRC treatment (36.98 g and 26.03 g in RC, respectively, $p = 0.10$, ANOVA). This effect was even more apparent in mixtures of *C. betulus* with one of the exotic species. In the nRC treatment, the biomass of *C. betulus* mixed with *R. pseudoacacia* or with *P. serotina* was higher than in the RC treatment (42.86 g and 24.51 g in mixture with *R. pseudoacacia*, $P = 0.04$, Kruskal–Wallis test; 77.46 g and 26.84 g in mixture with *P. serotina*, $P = 0.02$, Kruskal–Wallis test). Consequently, the proportion of *C. betulus* on total pot biomass differed between RC and nRC (7% and 13% if mixed with *R. pseudoacacia*; 5% and 19% if mixed with *P. serotina*; $P = 0.04$ and $P < 0.001$, Table 3).

Table 3: percentage of total pot biomass for monocultures and species mixtures distinguished between RC and nRC. Different characters indicate significant differences between the two treatments ($P < 0.05$, ANOVA and Kruskal–Wallis test). Mean plant biomass and significant differences between the species mixtures are shown in Fig. 2.

| Species			Mixed with			
			Q. robur	C. betulus	R. pseudoa-cacia	P. serotina
Q. robur	% of pot biomass	RC	—	41	8	4
		nRC	—	36	11	4
C. betulus	% of pot biomass	RC	59	—	7[a]	5[a]
		nRC	64	—	13[b]	19[b]
R. pseudoa-cacia	% of pot biomass	RC	92	93[a]	—	46
		nRC	89	87[b]	—	38
P. serotina	% of pot biomass	RC	96	95[a]	54	—
		nRC	96	81[b]	62	—

