INTRODUCTION

The urgency to take measures for mitigating climate change makes substitution for fossil fuels an increasingly important issue to address. Wood is a renewable source of energy with great potential to tackle this challenge (Canadell & Raupach, 2008; Demirbaş, 2001; Knust, 2009; Parikka, 2004). Besides forest stands, short rotation coppices (from here on referred to as SRC) on arable land are important sources of woody biomass (Butler Manning et al., 2015). SRCs are typically monocultures of fast-growing tree species with rotation lengths of 5 to 10 (15) years planted with high density (Knust, 2009; Stanturf & Oosten, 2014). Unfortunately, in spite of the steady increase in wood
biomass consumption in Germany (Ewald et al., 2017; Gößwein et al., 2018), cultivation of SRC rather stagnates (Liesebach, 2020). Optimizing wood production in SRC, would, on the one hand, reduce pressure on forests and, on the other hand, alleviate the negative impact of agricultural land-use on biodiversity (Butler Manning et al., 2015; Harris et al., 2017; Schmidt & Glaser, 2009). One way to further optimize wood production may be the cultivation of mixed cropping systems which may be a more sustainable alternative to monocultures with reduced input and stabilized yield, especially if legumes are involved (Knörzer et al., 2009; Vandermeer, 1989). By analogy with mixed-species forests lower the risk of fungal diseases (Pautasso et al., 2005) and pest damage (Jactel et al., 2005) can be expected and higher yield compared with monocultures may be achieved, if tree species show complementary ecological traits (Ammer, 2019; Pretzsch & Forrester, 2017). However, studies of mixed SRC, for example with commercial poplar clones and an admixed N-fixing, legume tree species are widely lacking (Oliveira et al., 2018).

*Populus* spp.-hybrids and *Robinia pseudoacacia* L. are, after *Eucalyptus* spp., the two most planted broadleaved tree species in the world (Nicoleșcu et al., 2020), and two of the most common trees species used for SRC in Germany (Knust et al., 2013). Poplars primarily grow on moist sites such a riparian forests with seasonal flooding (Knust et al., 2013; Rennenberg et al., 2010; Richardson et al., 2014), and its growth potential is highly correlated with nitrogen and water availability (Ehlting et al., 2007; Euring et al., 2016). Black locust, on the other hand, is preferably planted in dry regions and sites with low nutrient availability (Knust, 2009; Rédei, 2013). The species commonly grows in areas with 480–800 mm rainfall. It is native to North America but plays an important role in forest restoration worldwide (Qiu et al., 2010) and in the recultivation of postmining landscapes in Germany (Carl et al., 2018; Kanzler et al., 2014). Black locust does not only demand less water and nutrients but, as a legume tree species, it can enhance soil fertility by fixing nitrogen (Binkley, 1992; Knust, 2009; Nicoleșcu et al., 2020; Veste et al., 2013). *Populus* hybrids planted in SRC in Germany can yield between 0.8 and 14.6 t ha⁻¹ year⁻¹ dry wood matter (Landgraf et al., 2020), whereas 1–13.8 t ha⁻¹ year⁻¹ were reported for *R. pseudoacacia* (Carl et al., 2017) depending strongly on site and water availability. Integrating legume tree species into cropping systems can be an alternative strategy to mineral nitrogen additions (Rosenstock et al., 2014; Vandermeer, 1989). Subsequently, mixing both tree species in SRC could lead to complementarity and higher biomass growth. Oliveira et al., (2018) and Rédei et al., (2006) could indeed show that admixing black locust to white poplar (*Populus deltoides* Bartram ex Marshall) and black locust mixed SRC did not find improved poplar biomass growth (Gana, 2016). To our knowledge, no study has compared different *Populus* spp. genotypes growing in pure stands and mixtures with *R. pseudoacacia* yet.

The goal of this study is to assess the effect of the legume tree *R. pseudoacacia* on the growth of different *Populus* genotypes. Our hypotheses are (1) mixtures of *Populus* spp. and *R. pseudoacacia* in SRC show overyielding in comparison with SRC in pure culture, (2) the performance of the different poplar genotypes varies independent from site fertility, enabling the identification of some genotypes that are suited for mixed SRC with black locust.

