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From facilitation to competition: the effect of black locust (*Robinia pseudoacacia* L.) on the growth performance of four poplar-hybrids (*Populus* spp.) in mixed short rotation coppice

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Abstract
Short rotation coppices play an important role in providing biomass for energetic use. Mixing fast-growing tree species in short rotation coppices may show complementarity effects and increased yield. The aim of this study was to analyze the effect of species interaction in mixed short rotation coppices with fast-growing *Populus* spp.-hybrids and the N-fixing *Robinia pseudoacacia*. Four different *Populus*-hybrids (AF2, Fritzi Pauley, Hybride 275 and Max 1), planted alternately in pure and mixed stands with *R. pseudoacacia* were used for the analysis. Height and root collar diameter were measured once a year, over a period of four years (2014–2017). Additionally, in the third year, aboveground competition was surveyed with a terrestrial laser scanner and root biomass was analyzed to assess belowground competition. Soil nitrogen was also determined in order to verify enrichment properties of mixtures compared to pure stands. *Populus*-hybrids' stem volume showed no significant differences between stand types in the first year after planting. In the second and third year, however, two *Populus*-hybrids (AF2 and Max 1) had a higher stem volume increment of up to 3.8 times than stem volume increment in pure stands. This may be related to the fact that soil nitrogen was 39% higher in the mixtures than in pure stands. However, in the 4th year after stand establishment, *R. pseudoacacia's* crowns were so massive and broad, that this species was far more competitive than the *Populus*-hybrids. With the exception of *P.* 'Fritzi Pauley', which showed no significant differences between stand types, growth rates reversed for the other three *Populus*-hybrids. AF2, Max 1 and Hybride 275 showed up to 75% lower stem volume increment in mixtures compared to pure stands. We assume that, in spite of the initially observed facilitation between the species, the competition exerted by *R. pseudoacacia* started dominating after 4 years and began to surpass the benefits of facilitation.

Keywords Short rotation coppice · SRC · Poplar · Black locust · Competition · Facilitation

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Introduction

Wood production contributes to natural decarbonisation and subsequent climate change mitigation (Canadell and Raupach 2008; Knust 2009; Parikka 2004). As a renewable source of energy, wood has great potential as a fossil fuel substitute (Demirbaş 2001). In fact, the use of woody biomass increased in Germany (Ewald et al. 2017; Gößwein et al. 2018) while cultivation in short rotation coppices rather stagnated (Wühlisch 2016). However, intensifying wood production in SRC on agricultural lands would alleviate pressure on forests and reduce the impact of extensive agricultural management on biodiversity (Butler Manning et al. 2015; Harris et al. 2017; Schmidt and Glaser 2009). Short rotation coppices (from here on referred to as SRC) are typically high-density, single-species plantings of fast-growing trees with rotation lengths of less than 20 years (Knust 2009; Stanturf and Oosten 2014). Poplar hybrids (*Populus* spp.) and black locust (*Robinia pseudoacacia* L.) are two of the most often planted tree species in SRC for energy purposes in Germany (Knust et al. 2013). *Populus* hybrids planted in SRC in Germany can reach 6–14 t ha^{-1} $year^{-1}$ of dry wood matter and *R. pseudoacacia* yields around 3–10 t ha^{-1} $year^{-1}$ in rotation periods of 3 to 10 years depending on site and water availability (Knust et al. 2013). The genus *Populus* primarily grows on moist sites like fluvial plains with seasonal flooding (Knust et al. 2013; Rennenberg et al. 2010; Richardson et al. 2014). *Populus nigra* L. and *Populus deltoides* W.Bartram ex Marschall grow mainly along rivers, streams and flood plains. *Populus trichocarpa* Torr & A.Gray ex Hook grows on a wide range of soils and topography, but also prefers soils along riverbanks. *Populus maximowiczii* A.Henry grows along mountain rivers and streams with annual rainfall ranges from 600 to 1400 mm (Richardson et al. 2014). In contrast to *Populus* sp., *Robinia pseudoacacia* does not occur in wetlands or alluvial forests. Instead, it commonly occurs in areas with 480–800 mm rainfall per year (Vítková et al. 2017). In central Europe, *Robinia pseudoacacia,* is preferably planted in regions with poor precipitation and low nutrient availability (Knust 2009; Rédei 2013). *R. pseudoacacia* is not only less demanding regarding water and nutrients than *Populus* sp., but also, as a legume tree species, has the ability to fix nitrogen and enhance soil fertility (Binkley 1992; Kanzler et al. 2020; Knust 2009; Nicolescu et al. 2018; Veste et al. 2013).

Tree species combinations with complementary ecological traits might have the potential of higher yield compared to monocultures (Pretzsch and Forrester 2017). In forest stands, both reduction in competition and facilitation have been identified as underlying processes (Forrester and Bauhus 2016). Competition reduction occurs if interspecific competition is lower than intraspecific interference, while facilitation can be observed if one species positively influences another species (Ammer 2019). For instance, mixing N-fixing tree species may be beneficial for neighboring individuals of nitrogen-demanding species (Forrester et al. 2006; Hansen and Dawson 1982; Marron and Epron 2019). Indeed, Oliveira et al. (2018) and Rédei et al. (2006) were able to prove that mixing *R. pseudoacacia* to white poplar (*Populus alba*) can increase, under certain circumstances, *Populus*' biomass growth. However, another study on *Populus* spp. ('Dorskamp', *Populus deltoides* × *Populus nigra*) and *R. pseudoacacia* mixed SRC found no advantage regarding biomass growth (Gana 2016). Thus, the traits that trigger and determine differences in productivity in mixed *Populus* sp. and *R. pseudoacacia* SRC have not yet been fully understood.