While the mean plant biomass of the two exotic species increased if mixed with *Q. robur* or *C. betulus* (see above), only *R. pseudoacacia* was able to yield the same biomass if the two exotic species were mixed (Table 3). Overall, the mean plant biomass of *R. pseudoacacia* was higher in all mixtures if root competition was not excluded (Table 3). The same is true for *P. serotina*, except if mixed with *R. pseudoacacia*. Mean plant biomass of *P. serotina* was significantly lower in mixture with *R. pseudoacacia* than in monoculture, in nRC ($P = 0.02$, ANOVA) but even more in RC ($P < 0.001$, ANOVA) (Fig. 2). The biomass proportion per pot of *P. serotina* decreased from 62% in RC to 54% in nRC. Thus, even though *P. serotina* in mixture with *R. pseudoacacia* contributed more to the total pot biomass (see Fig. 4), the mean plant biomass was much lower than in monoculture or in mixtures with the two native species.
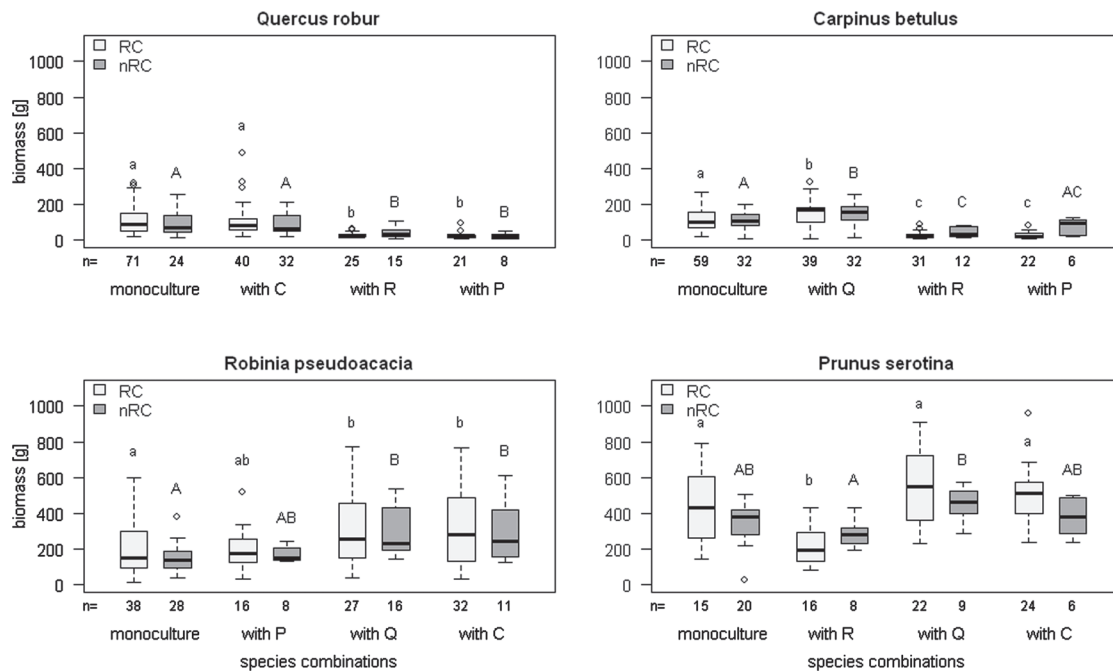
Figure 2: boxplots of mean biomass per plant for the different mixtures with (RC) and without (nRC) root competition. Horizontal lines in each box represent medians. Different characters over each box indicate significant differences between the species mixtures in RC (small characters) and nRC (capital characters) treatment ($P < 0.05$, ANOVA and Tukey test). Q = *Q. robur*, C = *C. betulus*, R = *R. pseudoacacia*, P = *P. serotina*.
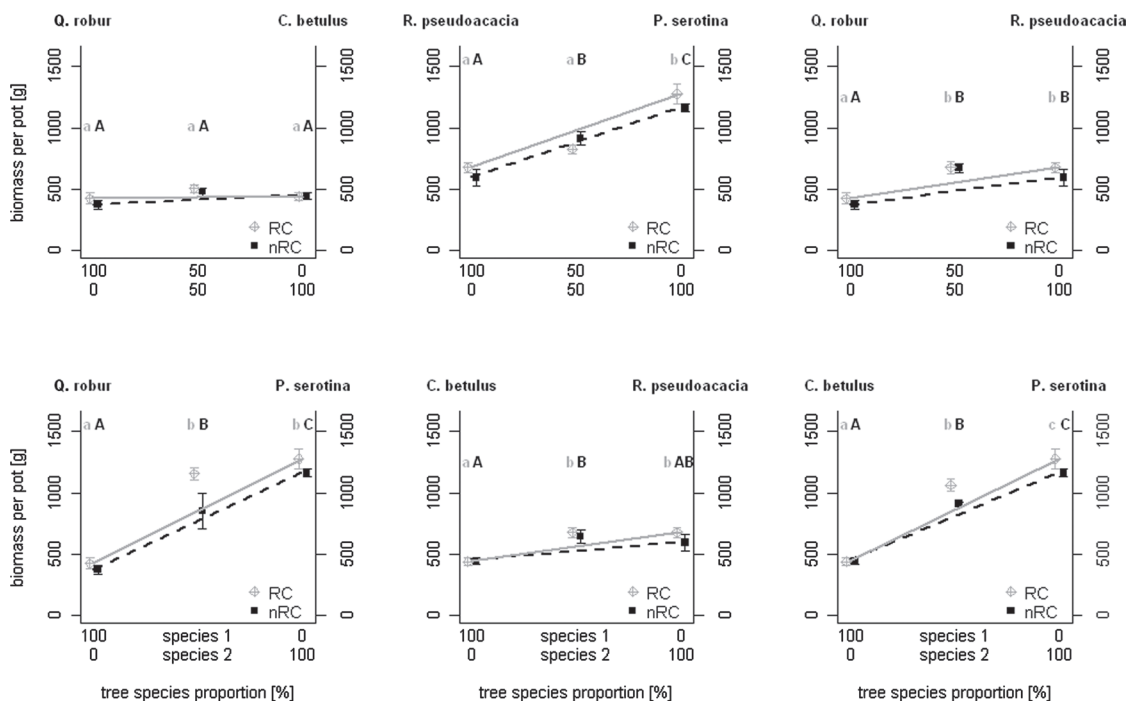
Figure 3: mean total biomass production per pot in monocultures and mixtures with (RC) and without (nRC) root competition. Dots show mean values ± SE. Dots on the left and right y-axes show the biomass production of two different species in monoculture. The dashed lines show the expected biomass productivity in mixture with neutral interactions between the two species (P_{exp}). Different characters above each boxplot indicate significant differences between the species monocultures or mixtures in RC (small characters) and nRC (capital characters) treatment ($P < 0.05$, ANOVA).
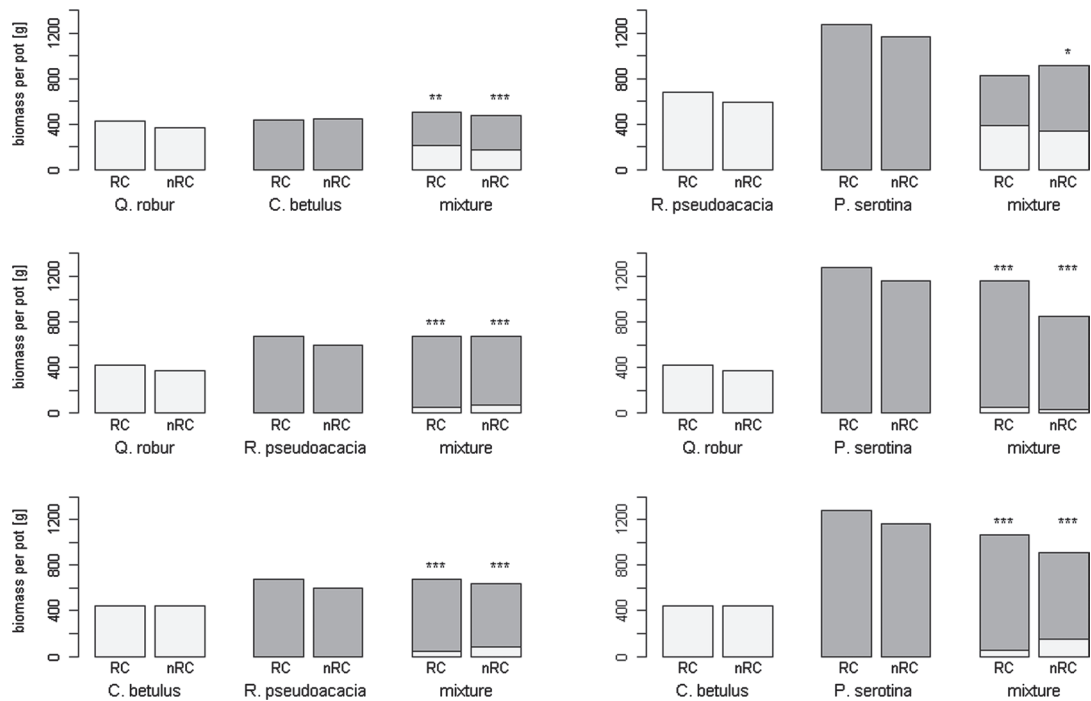
Figure 4: the first four bars in every figure show the mean biomass per pot of a given species in monoculture; the last two bars represent the proportion of the different species to total biomass in mixtures. Data are given for treatments with (RC) and without (nRC) root competition. Asterisks show significant differences between proportions of the different species in mixtures (ANOVA; *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Biomass productivity of monocultures vs. mixtures