## 2 | MATERIAL AND METHODS

### 2.1 | Study sites

Two plantations were established in April 2014 at the research farms of the Georg-August-University Göttingen in Deppoldshausen (51.581°N/9.967°E) and Reinhof (51.484°N/9.923°E) in Göttingen, Germany. Precipitation and mean temperature varied within the study period and included the particularly dry and hot year 2018 (Table 1), data from the DWD (Deutscher Wetterdienst - Climate Data Center, 2019).

The site at Deppoldshausen is situated on marginal land. The soils are shallow (<60 cm deep) and stony. According to the FAO classification system the soil type is a Calcaric Leptosol and characterized by a low water storage capacity. The soil at Reinhof (from here on referred to as ‘fertile site’) is classified as Gleyic Fluvisol, a young fertile soil with high water storage capacity (Rebola-Lichtenberg et al., 2019).

### 2.2 | Plant material and experiment design

For this study, we selected eight commercially used poplar genotypes, which represented different hybrids of *P. deltoides* W.Bartram ex Marshall, *Populus maximowiczii* A.Henry, *P. nigra* L., and *Populus trichocarpa*

| Year | 2014 | 2015 | 2016 | 2017 | 2018 |
|------|------|------|------|------|------|
| Temperature °C | 10.6 | 10.1 | 9.82 | 9.85 | 10.6 |
| Precipitation mm | 609 | 627 | 544 | 777 | 430 |
Torr. & A.Gray ex Hook (Table 2). One black locust (R. pseudoacacia L.) provenance was selected as mixture species (Northern German lowlands, HKG81902).

Four planting blocks were established at each site. The treatments within a block were exactly replicated at each site. Each block comprised either pure (Populus genotype or R. pseudoacacia) and mixed stands (alternately planted Robinia and a Populus genotype), resulting in a 50:50 mixture.

The following stand types were established on each block: 8 poplar plots (1 plot per genotype), 8 mixed plots (=8 Populus genotypes × 1 Robinia), 2 Robinia plots. Twenty-five trees were planted per plot in a 1 × 1 m spacing. Mixed plots consisted of 13 poplar and 12 black locust trees. Following standard practice in short rotation forestry and similar experiments (Oliveira et al., 2018) un-rooted poplar stem cuttings (25 cm in length) and rooted black locust nurseries were hand planted.

No fertilizers or herbicides were applied, since black locust, unlike poplar, is usually managed as a low-input system (Veste et al., 2013). Ground vegetation was mown on both sites once in June 2015 and twice in the summer of 2016. At the time of planting the trees were exposed to a severe drought. Therefore, the trees at the marginal site were irrigated two times in the weeks immediately after planting in 2014. There was no irrigation at any time at the fertile site or any further irrigation after stand establishment at the marginal site. Mice control was carried out twice a year in the first 2 years at both sites after planting by application of rodenticide to minimize rodent damage. More information on the establishment of the experiment can be found in (Rebola-Lichtenberg et al., 2019).

2.3 Field sampling and biomass calculation

The data set for biomass estimation for the eight different Populus genotypes was collected during three different felling activities, which occurred in February 2017 (n = 46), August 2017 (n = 31) and January 2019 (n = 286) to cover a wide range of stem diameters for biomass estimation. The number of sampled trees per genotype varied between 4 and 20 due to different mortality rates (Table 4). Height and root collar diameter were measured for each tree at the field while in dormancy. Height (measured in cm) was measured using a measuring pole for bigger trees and a ruler for smaller (<200 cm) trees and root collar diameter (in mm) was measured at 3 cm above ground using a digital calliper (Rebola-Lichtenberg et al., 2021). We used root collar diameter instead of dbh because most of the trees in the first 2 years were too small (<1.3 m). We kept with root collar diameter measurements throughout the whole experiment.

For the biomass estimation of black locust, we measured root collar diameter of all trees in all years and height between 2014 to 2016 during dormancy. After 2016, the trees became too high and the plots too dense. Therefore, we only measured height of trees that were sampled during the felling activities as explained in the following. 29 R. pseudoacacia trees, covering the whole range of diameter, were felled in January 2018. Based on the height to diameter relationship of 27 of these trees we estimated the height of all remaining trees by using the following function ($R^2 = 0.82$):

$$H = 188.74\ln(D) - 299.63,$$

where $H$ (cm) is estimated height of the tree and $D$ (mm) its measured diameter. Two trees were excluded from the measurements. The function was calculated using Microsoft Excel 2019 (Version 16.34 for Mac).