Pretzsch (2017a) pointed out the importance of studying mixing effects on an individual tree level in order to better understand "*competition, competition reduction through* *complementarity, and facilitation",* as mixing influences the environmental conditions resulting in altered tree and stand growth. It is well known that canopy structure affects light interception and carbon assimilation, which in turn have an impact on stand productivity (Broeckx et al. 2012; Forrester et al. 2018; Ishii et al. 2004; Kim et al. 2011). As a result individual tree growth is strongly depending not only on the proximity but also on the identity of the surrounding neighborhood (Fichtner et al. 2017; Metz et al. 2019; Pretzsch 2017a). Yet, it is not clear to what extent *Populus*-hybrids react differently, on the single-tree level, in mixed SRC with *R. pseudoacacia*.

In this study we hypothesized that *Populus*-hybrids in mixed stands with an N-binding legume tree like *R. pseudoacacia* would have an advantaged growth in comparison to monospecific stands. In addition, we addressed the following questions in order to assess the impact on *Populus*-hybrids at a single-tree level: (1) do the different *Populus*-hybrids react distinctly to the neighboring *R. pseudoacacia* in the first years of a recently established SRC? (2) does any of the *Populus*-hybrids and *R. pseudoacacia* have complementary ecological traits, which result in more efficient use of resources compared with monocultures?

Materials and methods

Study site

The plantation was established in April 2014 at the research farm of the Georg-August-University Göttingen in Reinshof (51.484°N/9.923°E), in the center of Germany in the state of Lower Saxony. Reinshof's soil is classified as Gleyic Fluvisol, a young fertile soil with high water storage capacity. During the study period rainfall was distributed very unevenly throughout the active growth period. Precipitation and mean temperature for the region of Göttingen were taken from the DWD ("Deutscher Wetterdienst—Climate Data Center," 2019) and can be seen on Table 1.

For this study, we analyzed four commercially used *Populus* hybrids: AF2 (*P. deltoides* × *P. nigra*), Fritzi Pauley (*P. trichocarpa* × *P. trichocarpa*), Hybride275 (*P. maximowiczii* × *P. trichocarpa*) and Max 1 (*P. nigra* × *P. maximowiczii*). As a complementary tree species for mixtures, we chose a single black locust provenance: *Robinia pseudoacacia* L., Northern German lowlands, HKG81901. Four planting blocks were established, each of which comprised one pure plot for each *Populus* hybrid, one *P.* hybrid/*R. pseudoacacia* mixed plot and one *R. pseudoacacia* pure plot (Fig. 1). On each plot, 25 trees were planted in a 1 × 1 m spacing. Unrooted *Populus* spp. stem cuttings (25 cm in length) and rooted *R. pseudoacacia* one year old nurslings were hand-planted. The *R. pseudoacacia* nurslings were cut down to the same size as *Populus*-hybrids stem cuttings right after planting.

The plantation was treated as a low-input system, i.e. no fertilizers or herbicides were applied. Instead, ground vegetation was mown in the second year in June and in the

Table 1 Total yearly precipitation (mm) and mean temperature (°C) for the region of Göttingen during the growing seasons of 2014 (1st year, stand establishment) until 2017 (4th year)

Year	2014	2015	2016	2017
ø °C	10.6	10.1	9.82	9.85
mm	609	627	544	777

Fig. 1 Exemplary block comprising the different stand types (mixed and pure *Populus* spp.). The black squares represent the plots (5 × 5 m) used for the competition survey. Aerial picture by Annika Ligner (IAPN, Göttingen), captured 26.7.2016

summer of the third year. There was no irrigation at any time. Mice control was carried out regularly to minimize rodent damage.

Plant growth survey

Height and root collar diameter were measured for each tree *in-situ* once a year while in dormancy. Height was measured using a measuring pole for bigger trees and a ruler for smaller (< 200 cm) trees and root collar diameter was measured at 3 cm above ground using a digital calliper. Height was expressed in cm and diameter in mm. Stem volume, was estimated using the simplified equation $V = D^2H$, with root collar diameter D and height H and expressed in cm^3. V is known to be very closely related to woody biomass (Annighöfer et al. 2016). Volume increment of a specific year was analysed by subtracting the volume of the year before to the year being analysed and expressed in cm^3 $year^{-1}$. No volume increment was calculated for the first year, since the first measurement of the trees was done after the first growing season.

Competition survey

In the first two years after stand establishment there were no crown overlapping, so there was no measurable aboveground competition. In the third year, however, some crowns started overlapping. After the growing season in that year (in the Winter of 2016/2017) we conducted an aboveground competition survey to assess crown overlapping over *Populus* spp. trees. All 16 mixed plots and 16 pure *Populus* spp. plots were selected, resulting in a total of 32 surveyed plots. In every plot, we chose the *Populus* spp. tree that was planted centrally in order to minimize edge effects. A terrestrial laser scanner, Faro Focus 3D 120 (Faro Technologies Inc., Lake Marry, USA), was used to quantify the competition strength enforced on these trees. Therefore, we placed the scanner on a tripod at 1.3 m directly over the study trees while bending the study tree towards the ground (under the scanner level). We conducted a single scan at each tree, using a field of view of 180° in vertical direction (upper hemisphere) and 360° in horizontal direction. The scan resolution was set to 0.035 degrees and all objects within a distance of 120 m were captured. After transferring the scan data to the computer we used Faro Scene (Faro Technologies Inc., Lake Marry, USA) software to filter each scan for erroneous scan points (stray points, etc.) using the standard filters and filter settings of the software. Then, each scan was exported as xyz-file for further processing. Using an algorithm written in Mathematica (Wolfram Research, Champaign, USA) we applied a 1-cm point cloud grid to the data, homogenizing the data density to reduce effects of varying distance to the scanner (see Seidel et al. 2011 for details). Finally, we determined the aboveground competition enforced on each study tree by counting the number of laser hits in a vertically orientated, upward-facing search cone with 60 degree opening angle in accordance with Seidel et al. (2015). Some of the trees, that were initially selected, died after the survey and were excluded from the final analysis. In the end we had $n_{pure} = 15$ and $n_{mix} = 10$ *Populus* hybrids trees for the analysis.