Total pot biomass differed between mixtures and monocultures (Fig. 3). Independent of treatment or species mixture, *Q. robur* had the lowest pot biomass (Table 3, Figs 3 and 4). The highest productivity was observed for *P. serotina* monocultures (Figs 3 and 4). Only in one case we observed an underyielding of productivity, i.e. in the mixture of *R. pseudoacacia* and *P. serotina* exposed to RC (Fig. 3, Table 4). This mixture produced 15.15% less biomass than expected if no interaction had taken place (i.e. [P_{exp} = productivity$_{species\ 1}$ in monoculture + productivity $_{species\ 2}$ in monoculture]/2). The mean biomass of *P. serotina* in monoculture pots was approximately twice as high as the biomass of *R. pseudoacacia*. Biomass production per pot of the mixture of both exotic species was higher in the nRC than in the RC treatment, but the opposite was found in monocultures (Fig. 3). In all other mixtures, an overyielding of biomass productivity was found; three mixtures even showed transgressive overyielding (Table 4). Overyielding of all other mixtures compared to the expected productivity (P_{exp}) and the more productive monoculture ranged up to 38.75% for the mixture of *Q. robur* with *P. serotina* (nRC treatment, Table 4). The total pot biomasses of mixtures of *Q. robur* with *C. betulus*, *Q. robur* with *R. pseudoacacia*, and *C. betulus* with *R. pseudoacacia* were even higher than the biomass of the most productive monoculture, indicating transgressive overyielding. In all cases where