The selection of the trees to be harvested was made by choosing vital and undamaged individuals. All sampled trees were harvested as a whole and used to estimate biomass. They were felled close to the ground, cut in smaller parts and put right away in paper bags. To determine dry weight (DW), all woody samples were dried at 95°C in a temperature-controlled oven until they achieved a constant weight. The bags with the woody samples were weighted in the lab using two different scales. Smaller samples (<200 g) were weighted with a smaller scale with accuracy of 1 g. Heavier samples (>200 g) were weighted with a scale with the accuracy of 20 g.

We used the standard method to fit allometric equations to sample data using the equation form (Sprugel, 1983):

$$DW = 81(D^2H)^{0.82},$$

using root collar diameter ($D$ in mm) and height ($H$ in cm) as explanatory variables, to estimate biomass of all trees on the individual tree level (DW in g). To increase validity of the

| Name of genotype | Parentage               |
|------------------|-------------------------|
| AF2              | *P. deltoides* × *P. nigra* |
| Fritz Pauley     | *P. trichocarpa*         |
| Hybride 275      | *P. maximowiczii* × *P. trichocarpa* |
| I214             | *P. deltoides* × *P. nigra* |
| Matrix 11        | *P. maximowiczii* × *P. trichocarpa* |
| Matrix 49        | *P. maximowiczii* × *P. trichocarpa* |
| Max 1            | *P. nigra* × *P. maximowiczii* |
| Muhle Larsen     | *P. trichocarpa*         |
analysis, the variance was homogenized by fitting the models to logarithmically transformed data (using function ‘lm’ in R package ‘stats’; Chambers, 1992) and estimate coefficients \( \beta_1 \) and \( \beta_2 \) in dependence of \( D^2H \) (in cm\(^3\)) (Annighöfer et al., 2016; Sprugel, 1983). The transformed equation becomes:

\[
\ln(DW) = \beta_1 + \beta_2 \ln(D^2H),
\]

where \( \ln \) is natural logarithm, \( DW \) is wood biomass dry weight (g), \( D \) (cm) is root collar diameter, \( H \) (cm) is height and \( \beta_1 \) and \( \beta_2 \) are fitted coefficients (Table 3).

As suggested by Sprugel (1983) we used the first-order correction factor by multiplying the anti-log of the intercept of the logarithmically transformed models.

\[
CF = \exp \left( \frac{\text{SEE}^2}{2} \right)
\]

with CF as the correction factor, SEE as the standard error of the estimate based on natural logarithms.

### 2.4 Analysis of genotypical performance

The analysis of genotypical performance was made by juxtaposing the variables mortality (%) and biomass per poplar tree (g tree\(^{-1}\)) with genotype and stand type as explanatory variables, distinguishing sites. Deceased poplar and black locust trees were registered to assess mortality. Mortality was analysed on a plot level, which was described as proportion data (deceased trees/initial trees).

### 2.5 Effect of complementary

For comparison of biomass growth development between pure and mixed stands, Pretzsch’s (2005) ‘non-transgressive overyielding’ (\( \Delta p_{rel} \)) approach was used. A mixture shows over- or underyielding if it yields higher or lower values than expected based on the weighted average of the monoculture outcomes of the component species (Rebola-Lichtenberg et al. 2020). Over- and underyielding were calculated as:

\[
\Delta p_{rel} = \frac{p_{1,2}}{(m_1p_1 + m_2p_2) - 1} \cdot 100,
\]

where \( p_{1,2} \) was total aboveground biomass in mixtures, \( p_1 \) and \( p_2 \) are the total aboveground biomass in pure stands for poplar and black locust and \( m_1 \) and \( m_2 \) are the proportions of both tree species in mixtures (in our case 0.5). Results are given in percentage (%).