Root survey

Belowground biomass of pure and mixed stands of the *Populus* 'Max 1' and *R. pseudoacacia* were studied. Since surveying roots is a very laborious and difficult work, we focussed on only one hybrid. We chose the hybrid that seemed to be most vital and fast-growing. Three plots (pure *Populus* spp., mixed and pure *R. pseudoacacia*) per block were assessed. Root sampling was conducted using a metal root auger (2 cm diameter) down to 30 cm soil depth in October 2016 (third year after planting). In each plot, a central tree with four neighboring trees was selected. Four soil samples per plot were taken mid-way between the central and the neighboring tree. Soil samples from three different soil layers (0–10, 10–20 and 20–30 cm) were transferred into plastic bags and stored separately at 4 °C. In order to extract roots, soil samples were rinsed over a sieve (mesh size 0.4 mm) using tap water and cleaned of soil residue. Coarse and fine roots were manually sorted into *Populus*, *R. pseudoacacia* and grass roots using a stereomicroscope by inspecting the root colour, elasticity, surface structure and mode of branching (Jacob et al. 2013; Kubisch et al. 2015). Root material was then dried at 55 °C for 72 h until constant weight. Data was expressed as poplar (*Populus* spp. 'Max 1') and black locust (*R. pseudoacacia*) and grass root biomass for 0–10, 10–20 and 20–30 cm soil depth per area in mg cm^{-2}.

In order to compare root development between pure and mixed stands we used the "non-transgressive" approach (Pretzsch 2005). A mixture shows over- or underyielding if its performance is greater or lower than expected based on the weighted average of the monoculture outcomes of the component species. It was calculated as:

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

where $p_{1,2}$ was total root biomass in mixtures. p_1 and p_2 are the total root biomass in pure culture for *Populus* spp. 'Max 1' and *R. pseudoacacia* and m_1 and m_2 are the proportions of both tree species in mixtures (in our case 0.5). Results are expressed in percentage (%).

Nitrogen analysis

Soil cores for nitrogen analysis were sampled using a metal soil auger (2 cm diameter) in October 2016 (3 years after planting). Three random samples per plot were taken down to 30 cm soil depth. Soil samples were transferred into plastic bags and stored at − 18 °C. For the analysis, 100 g of soil was diluted in 250 ml of 0.01 M $CaCl_2$ solution and shaken for one hour at room temperature. After filtration, the content of soil mineral nitrate and ammonium of the solution was determined photometrically (AutoAnalyzer 3 SEAL, Norderstedt, Germany). The gravimetric soil water content was determined by drying the soil samples for 24 h at 105 °C. Data was expressed as total soil nitrogen ($N_{total} = NH_4^+ + NO_3^-$) for 0–30 cm soil depth averaged over plots in kg ha^{-1}.

Statistical and data analysis

All statistical analyses were conducted using the R software version 3.5.1 (R Development Core Team 2018, Vienna, Austria). Stem volume, diameter and height of the trees were analysed on single-tree level. Root biomass and N_{total} where analysed on the plot level using stand type as explanatory variable in linear models (ANOVA). All data compared was normal distributed. First we compared the variances by using Fisher's F test. In case of lack of significance we used ANOVA to compare the differences between the stand types. If the variance was significantly different, we applied the Welch Test. The relationship between *Populus*-hybrids height increment and competition was analyzed using linear regression.

Results

Tree growth

In the first year after planting, *Populus* spp. stem volume did not differ between stand types: mean volume was 39 cm^3 for trees in mixed and in pure stands (Fig. 2). In the second year, a significantly higher stem volume was registered for *Populus* in the mixtures (132 cm^3) compared to pure stands (95 cm^3) (Fig. 2), which corresponds to a higher stem volume in mixtures of 39%. In the third year, the pattern of an advanced increment in mixtures persisted. Similar to the year before, *Populus*' trees had an overall 43% higher stem volume in mixtures (Fig. 2).

The degree of the effect on the four hybrids, however, differed. In the third year after stand establishment, *Populus* height in particular was, for 3 out of 4 *Populus* hybrids, significantly higher in mixtures than in pure stands. Only Fritzi Pauley showed no significant differences between stand types (Fig. 3). AF2 showed a 66% and Max 1 a 30% higher annual stem volume increment in mixtures than in pure stands (Fig. 4). Fritzi Pauley and Hybride275 showed, however, no significant differences between the means for annual stem volume increment of the different stands (Fig. 4).

In the 4th year after stand establishment, however, growth relations reversed. *Populus* trees annual mean stem volume increment in mixtures was in general 44% lower than in pure stands (4638 cm^3 year^{-1} in pure and 3066 cm^3 year^{-1} in mixed stands) (Figs. 2, 3). The recess in stem development was particularly high for the hybrid AF2 (Fig. 4). Its annual mean stem volume increment in pure stands was over four times higher than in pure stands (Fig. 4). Also, for Hybride275 and Max 1 annual stem volume increment was significantly lower in mixed than in pure stands (42% and 53% respectively) (Fig. 4). *Populus* spp. 'Fritzi Pauley', once again, didn't show any significant difference between the stands (Figs. 3, 4). The *R. pseudoacacia* showed advantaged growth in comparison to the *Populus* hybrids (Fig. 3e). In the third year, as crowns started overlapping, *R. pseudoacacia* trees were between 26% (for Max 1) and 73% (for Fritzi Pauley) higher than *Populus* spp. trees (Fig. 3).

