Genotype identity has a more important influence than genotype diversity on shoot biomass productivity in willow short-rotation coppices

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Abstract
Willow (Salix spp.) short-rotation coppice is commercially grown to produce lignocellulosic biomass to meet renewable bioenergy demands. Most commercial willow coppices are grown in stands of a single genotype, but biomass productivity may be greater in mixed communities, and the productivity in mixed communities may depend on the specific genotypes involved. We assessed the biomass production of four different Salix genotypes (“Björn,” “Jorr,” “Loden,” “Tora”) grown without additional nutrient fertilization during one cutting cycle at three locations in Europe (Uppsala in Sweden, Rostock and Freiburg in Germany) in plots of pure and mixed communities. We evaluated (i) the effect of genotype diversity on shoot biomass productivity, including the evidence for complementarity and selection effects; (ii) the influence of individual genotypes on mixed community productivity; and (iii) the productivity of individual genotypes in response to pure vs. mixed culture. Mean shoot biomass production after the first cutting cycle decreased in the order Rostock (8.7 Mg ha\(^{-1}\)) > Freiburg (6.9 Mg ha\(^{-1}\)) > Uppsala (5.7 Mg ha\(^{-1}\)), with values similar to those for other nonfertilized willow stands after the first growth cycle. Consistently across all three locations, increasing genotype diversity did not significantly affect shoot biomass production. Using Bayesian statistics, the addition of the genotypes “Jorr” and “Loden” was predicted to enhance shoot biomass production, while “Tora” and “Björn” are more likely to reduce shoot biomass production in mixed communities. In addition, we found evidence for a negative selection effect due to the genotype “Tora” performing better in mixed than in pure communities in two of the sites (Freiburg, Uppsala). In conclusion, our results imply that increasing genetic richness has no negative effect on productivity and that there is a potential to design site-specific genotype mixtures of short-rotation coppice promoting both high genetic diversity and high biomass production.

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1 | INTRODUCTION

There have been periods of intense interest in renewable alternatives to fossil fuels, starting with the oil crisis of the 1970s and, more recently, due to global climate change. Currently, a variety of renewable biomass types are used to satisfy the demand for bioenergy. Among these are second-generation biofuels made from lignocellulosic biomass obtained from pure (monocultures) or mixed communities of herbaceous crops (e.g., Miscanthus or switchgrass Panicum ssp.) and woody crops (e.g., willow Salix spp. or poplar Populus spp.) cultivated in short-rotation coppice plantations (Keoleian & Volk, 2005). A considerable amount of research focuses on the breeding of new high-yielding genotypes (Fontana, Lafleur, Labrecque, Courchesne, & Bélanger, 2016) and the link between genotype functional traits and growth. Genotypes with different functional traits can influence ecosystem functions and thus biomass productivity due to variation in their morphological, phenological or ecophysiological attributes (Violle et al., 2007). At the species level, several studies focusing on the relationship between plant trait diversity and productivity have shown that biomass production often increases with increasing species richness and trait dissimilarity (Cardinale et al., 2011; Duffy, Godwin, & Cardinale, 2017; Hooper et al., 2005; Tilman, Isbell, & Cowles, 2014). Although rarely tested to date at the genotype level, biomass production may increase with increasing number of genotypes in a community and the associated increase in trait diversity (Barot et al., 2017).

The often observed increase in productivity with species richness, or net biodiversity effect, can be explained by two mechanisms: the complementarity effect, due to either niche differentiation or facilitation, and the selection effect (Loreau & Hector, 2001; Tilman, Lehman, & Thomson, 1997). Facilitation, where the presence of one community component can improve growing conditions for the other community components, and niche differentiation, where co-existing species occupy different parts of the niche space, can be promoted by functional trait variation between species or genotypes. Niche differentiation can occur when functionally different community components use resources differently in space and/or time, either due to their difference in canopy or due to root system size (Bayer, Seifert, & Pretzsch, 2013; Craine & Dybzinski, 2013) or the timing of important phenological events such as bud burst or bud set (Weih, 2009). The resulting partitioning of resources can improve community productivity (Brassard, Chen, Bergeron, & Pare, 2011; Chamagne et al., 2017; Hooper & Vitousek, 1997). Positive selection effects arise when a highly productive species or genotype dominates mixtures, which can lead on average to a higher biomass production. Conversely, negative selection effects occur when a less productive species or genotype dominates mixtures (Loreau & Hector, 2001; Tilman et al., 1997). Thus, complementarity and selection effects occurring in mixed stands can result in an increased community productivity compared to their respective pure stands.