### 2.6 Statistical analysis

Biomass of the different poplar genotypes was analysed on tree level using genotype and stand type as explanatory variables, distinguishing the fertile and the marginal site. Biomass was described as g DW tree\(^{-1}\). All data were normally distributed. Significant differences between comparisons were determined at the level \( p < 0.05 \). First, we compared the variances by using Fisher’s F test. If significance was lacking, we applied one-way ANOVA to compare the differences between the groups. If the variance was significantly different, we applied the Welch test. For analyzing mortality on the plot level, we used genotypes, stand types and sites as explanatory variables. Generalized linear models with binomial error structure were used to quantify the effect of explanatory variables on plot level mortality. In the case of overdispersion, we used a quasibinomial error structure (Crawley, 2007). Differences between genotypes, between stand types and between sites were analyzed using the glht function of the ‘multcomp’ package (Hothorn et al., 2008) with Tukey contrasts. Correlation between the means of the different Populus hybrids biomass in oven dried tons per hectare (odt ha\(^{-1}\)) and \( R. \ pseudoacacia \) in mixtures was analysed using linear regression. All statistical analyses were done using R software, version 3.5.1 (R Development Core Team, 2018).

### 3 Results

#### 3.1 Growth of poplar and black locust in monoculture at contrasting sites

The poplar genotype Max 1 performed best at both sites, followed by Hybride 275, Matrix 11 and AF2. Also consistent
for both sites was the ranking of poorest performers with Muhle Larsen, Fritzi Pauley and I214 bringing up the rear (Figure 1a). Biomass yield at the fertile site ranged from 0.96 ± 0.84 kg tree⁻¹ for I214 to 2.30 ± 1.49 kg tree⁻¹ for Max 1 (Figure 1a; Table 4). The yields at the marginal site ranged from 0.06 ± 0.04 kg tree⁻¹ (Muhle Larsen) to 0.38 ± 0.19 kg tree⁻¹ (Max 1) DW biomass (Figure 1b; Table 4). At both sites, black locust grew much better than all poplar genotypes. At the fertile site, it reached a mean of 5.9 ± 4.9 kg tree⁻¹ and at the marginal site 3.9 ± 2.9 kg tree⁻¹ in pure stands (Table 4).

### 3.2 Performance of the different poplar genotypes in mixtures

The performance of the different poplar genotypes was assessed by comparing DW wood biomass per tree and survival rate between mixed and pure stands at both sites (Figure 2). Max 1 performed best because both biomass growth and survival were above average at both sites and stand types (Figure 2). Hybride 275 was the second-best performer. Only mixed stands at the fertile site performed lower than average. Matrix 11 performed, at both sites, only in pure stands above average. Fritzi Pauley, I214, Matrix 49 and Muhle Larsen performed lower than average in terms of biomass and survival rate (Figure 2).

The genotypes AF2 and I214 did not show significant differences between mixed and pure stands at any sites, whereas Fritzi Pauley, Hybride 275, Matrix 11 and Matrix 49 showed significantly higher biomass per tree in pure than in mixed stands at both sites. The poplar genotypes Max 1 and Muhle Larsen had significantly higher biomasses per tree in the pure stands at only one site: at the marginal site for Max 1 and at the fertile site for Muhle Larsen. None of the genotypes showed at any site significantly higher biomass production in the mixed stands (Table 4).

**Table 4** Biomass (mean ± SD in g tree⁻¹) of standing poplar trees with sampling size *n*

| Genotypes       | Fertile site                | Marginal site               |
|-----------------|-----------------------------|----------------------------|
|                 | Mixed | *n* | Pure | *n* | *p* | Mixed | *n* | Pure | *n* | *p* |
| AF2             |       | 1191 ± 1437 | 11  | 1921 ± 1374 | 10  | 0.0861 | 115 ± 120 | 5  | 196 ± 234 | 8  | 0.315 |
| Fritzi Pauley  |       | 250 ± 124  | 4   | 1467 ± 1123 | 12  | 0.0407* | 50 ± 29 | 7  | 111 ± 115 | 9  | 0.0227* |
| Hybride 275    |       | 1186 ± 1056| 19  | 1923 ± 1036 | 18  | 0.00121** | 160 ± 136 | 15 | 265 ± 168 | 14 | 4.34 e⁻⁴*** |
| I214            |       | 939 ± 1.034| 10  | 962 ± 836   | 9   | 0.924  | 103 ± 156 | 6  | 91 ± 80  | 10 | 0.609  |
| Matrix 11      |       | 870 ± 944  | 15  | 2.266 ± 1.547| 12  | 2.47e⁻⁵*** | 112 ± 84 | 10 | 221 ± 168 | 8  | 1.12e⁻⁰³*** |
| Matrix 49      |       | 527 ± 527  | 13  | 1.127 ± 750 | 17  | 4.85e⁻⁵*** | 75 ± 73 | 11 | 134 ± 92  | 10 | 0.00758** |
| Max 1           |       | 1957 ± 1.581| 17 | 2.299 ± 1.489 | 20  | 0.205  | 199 ± 150 | 15 | 381 ± 186 | 14 | 1.06e⁻⁰⁸*** |
| Muhle Larsen    |       | 513 ± 493  | 10  | 1.257 ± 768 | 10  | 9.52e⁻⁴*** | 50 ± 30 | 4   | 56 ± 39  | 10 | 0.606  |
| R. pseudoacacia |       | 7226 ± 5347| 8   | 5914 ± 4915 | 5   | 0.0164* | 4415 ± 2780 | 10 | 3867 ± 2941 | 4 | 0.0482* |