exotic and native species were mixed, the exotic species were much more productive (Fig. 4). In general, mixtures of one native and one exotic species led to relative or even absolute biomass overyielding.

Table 4: non-transgressive and transgressive overyielding/ underyielding of mixtures with (RC) and without root competition (nRC). Relative percentage (Δp_{rel} [%]) shows the higher (positive values) or smaller (negative values) productivity of mixtures compared to the expected productivity calculated as the average of the two monocultures. Absolute percentage (Δp_{abs} [%]) refers to the productivity of the more productive species of a given mixture and shows transgressive overyielding of mixtures

Mixture of	More productive species	RC		nRC	
		Δp_{rel} (%)	Δp_{abs} (%)	Δp_{rel} (%)	Δp_{abs} (%)
Q. robur with *C. betulus*	*C. betulus*	15.49	14.61	17.26	7.45
R. pseudoacacia with *P. serotina*	*P. serotina*	-15.15	—	4.03	—
Q. robur with *R. pseudoacacia*	*R. pseudoacacia*	22.49	0.46	38.75	12.69
Q. robur with *P. serotina*	*P. serotina*	35.38	—	10.87	—
C. betulus with *R. pseudoacacia*	*R. pseudoacacia*	21.20	0.01	23.36	7.93
C. betulus with *P. serotina*	*P. serotina*	23.81	—	0.85	—

DISCUSSION

Are exotic species more competitive due to a higher productivity?

Many studies suggest a better competitiveness of exotic tree and herbaceous species compared to native plants under adequate environmental conditions (Fuentes-Ramirez et al. 2011; Gorchov and Trisel 2003; Hager 2004; Littschwager et al. 2010; Osunkoya et al. 2005). Generally, invasive species, like P. serotina, are thought to be characterized by certain biological features giving them at least short-term advantages over native species. The predominance of invasive exotic species over native species is mainly related to a higher biomass production. Many studies confirmed biomass productivity being the most important attribute of highly competitive exotic tree species (e.g. Gyenge et al. 2008; Heidingsfelder and Knoke 2004; Hildebrandt et al. 2009; Lamarque et al. 2011). Like in other studies (e.g. Closset-Kopp et al. 2007; Lee et al. 2004), the two exotic species, P. serotina and R. pseudoacacia, showed a significant higher biomass production compared to the native species, Q. robur and C. betulus, in our experiment. According to MacArthur and Wilson (2001), high growth rates, especially during the first years of life, are a typical attribute of r-strategists, which generally dominate plant communities in early successional stages (Closset-Kopp et al. 2007). However, P. serotina seems to be able to ensure a permanent existence being adapted to various stages of succession (Closset-Kopp et al. 2007). Due to their fast growth combined with high fecundity, exotic species, like P. serotina, are able to rapidly occupy new habitats, giving inferior native species no chance to establish (Closset-Kopp et al. 2011). Another important characteristic of P. serotina seedlings is their ability to survive under shady conditions under closed canopies ('Oskar syndrome') and to grow rapidly when light conditions improve (Closset-Kopp et al. 2007; Silvertown 1984). Hence, on the one hand, P. serotina behaves as a shade-tolerant K-strategist focusing on persistence in juvenile stages. On the other hand, this species seems to be a superior competitor in gaps by shifting towards fast growth responses and reproduction (r-strategist). This combination of traits may explain the high competitiveness and invasiveness of P. serotina. Other invasive exotic species, such as Acer platanoides in North America or Ailanthus altissima Mill. Swingle and R. pseudoacacia in Europe, are known to behave alike (Closset-Kopp et al. 2007). In contrast to P. serotina, R. pseudoacacia is characterized as shade-intolerant (Motta et al. 2009; Rédei et al. 2012), but also has a rapid juvenile growth particularly under high light levels (González-Muñoz et al. 2011; Lee et al. 2004; Nasir et al. 2005).