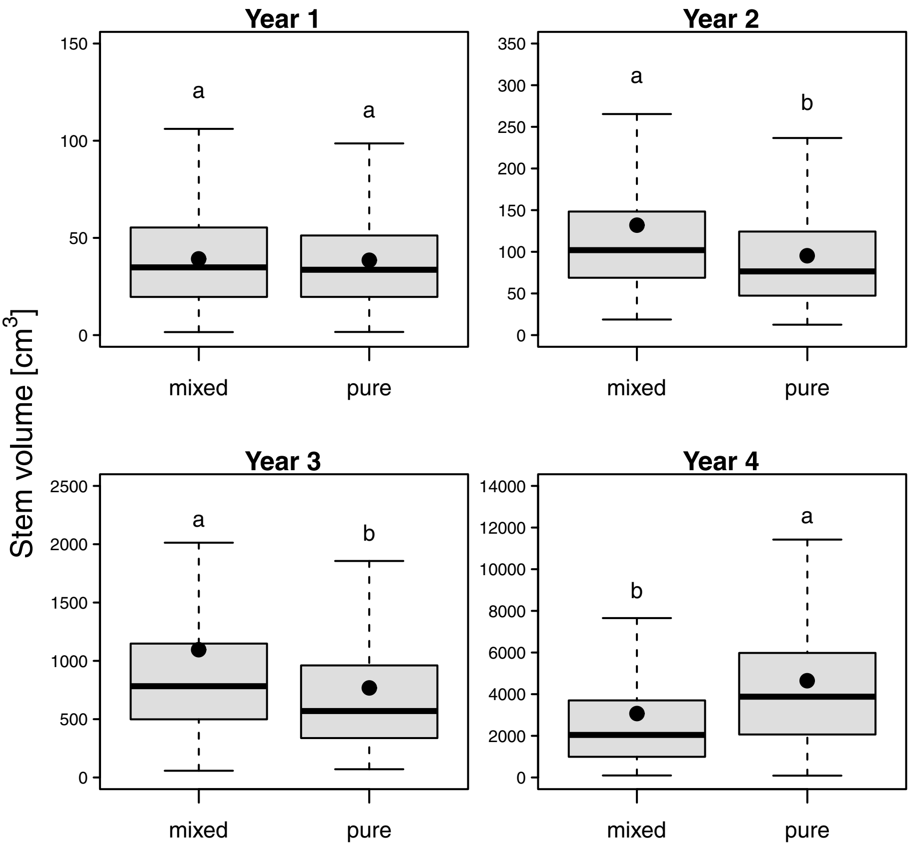

Fig. 2 Stem volume per *Populus* tree (cm^3) across all hybrids for the first 4 years after stand establishment in mixed and pure stands. Mean values are marked by black dots. Solid lines in the boxes represent the median, the bottom and the top of the box represent first and third quartile (IQR). Each whisker represents 1.5 IQR. Different letters (a, b) indicate significant differences between the stand types at significance level $p < 0.05$

Competition effects

Populus hybrids in mixtures were exposed to a much higher aboveground competition in mixed than in pure stands (6306.80 voxels in mixtures and 57.47 voxels in pure stands, $p < 0.005$). A strong negative correlation was found between height and root collar diameter increment of *Populus* hybrids in the 4th year after stand establishment with increasing competitive pressure (Fig. 5).

Roots and nitrogen content in the soil

The means of total root biomass at a soil depth of 0–30 cm for *Robinia pseudoacacia* and *Populus* spp. 'Max 1' differed significantly between pure and mixed stands. *R. pseudoacacia's* total root biomass was, in both mixed and pure stands, approximately