Comparisons were made between means of the different stand types showing significance level: "***" *p* ≤ 0.001; "**" *p* ≤ 0.01; "*" *p* ≤ 0.05.

![Figure 1](image_url) Mean of biomass in g per tree of the different poplar genotypes growing in pure stands at the fertile (a) and the marginal (b) site after a rotation time of 5 years. The different letters (a-e) indicate significant differences between the genotype means (*p* < 0.05).

At the fertile site, mortality of poplar did not differ between pure and mixed stands, with one exception (Hybride 275, Table 5). At the marginal site, however, 5 out of 8 genotypes...
Comparisons were made between means of the different stand types showing significance level '*' $p \leq 0.05$. 

**TABLE 5** Mortality at plot level (mean ± SD in %)

| Genotypes          | Fertile site |         |         |         | Marginal site |         |         |         |
|--------------------|--------------|---------|---------|---------|---------------|---------|---------|---------|
|                    | Mixed        | Pure    | p       | Mixed    | Pure          | p       | Mixed    | Pure    |
| AF2                | 67 ± 7.4     | 67 ± 12 | 0.993   | 83 ± 17  | 29 ± 21       | 0.0214* |
| Fritzi Pauley     | 92 ± 6.3     | 71 ± 15 | 0.465   | 63 ± 30  | 26 ± 13       | 0.081   |
| Hybride 275       | 44 ± 21      | 10 ± 4.0| 0.0187* | 15 ± 20  | 7.0 ± 6.0     | 0.436   |
| I214              | 61 ± 21      | 51 ± 26 | 0.764   | 46 ± 22  | 16 ± 5.6      | 0.0349* |
| Matrix 11         | 46 ± 14      | 32 ± 15 | 0.683   | 44 ± 19  | 6.0 ± 4.0     | 0.0111* |
| Matrix 49         | 33 ± 0.7     | 29 ± 26 | 0.910   | 60 ± 27  | 7.0 ± 6.0     | 0.0188* |
| Max 1             | 5.8 ± 7.4    | 8.0 ± 7.3| 0.901  | 1.9 ± 3.8| 2.0 ± 2.3     | 0.994   |
| Muhle Larsen      | 69 ± 6.3     | 67 ± 13 | 0.946   | 75 ± 16  | 30 ± 17       | 0.0168* |
| Robinia pseudoacacia | 22 ± 14  | 25 ± 9.1| 0.601   | 12 ± 9.8 | 23 ± 9.3      | 0.0116* |

Comparisons were made between means of the different stand types showing significance level '*' $p \leq 0.05$. 

**FIGURE 2** Performance of the different poplar genotypes regarding mean biomass (g tree$^{-1}$) and mean survival rate (%) in mixed and pure stands after a 5-year rotation period in the fertile (a) and in the marginal site (b). Dashed lines show the mean values across all poplar genotypes and stand types at the given site.
showed significant higher mortality when growing in mixtures. None of the genotypes showed statistically significant higher mortality in pure stands at any site (Table 5).

3.3 | Biomass yield of the different stand types

Productivity differed between pure and mixed stands, between sites and poplar genotypes. *R. pseudoacacia* in monoculture yielded an estimated aboveground wood biomass production of 45 odt ha⁻¹ (oven dry tonnes per hectare) at the fertile site (Figure 3). At the marginal site, it produced one-third less biomass (30 odt ha⁻¹), (Figure 3). The estimated biomass production of poplar differed between genotypes. At the fertile site, total estimated biomass of the pure stands ranged from 4.1 odt ha⁻¹ for Muhle Larsen and 21 odt ha⁻¹ for Max 1. At the marginal site the same genotypes built the top and the rear of the ranking, ranging from 0.39 odt ha⁻¹ for Muhle Larsen and 3.7 odt ha⁻¹ for Max 1 in pure stands.