In our experiment, it was evident that the exotic species had a strong negative impact on the growth of native species (Table 3, Fig. 4). Mean plant biomass of both native species decreased significantly when growing together in one pot with P. serotina or R. pseudoacacia. Interspecific competition with the exotic species had a much stronger influence on mean plant biomass than had interspecific competition

with the other native species. The most evident reason for the superiority of the two exotic species in our experiment was their significantly higher biomass productivity resulting in a much higher competitiveness compared to Q. robur and C. betulus.

Does root competition affect biomass production of the inferior species?

Root competition affects plant growth in positive ways through niche partitioning and facilitation, but also in negative ways through competitive exclusion (Berendse 1982; Rajaniemi 2003; Silvertown 2004). Vertical belowground niche partitioning, i.e. the variation of the rooting depths, could not be studied here due to the limited pot height (33 cm). However, biomass production of the inferior species was lower when root competition by the exotic species took place, which may indicate competitive exclusion, simply by affecting space occupation. Hence, root competition seems to have an important influence on plant interactions for the studied species. Accordingly, Leuschner et al. (2001) assumed that the amount of belowground biomass of the superior competitor has a negative correlation to tree growth and vitality of inferior species in species mixtures. The strong competitiveness of the superior species led to a substantial decrease of the root biomass of the less competitive species. Similarly, in our study, the high competitive exotic species had negative effects on the biomass production—belowground as well as aboveground—of the native species. In mixtures with the native species, R. pseudoacacia as well as P. serotina had a significantly higher belowground biomass compared to monocultures. The two exotic species enhanced root growth in mixtures in order to pre-occupy the rooting space. Other studies found that competitive species are able to increase their fitness by growing roots into the soil shared with another co-occurring species. This does not only lead to an additional acquisition of resources from that space but also to a decreasing fitness of the competitors by reducing their resource supply (Aerts et al. 1991; Robinson et al. 1999). In our experiment, most of the available rooting capacity per pot was occupied by the exotic species. The two native species, Q. robur and C. betulus, only had limited access to free resources, resulting in reduced biomasses in mixtures with exotic species. Accordingly, Rewald and Leuschner (2009) found that Q. robur and C. betulus had the lowest belowground interspecific competitive ability compared to other native tree species. In the nRC treatment, inferior species were spatially separated belowground from the superior competitors. Rooting capacity of every tree was limited to one-fourth of the pot volume due to installed partitions, which had a negative effect on the growth of both exotic species. Our results showed that the inferior species managed to increase their biomass production when root competition was excluded. Thus, even a limited rooting volume seemed to provide better growing conditions than direct root interactions by superior competitors.

Do species mixtures produce more biomass than monocultures?

In accordance with other studies (e.g. Bauhus *et al.* 2000; Brown 1992; Erskine *et al.* 2006; Pretzsch *et al.* 2010; Vilà *et al.* 2007), we found that species mixtures are more productive than are monocultures. Various reasons for this phenomenon, like niche partitioning and hence complementary resource use and facilitation, have been discussed in literature (Fridley 2001; Hector *et al.* 2002; Kelty 2006; Perot and Picard 2012; Pretzsch and Schütze 2009).