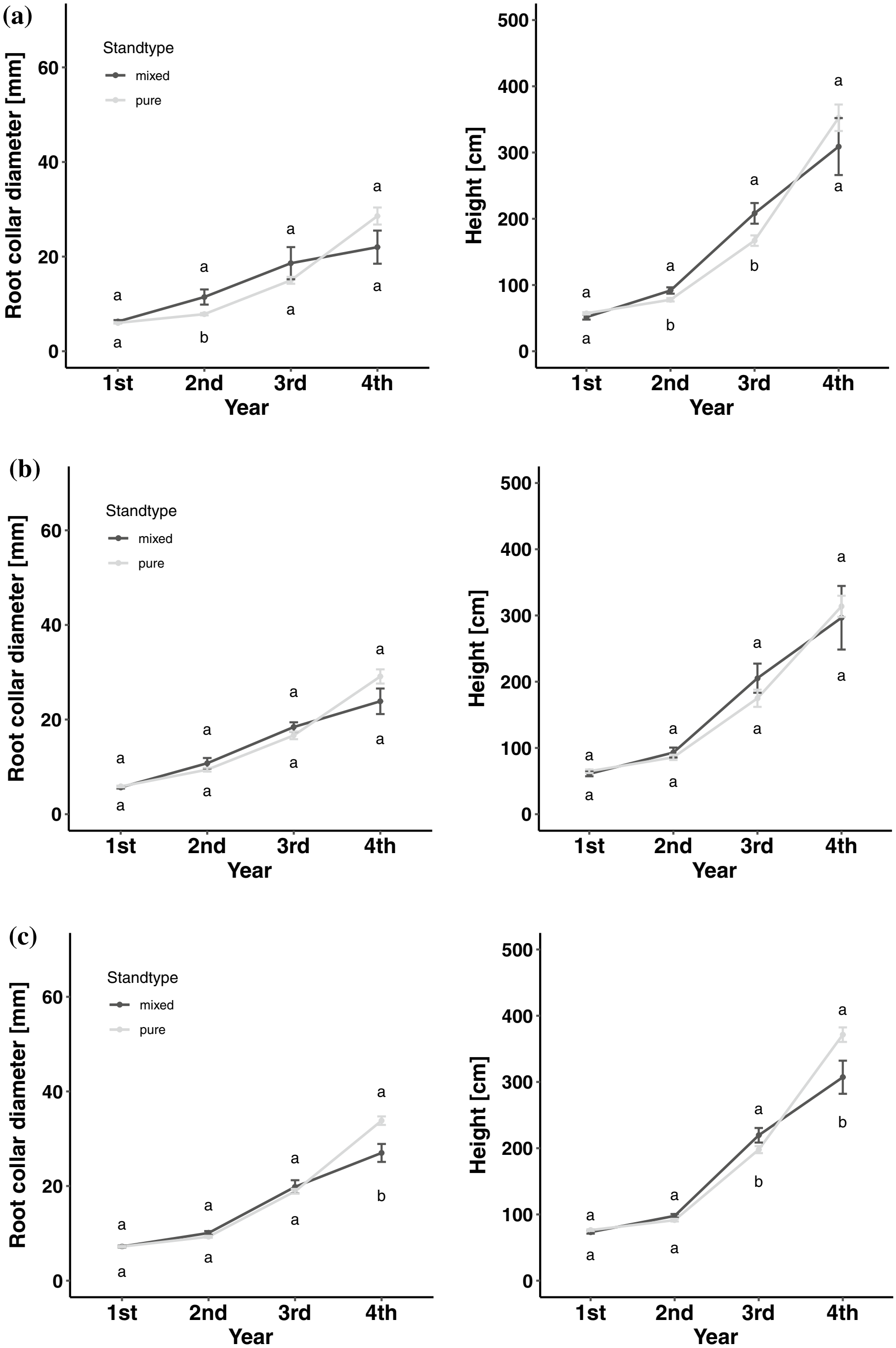

Fig. 3 Progression of root collar diameter (mm) and height (cm) of the different *Populus* hybrids and the *R. pseudoacacia* over a period of 4 years in mixtures and in pure stands. Error bars represent standard error of the means. Different letters (a, b) represent significant differences between mixed and pure stands for each year

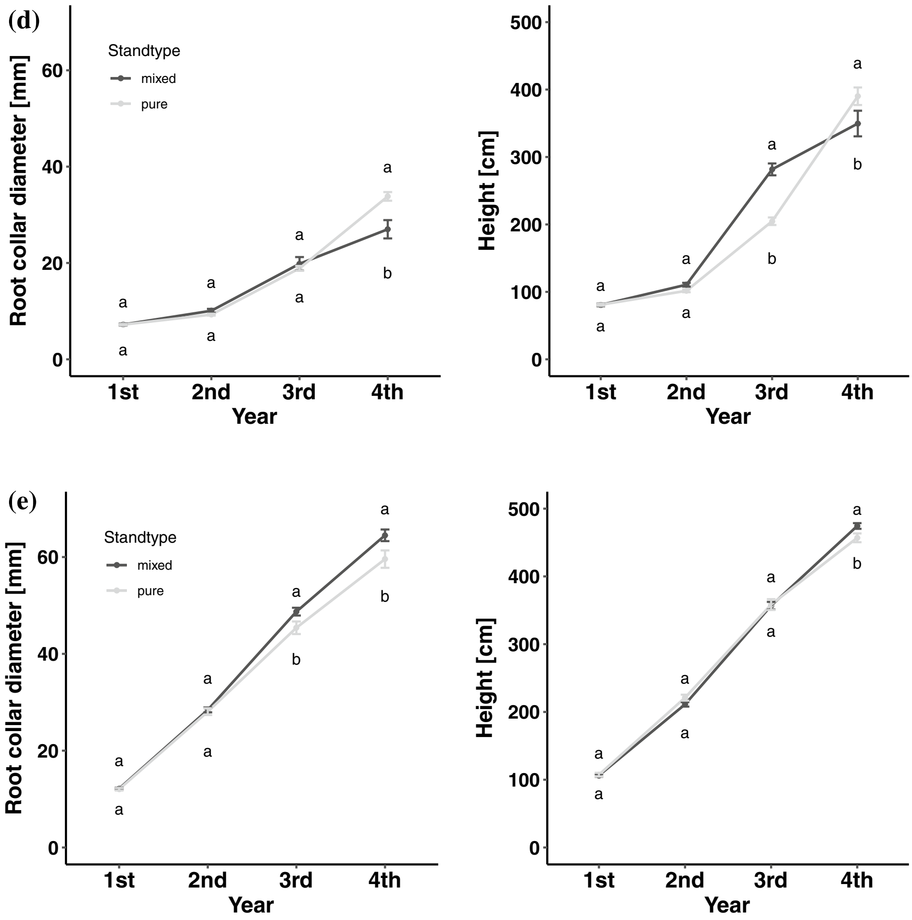

Fig. 3 (continued)

three times higher than that of *Populus*. Root biomass of all species declined with depth (Fig. 6). The total root biomass dropped substantially in mixtures reflecting an underyielding. The mean of *R. pseudoacacia's* total root biomass per plot was 1.13 mg cm^{-2} in pure stands and 0.44 mg cm^{-2} in mixed stands, *Populus* hybrids' root biomass was 0.40 mg cm^{-2} in pure and 0.14 mg cm^{-2} in mixed stands. *R. pseudoacacia's* root biomass (Δp_{rel}) dropped 22% and *Populus* spp. 'Max 1' 30%. Grass roots predominated each stand type at every soil depth (Fig. 6), but no significant differences were found between the stand types for the total grass root biomass.

The total soil nitrogen content (N_{total}) in the third year significantly differed between stand types ($p < 0.05$): pure *Populus* stands had the lowest N_{total} content (5.4 kg ha^{-1}), followed by mixed stands (7.5 kg ha^{-1}). *R. pseudoacacia's* stands had the highest N_{total} content with 10.3 kg ha^{-1}.