The estimated total biomass production of the mixtures ranged from 23.85 to 40.30 odt ha⁻¹ (mixtures with Muhle Larsen and I214, respectively) at the fertile site and 15.44 to 21.20 odt ha⁻¹ (mixtures with Max 1 and AF2) at the marginal site. There, poplar’s proportion in the mixtures varied between <1% of the total biomass (Fritzi Pauley, AF2, Matrix 49 and Muhle Larsen) to 7% (Max 1). At the fertile site the contribution of poplar ranged varied between <1% (Fritzi Pauley) and 32% (Max 1).

By comparing productivity at the non-transgressive level, we observed significant overyielding only for two of the poplar–black locust mixtures at the fertile site, namely the mixtures with the genotypes AF2 and I214 (Figure 3; Table 6). At the fertile site, the highest overyielding rate was reached by the mixture with the genotype I214 with 63% more biomass. At the marginal site, four genotypes in the mixtures showed significant overyielding (Figure 3; Table 6). At the marginal site, the mixtures with AF2 and Fritzi Pauley topped the ranking with rates around 35% and 36% overyielding.

The growth of *R. pseudoacacia* in the mixtures was influenced by the genotype with which it was growing with (Figure 4). At the marginal site, there is a significant negative relationship between poplar’s biomass in mixture and the biomass of black locust. The most productive genotype (Max 1) drove to the lowest black locust biomass production in mixtures. No such significant relationship could be found at the fertile site.

4 | DISCUSSION

The aim of mixing a nitrogen demanding tree species such as *Populus* sp. with a legume tree species (*R. pseudoacacia*) was to increase tree growth by improving N availability. How successful such combinations of N-fixing and N demanding tree species can perform in short-rotation plantings were shown by Forrester et al. (2004) and Hansen and Dawson (1982). Whereas the former studied mixtures of *Eucalyptus globulus* Labill. and *Acacia mearnsii* De Wild., the latter reported on combinations of *Alnus glutinosa* (L.) Gaertn. and *Populus* hybrids. Beneficial effects of a N-fixing species on a N demanding were also found in mixtures of black locust on poplar. For example, Oliveira et al. (2018) observed transgressive overyielding in SRC mixtures of *R. pseudoacacia* and *Populus alba* at the end of the first rotation at a mixed rate of 75% *Populus* and 25% *Robinia*. Rédei et al. (2006) also reports overyielding in mixed forest stands with *Populus alba* and *R. pseudoacacia*. In our previous work about mortality (Rebola-Lichtenberg et al., 2019) and facilitation and competition (Rebola-Lichtenberg et al., 2021) in mixed poplar-black locust SRC, we came, however, to the conclusion that *R. pseudoacacia* affected the overall performance of poplar mostly negatively due to its advanced growth and dominance in the crown layer. This study assessed total biomass yield at the end of the first short rotation of 5 years and underpins the findings of our previous studies.