Mixtures of the two native species and mixtures of the native species with *R. pseudoacacia* showed transgressive overyielding, which means that the biomass production of the mixture was higher than that of the more productive species. In contrast, mixtures of both native species with *P. serotina* only resulted in non-transgressive overyielding. Thus, *P. serotina* was so much more productive in monoculture that the loss of total biomass, caused by the admixed native plants, was not counterbalanced by the remaining individuals. According to Loreau (2004), transgressive overyielding occurs if interspecific competition for both species is lower than intraspecific competition due to 'competitive reduction', i.e. the two species are subjected to reduced competition in mixture compared to monocultures (Pretzsch and Schütze 2009). However, in our study, in mixtures interspecific competition was lower than intraspecific interference for the exotic but not for the native species. Thus, transgressive overyielding may even occur if just one species in a mixture benefits from reduced intraspecific competition. For both native species, interspecific interactions with an exotic species had a stronger negative impact on biomass production than had intraspecific competition or interference by the other native species.

Even though *Q. robur* and *C. betulus* did not contribute to overyielding, they seemed to have a stimulating effect on the two exotic species based on their low competitiveness. Forrester *et al.* (2007) found the biomass production of the mixture of *Eucalyptus globulus* Labill. and *Acacia mearnsii* de Wildeman to be twice as high compared to monocultures of the two species growing on the same sites. The authors explained their finding with the nitrogen fixation of *A. mearnsii*. Therefore, it was expected that *R. pseudoacacia*, being also a nitrogen-fixing species, facilitates the growth of all other species in mixture by changing the soil conditions, causing overyielding in species mixtures (Forrester *et al.* 2006; Huston *et al.* 2000; Kowarik 2010). However, we found the opposite. In our pot experiment, *R. pseudoacacia* had always a negative impact on mean plant biomass of the admixed species. Mean plant biomass of *P. serotina* and the two native species was even lower in the RC treatment, which allowed root interactions. A possible explanation for not observing growth improvement by *R. pseudoacacia* may be that the soil used for the pot experiment was already fertilized with nitrogen. Hence, nitrogen may not have been the limiting resource. Bauhus *et al.* (2000) gave examples where nitrogen-fixing species have suppressed the growth of the admixed species.

If not nitrogen but other resources like phosphorus or water are limited, the nitrogen-fixing species have to compete for these resources, and thus there will be a shift from facilitation to competition.

In our experiment, only the mixture of the two exotic species, *R. pseudoacacia* and *P. serotina*, together did not show a positive mixing effect on the total biomass production (Table 4, Fig. 3). Interestingly this was only the case if root competition was not excluded. Thus, in the RC treatment, biomass productivity was 15.15% less than expected (P_{exp}). The substantially lowered mean plant biomass of *P. serotina* when growing in mixture with *R. pseudoacacia* indicates a negative impact of *R. pseudoacacia* on *P. serotina* by root competition. Therefore, *R. pseudoacacia* seemed to be more effective in acquiring belowground resources if the two species grow together. However, the competitiveness of *P. serotina* compared to *R. pseudoacacia* may increase with decreasing light availability. It seems as if the ability of *R. pseudoacacia* to successfully compete for belowground resources is substantially reduced in the shade. However, this assumption could not be tested in our experiment as we could not realize another variant with reduced light. Actually, at the study site in Italy, *P. serotina* is more invasive under the canopy of overstorey trees than is *R. pseudoacacia*. Overall, the results of our study correspond quite nicely with the situation within the regeneration at the study site: the native species are much less competitive than the dominating *R. pseudoacacia* and *P. serotina* (Annighöfer *et al.* 2012).

It was evident that, in the early life stages of the investigated tree species, the native tree species are clearly inferior—especially when they are exposed to root competition by the exotic species.

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