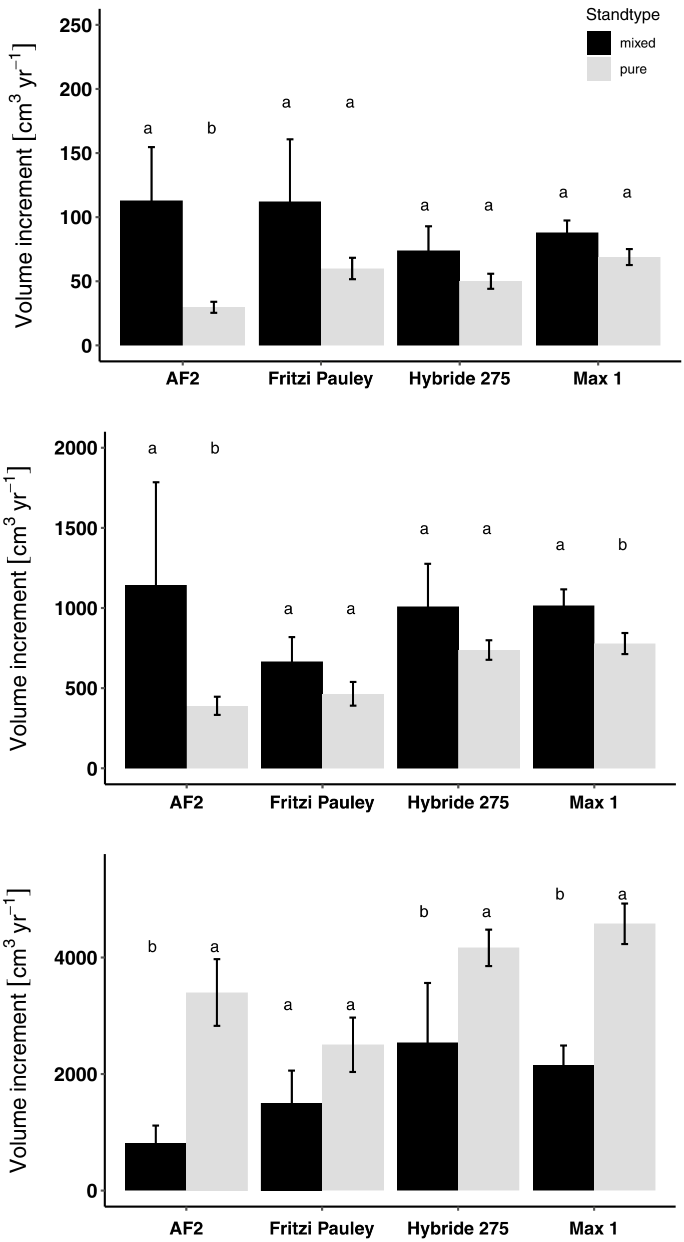

Fig. 4 Mean tree stem volume increment per year (cm^3 year^{-1}) for the different *Populus* hybrids in mixed and in pure stands. Error bars represent standard error of the means. Different letters (a, b) represent significant differences between mixed and pure stands for each *Populus* hybrid

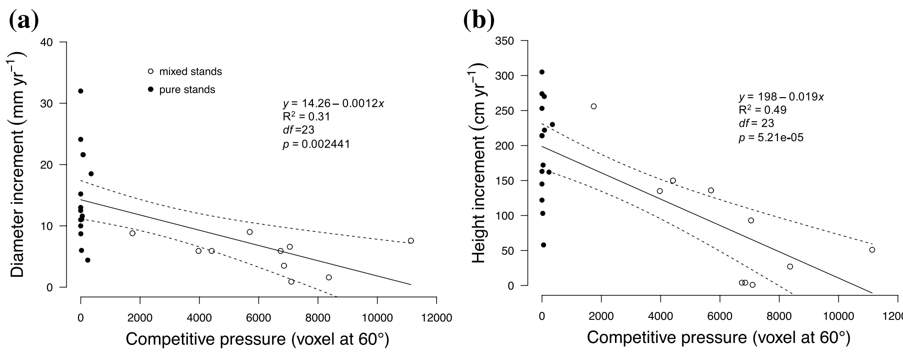

Fig. 5 **a** Relation between *Populus*' hybrids root collar diameter increment (mm year^{-1}) in the 4th year and the competitive pressure caused by neighboring trees (number of voxels in 60° cone); **b** Relation between *Populus*' hybrids height increment (cm year^{-1}) in the same year and the competitive pressure. Both plotted with 95%-confidence interval, n = 25

Discussion

Our recently established mixed stands of *Populus* hybrids and *R. pseudoacacia* showed that interactions between the tree species are dynamic and vary as stand develops. While in the first years the positive mixing effects on *Populus* hybrids were predominant, canopy closure, negatively affected the growth performance of the hybrids. This outcome may explain contrasting findings of past studies addressing this kind of mixture. While facilitation and increased yield in mixed culture of *Populus* sp. and *R. pseudoacacia* were observed by some authors (Oliveira et al. 2018; Rédei et al. 2006), others showed no facilitation or even strong interspecific competition (Gana 2016; Marron et al. 2018). Our main hypothesis, which stated that *Populus* hybrids with an N-binding legume tree like *R. pseudoacacia* would have an advantaged growth compared to *Populus* hybrids in monoculture, could not be completely disproved nor confirmed. Positive and negative interactions between species probably occurred simultaneously (D'Amato and Puettmann 2004; Forrester 2017), varying spatially and temporally depending on resource availability, climatic conditions (Forrester 2017) and stand development (Forrester et al. 2004; Pretzsch and Forrester 2017). Our study suggests, that the predominant process of interaction, very much depends on the point in time at which the stands are investigated.