4.1 | Biomass production in pure stands

Although for black locust the biomass production of 8.9 odt ha⁻¹ yr⁻¹ at the fertile site and 5.9 odt ha⁻¹ yr⁻¹ at the marginal in pure stands was rather satisfactory, the performance of poplar was generally very low. At the fertile site, even the best-performing genotype (Max 1) produced less than half of the biomass of black locust in monoculture. The biomass production ranged from 0.82 odt ha⁻¹ yr⁻¹ for Muhle Larsen to 4.2 odt ha⁻¹ yr⁻¹ for Max 1. At the marginal site, production ranged from 0.08 to 0.75 odt ha⁻¹ yr⁻¹ with the same genotypes occupying the upper and lower limits as at the fertile site. Although poplars belong to the fastest growing tree species in the temperate zone, it seems as if high productivity can be expected only under high below- and aboveground resource availability (Monclus et al., 2006; Stanturf & Oosten, 2014; Stettler & Bradshaw, 1996; Vítková et al., 2017). It is, for example, well known that highly productive hybrids used in SRC are usually intolerant to drought (González-González et al., 2017; Monclus et al., 2006). All four poplar species involved in the parentage (*P. nigra*, *P. deltoides*, *P. trichocarpa* and *P. maximowiczii*) grow naturally on moist sites along rivers, streams and flood plains (Richardson et al., 2014). Therefore, repeated irrigation is recommended for poplars in SRC (Knut, 2009; Stanturf & Oosten, 2014). The fact, that our sites differ from the...
FIGURE 3  Dry biomass yield estimation for the different poplar genotypes and black locust in pure and mixed stands under fertile and marginal site conditions. Biomass given in oven dry tons per hectare (odt ha\(^{-1}\)) after a first rotation of 5 years. The dashed lines represent no interaction effects between *Populus*-genotypes and *Robinia pseudoacacia*. The continuous lines represent the positive and negative effects (over- or underyielding) in the species mixtures. The significant best model is drawn bold.
FIGURE 3  Continued
natural habitat of poplar and that the experiment was implemented as a low-input-system without irrigation, may have led to water deficits. If water is restricted, photosynthesis is also limited, resulting in inhibited growth (Liu & Dickmann, 1993; Mitchell, 1992). The contrasting performances of the *Populus* hybrids and *R. pseudoacacia* show evidence of the high drought tolerance of the latter, which tolerates dry and poor soils (Nicolescu et al., 2020).

### 4.2 Mixture effects and impact on biomass production

Oliveira et al. (2018) and Rédei et al. (2006) reported a slower growth dynamic of black locust in comparison to poplar. In these two studies, the poplars were able to profit from the natural fertilization without suffering
adverse effects from the competitive pressure exerted by the black locust. In our study, however, we observed, that poplar had a clearly inferior wood biomass growth in comparison with the black locust’s (Figure 3). Because of this extremely high discrepancy, there was soon no expectation of a transgressive overyielding in our mixtures of equal species proportions in comparison with pure stands. Although the lack of absolute – transgressive – overyielding is evident, we still found interactions – positive and/or negative – between the two species. Thus, the poplar genotypes differed in their response to the admixed black locust.

Even though poplar showed lower performance in mixed culture with black locust (Figure 2; Tables 4 and 5; Rebola-Lichtenberg et al., 2019, 2021), a significant non-transgressive overyielding was observed for two mixtures (P. ‘AF2’/R. pseudoacacia and P. ‘I214’/ R. pseudoacacia) at the fertile site and for 4 out of 8 at the marginal site (Figure 3; Table 6). However, in all these cases, it was not poplar that profited from the mixed culture with black locust (Figure 2). Instead, in comparison with monoculture R. pseudoacacia, showed an advanced growth in mixtures at both sites (Table 4). For example, R. pseudoacacia growing in mixtures with the Populus genotype AF2 resulted in a significant overyielding of 28% at the fertile and 36% at the marginal site (Figure 3). Analyzing this result at a species level, it turned out that, at the fertile site, proportionally, a 37% higher biomass production for black locust and a 36% lower biomass production for poplar was found. At the marginal site, these differences were even more severe (with 41% higher biomass for black locust and 78% lower biomass for poplar). This result was surprising since we had expected from other studies that poplar would be the species profiting from black locust neighbours through nitrogen enrichment in the soil (Marron & Epron, 2019; Oliveira et al., 2018; Rédei et al., 2006). Actually, it turned out that R. pseudoacacia had exerted highly competitive pressure on poplars throughout the 5 years. This can be explained by its crowns, which occupied the entire space and received full light from above and partly from the side (Rédei et al., 2018). It seems as if R. pseudoacacia took advantage of the rather narrow crowned poplar genotypes and was able to find the required space that they need for optimal growth (Nicolescu et al., 2020). The dominance of black locust in mixed stands had not only a positive effect on its own growth, but it was also the reason why poplars performed so poorly in mixture (Rebola-Lichtenberg et al., 2021). A recent study did also find evidence of overyielding in mixtures of a poplar hybrid (P. maximowiczii ß P. trichocarpa) and black locust (Schweier et al., 2019). However, like in our study, poplars biomass did not positively respond in the mixture. Instead, the higher black locust growth drove to overyielding of the mixture (Schweier et al., 2019). Comparable results were obtained in a pot experiment (Kawaletz et al., 2013). In that study, black locust when growing together with Quercus robur or Carpinus betulus, showed high growth while suppressing the growth of the two admixed species.