Facilitation

The objective of admixing the legume tree *Robinia pseudoacacia* with *Populus* hybrids was to increase the N availability to the SRC-system and promote higher growth of the N demanding species *Populus* sp.. Successful combinations of N-fixing with N demanding tree species in short-rotation plantings was already reported by Forrester et al. (2004) with *Eucalyptus globulus* and *Acacia mearnsii* and by Hansen and Dawson (1982) with *Alnus glutinosa* and *Populus*-hybrids.

Our experiment showed that on the second and third year after stand establishment, *Populus'* single tree stem volume was significantly higher in mixture than in pure stands (Fig. 2). Looking closely at the different hybrids (Fig. 3, Fig. 4), we observe that degree of

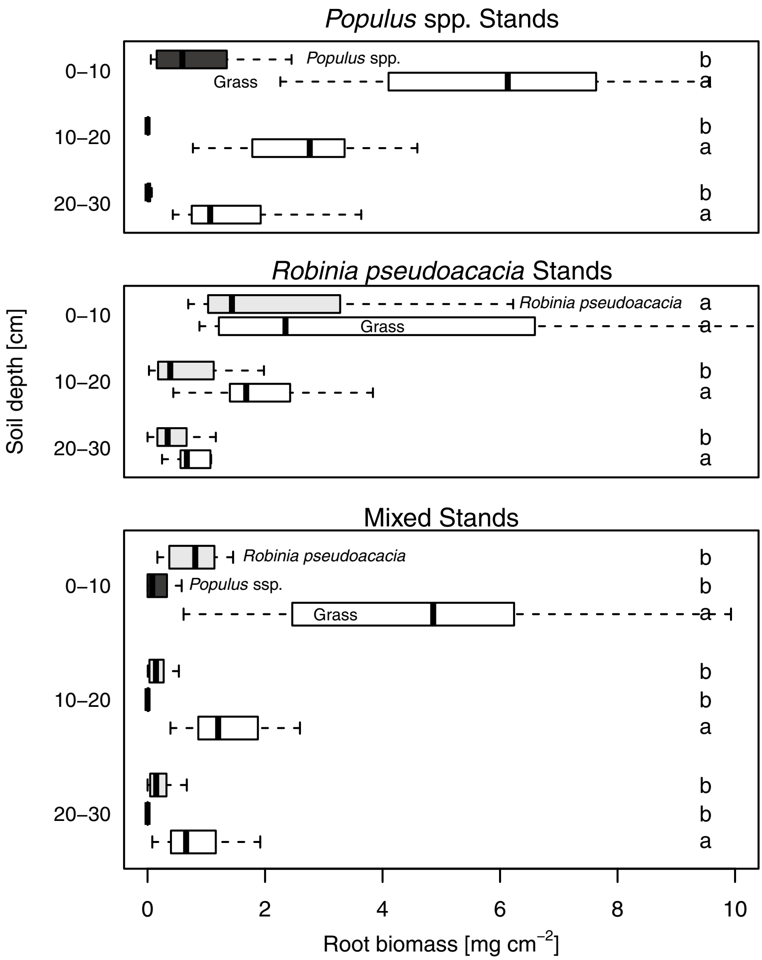

Fig. 6 Root biomass distribution at different soil depths (0–10, 10–20 and 20–30 cm) in pure and mixed stands of black locust (*Robinia pseudoacacia*) and poplar (*Populus* spp. 'Max 1') in the 3rd year after stand establishment. Different letters (a, b) indicate significant differences between the species (black locust, poplar and grass) in the stands at the given soil depth (significance level $p<0.05$)

the effect of interspecific facilitation was distinct between the different hybrids. Facilitation was most obvious for AF2, which showed an advantaged stem volume increment in the mixtures in the second and third year of respectively 3.8 and 3 times more than stem volume increment in pure stands (Fig. 4). Max 1 showed only in the third year a 1.3 times faster growth in mixtures compared to pure stands (Fig. 4). Even though Hybride275 and Fritzi Pauley showed a tendency for higher growth in mixtures at the same period of time, the differences were not significant (Fig. 4). *Populus* hybrids are known for taking up N rapidly from the soil resulting in higher growth rates (Cooke et al. 2005; Liu and Dickmann 1993). In the context of SRC, N fertilization is used to improve harvest yields and reduce rotation age (Cooke et al. 2005; Rennenberg et al. 2010). In our case, it is likely that presence of *R. pseudoacacia* led to an increase in N availability for the hybrids. In fact, in the third year after stand establishment, N_{total} was 39% higher in mixtures than in pure *Populus* stands. Since no fertilizer was added in our study, we assume that *R. pseudoacacia* led to a "natural" fertilization of the soil. This facilitation effect continued into the third year after stand establishment and seemed to confirm the findings of Marron and Epron, (2019), who stated that mixed tree plantations with N-fixing tree species are generally more productive (24%) than monocultures under temperate conditions.