The highest performers of the genus Populus were found for the genotypes Max 1 (P. nigra ß P. maximowiczii), Matrix 11 and Hybride 275 (both P. maximowiczii ß P. trichocarpa) across sites and stand types (Figures 1 and 2). Interestingly, the mixed stands with the best performing poplar genotypes were the ones showing a tendency to non-transgressive underyielding (Figure 3; Table 6). This may be explained by the finding that the higher the genotypes biomass production, the lower the corresponding value of black locust, at least at the marginal site (Figure 4). More specifically, while Max 1 performance (growth and mortality) excelled across sites and stand types in
comparison to the other poplar genotypes, the total biomass production of the mixed stands with this genotype was only average at the fertile site and very poor at the marginal site (showing the lowest total biomass of all mixed stands). It seems as if black locust's biomass growth in those mixed stands was hampered by the relatively strong growth of Max 1. However, the latter could not over-compensate the reduced biomass production of the former. Tree growth is dependent on the efficiency of resource use, which, in return, depends on tree species and stand structure (Binkley, 2011). Both poplar and black locust are dominant, strong light-demanding tree species, intolerant of shade and competition (Bärwolff et al., 2012; Nicolescu et al., 2020; Richardson et al., 2014). The fact that those poplar genotypes were good performers, meant for the black locust higher interspecific competition and lower dominance in the stands. This may be support the theory that competition for light appears to be most critical in mixtures of N-fixing and N demanding trees species (Binkley, 1992). Moreover, the finding suggests that the two best performing genotypes (Max 1 and Hybride 275) were not limited by low N availability, otherwise their growth in mixture with black locust should have been higher than in monoculture.

4.3 Managing mixed short rotation coppice

The main purpose of SRC is usually the production of woody biomass. Increasing productivity is therefore the major objective when analyzing SRCs. Transgressive over-yielding in mixtures is, however, not so often observed, which is why, in most cases, biomass production is still being better achieved in monocultures (Bauhus et al., 2017). Nevertheless, it is possible to achieve transgressive over-yielding in poplar/black locust SRC as observed in Oliveira et al. (2018). Their experiment showed the same high planting density as ours, but the coppices were not, in contrast to ours, managed as a low-input system. Moreover, besides using herbicide (hence preventing weed competition), the plantations were irrigated. In that way, stress caused by water scarcity, as observed in our experiment, was avoided (Stanturf & Oosten, 2014). At Oliveira’s et al. (2018) experiment, the most negative growth response resulted from a mixture of equal proportion of tree species numbers (50% Populus, 50% Robinia). Comparing their results to ours, it seems as if irrigation and/or chemical vegetation management is needed if the aim of the coppice is the maximization of biomass production. Oliveira et al. (2018) obtained highest yield by reducing the number of black locusts to a ratio of 25R:75P. That probably decreased the strength of interspecific competition on poplar. Another option may be the delayed planting of the black locust. However, since the best performing poplar genotypes in our experiment did not benefit from neighboring Robinia, delayed planting is unnecessary on comparable sites, not least for economic reasons. This may just make sense on very poor sites where chemical fertilization may be prohibited for reasons of nature conservation purification of drinking water. For the success of the mixed SRC and achievement of higher biomass yield in comparison with monospecific SRC, it is of utmost importance that, by balancing the mentioned factors, poplars take a dominant or co-dominant role in the stands.

The primary focus of mixing trees species in a stand is, however, usually the improvement of the ecological stability of the system. Structurally diverse ecosystems are more resistant, resilient and adaptable to climate change (Bauhus et al., 2017). In the face of climate change's unpredictability, it is of increasing importance that land-use systems get strengthened in their ability to resist extreme weather conditions. Even though in our experiment monocultures were more productive, the focus on future plantings should be put on more resistant and resilient ecosystems. The dry years and in particular dry spring seasons were advantageous for R. pseudoacacia. More and intensive precipitation over the rotation period could have reversed the outcome, by impacting positive the growth of the Populus hybrids and negative of R. pseudoacacia. Thus, future research will need to explore the various options such as mixture proportions, time of planting etc., to achieve both, high biomass production and creating sustainable and resilient production systems at the same time.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.
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