Aboveground competition

The mode of interaction between trees in forests is predominantly the competition for resources (D'Amato and Puettmann 2004). Mixing ecologically complementary species can increase the inequality of size and growth distribution between small and tall trees (Pretzsch 2017b) and differences in size among trees in their early growth rates may increase as stands develop (D'Amato and Puettmann 2004). Negative mixing effects due to inequal growth distribution was observed in young mixed plantations of red alder (*Alnus rubra* Bong.) with Douglas-fir (*Pseudotsuga menziesii* Franco) (Radosevich et al. 2006) and of *Pinus radiata* with *Acacia* spp. (Forrester et al. 2007). Indeed, our study shows, that 4 years after stand establishment, the effects of competition enforced on the *Populus* hybrids by *R. pseudoacacia* began to surpass the benefits of the facilitation (Fig. 2). After the third year, crown cover in the mixtures was on average more than a 100 times higher than in pure *Populus* stands (Fig. 5). *R. pseudoacacia's* crowns were so massive and broad, that they were far more competitive than *Populus* trees. Three (out of four) *Populus* hybrids, therefore, reversed growth rates (Fig. 3), by showing a significantly lower stem volume increment in mixed stands in comparison to pure stands (Fig. 4). The hybrid AF2 had the highest negative impact, by growing in mixtures only ¼ of the growth in pure stands. The hybrids Max 1 and Hybride275 reduced growth in mixtures to around half of the growth in pure stands. Oliveira et al. (2018) showed that SRC mixture of *R. pseudoacacia* and white poplar (*Populus alba*) had a notable influence on yield: *Populus alba*, however, only showed overyielding in mixtures if the proportion of *R. pseudoacacia* was lower (25%). Our experiment had a mixture proportion of 50%. The high density of *R. pseudoacacia*, with a strong canopy cover (Fig. 5) and their presumably well distributed roots (Fig. 6) led to increased competition over *Populus* and subsequently to a regression on height (Figs. 3, 5b) and diameter (Figs. 3, 5a) increment of the latter. The genus *Populus* belongs to the fastest growing trees in the temperate zone, but their high productivity depends on high water availability and full sunlight (Monclus et al. 2006; Stanturf and Oosten 2014; Stettler and Bradshaw 1996; Vítková et al. 2017). In addition, highly productive hybrids used in SRC usually have a low level of drought tolerance (González-González et al. 2017; Monclus et al. 2006). For a successful seedling growth it is recommended to irrigate the plantation in the first year after planting (Knust et al. 2013). The fact that our experiment was implemented as a low-input-system very likely resulted in *Populus* trees struggling with water scarcity, since there was no irrigation at any time. When soil water is restricted, photosynthesis of high-N demanding plants like *Populus* is also restricted (Liu and Dickmann 1993; Mitchell 1992). In contrast, the much more drought resistant *R. pseudoacacia* was able to outcompete, at a very young stage, all four *Populus* hybrids and, at some point, suppressed the growth of three out of four hybrids. Not even *Populus* spp. 'Max 1', which is considered to be highly productive and drought resistant (Euring et al. 2016; Schildbach et al. 2012), was able to compete with *R. pseudoacacia*. This findings give the answer to our first research question: do the different *Populus*-hybrids react distinctly to the neighboring *R. pseudoacacia*? *Populus* spp. 'Fritzi Pauley', didn't show, at any time, significant differences in its growth compared to monospecific stands. All other three *Populus*-hybrids showed in first place positive mixing effects followed by negative effects due to competition. The intensity of the impact varied slightly between the different hybrids, but none of them stood out. In an earlier paper, we could show that the mortality of *Populus*-hybrids was higher if planted at the same time in mixed stands with *R. pseudoacacia* than in pure plots (Rebola-Lichtenberg et al. 2019), which underpins the high dominance and competitiveness of *R. pseudoacacia* in a low-input-system.

Belowground competition

Root development affect availability of nutrients and have considerable influence on growth (Mitchell 1992) but is not a reliable indicator of *Populus*' aboveground biomass (Al Afas et al. 2008). In our experiment, the biomass of the peripheral root system, where tree roots of both tree species were expected to get into contact, dropped significantly in the mixtures for both species, indicating belowground underyielding. While this result could rather be expected for *Populus* from the findings on the lower annual stem increment in mixtures, it was unexpected for *R. pseudoacacia*. In fact, we expected belowground overyielding of *R. pseudoacacia*. A potential explanation may be that the competition by grass was much higher in the mixed plots than in the pure *R. pseudoacacia* plots (Fig. 6). Nevertheless, *R. pseudoacacia's* root biomass in mixtures was less reduced than *Populus'* in comparison to pure stands, highlighting the competitive ability of *R. pseudoacacia* not only aboveground, but also belowground. Finally, we can answer our second research question, whether at least one of the *Populus*-hybrids have complementary ecological traits with *R. pseudoacacia*. Even though there seems to be positive mixing effects between both species that could enhance *Populus* growth, the competition is, under a low-input system and a mixing species ratio of 50:50, too high for any of the *Populus*-hybrids to be able to compete. Hence, there is no clear sign of long-term facilitation or competition reduction for any of the *Populus*-hybrids.

Conclusions

The variability we observed in the mixing responses is the evidence that there is a risk in prematurely generalizing mixing effects found in short-term experiments (Pretzsch and Forrester 2017). From a management point of view our results have important implications. Given that there was facilitation in the beginning of our experiment, future studies should explore options to reduce the competition by *R. pseudoacacia* on time, but only to a degree that ensures a positive net effect. Oliveira et al. (2018) reduced the amount of *R. pseudoacacia* trees successively, which may be a plausible solution. In practical terms, planting designs should take into account that *R. pseudoacacia* develops large crowns exerting strong aboveground competition. Planting *R. pseudoacacia* in rows with greater distance to *Populus* trees, would reduce the competition while maintaining a certain level of natural nitrogen enrichment of the soil. Another option may be the delayed planting of the N-fixing species a few years after planting *Populus* (Radosevich et al. 2006). It is well known from other studies that delayed planting can help to control competition between tree species that differ in their growth pattern (Radosevich et al. 2006). Furthermore, the probability of drought episodes and more severe climatic events is increasing (Lindner et al. 2010; Monclus et al. 2006). The productivity of European forests is therefore expected to decline, resulting in yield reduction (Lindner et al. 2010). Against this background the mixture of the drought resistant *R. pseudoacacia* and the fast-growing *Populus* sp. is, even though our study pointed towards some trade-offs, still a promising SRC mixture, which needs to be further studied.

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