Besides species richness, genetic richness plays an equally important role in productivity, especially when trait variation is high (Barot et al., 2017), as is the case in many Salix hybrids bred for biomass production (Kuzovkina et al., 2008). The rapid growth rate, high genetic variation and short breeding cycle in Salix are beneficial features for breeding a high diversity of hybrids. Early breeding programs aimed at developing high-yielding genotypes which resulted in the generation of highly variable hybrids with different expressions of various growth-related phenological, functional and morphological traits (Berlin et al., 2014; Shield, Macalpine, Hanley, & Karp, 2015). This enhanced trait space, potentially available in the combination of different high-yielding Salix genotypes, could lead to niche differentiation when realized by cultivating different genotypes together.

In this study, we focus on the productivity of four selected Salix genotypes planted at three sites along a latitudinal gradient. The four Salix genotypes are planted commercially and differ in their phenology, morphology and nitrogen-use characteristics (Weih & Nordh, 2002). For example, the two taxonomically closely related genotypes “Björn” and “Tora” differ in their morphological (e.g., diameter and leaf area) and functional characteristics (e.g., leaf nitrogen concentration) whereby “Tora” is one of the highest productive genotypes and “Björn” one of the lowest productive ones among the four genotypes investigated here (Weih & Nordh, 2002; Figure 1). “Jorr” has high leaf area productivity, and the broad-leaved genotype “Loden,” taxonomically most distant from the other three genotypes, is characterized by high leaf area ratio (Weih & Nordh, 2002). Results from a limited number of previous long-term studies have shown that mixing willow genotypes may

**KEYWORDS**

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enhance biomass production, but also that a positive effect of mixing genotypes on production is not consistent and depends on the specific genotype mix (Dawson & McCracken, 1995; McCracken et al., 2011). These results suggest a prominent role of genotype identity for the expected effect of genotype mixtures on productivity, but the specific effects of genotype identity on the productivity in mixtures have only rarely been investigated (Dillen et al., 2016). Based on previous results and ecological theory (e.g., Loreau & Hector, 2001), we expect that (1) community shoot biomass in willow plantations increases with increasing genetic richness (i.e., number of genotypes grown in the community) and (2) the increase in community biomass production (net diversity effect) is promoted more by a complementarity effect than by a selection effect. To test these hypotheses, shoot biomass of all willow plants grown in planted communities (plots) with different mixtures was assessed.

In addition to investigating the effect of genotype diversity on shoot biomass productivity, including the associated mechanisms, we were interested in testing the specific effects of genotype identity on the productivity in mixed communities (plots). Specifically, we aimed at testing the influence of the presence or absence of individual genotypes on mixed community (plot) productivity and the productivity of individual genotypes in response to pure vs. mixed culture. A previous study using two Salix genotypes (“Tora” and “Loden”) with contrasting functional traits, container-grown under semicontrolled conditions, showed a higher biomass production in one of the genotypes when grown in mixtures as opposed to monocultures, while the other genotype showed the opposite pattern (Hoeber, Fransson, Prieto-Ruiz, Manzoni, & Weih, 2017). Based on these results, we sought to estimate probabilities for increased biomass productivity when specific genotypes were grown in mixed communities (plot) compared to monoculture. To estimate these effects, we used Bayesian statistics to extract genotype- and community-specific predictions from our models, where the probability and magnitude of differences between groups could be easily calculated from posterior distribution estimates. Thus, we tested whether (3) the addition of individual genotypes to a given community increases community (plot) productivity and whether (4) individual genotype productivity is greater when grown in mixture as compared to monoculture. Due to the high trait variation in the four Salix genotypes used here, we expect positive and negative effects of the individual genotypes on the overall community (plot) productivity. More specifically, we expect that the genotype “Loden” has a negative effect on the overall community (plot) productivity considering its higher leaf area (Figure 1) and that “Tora,” as a result of its higher productivity in monoculture, benefits from the presence of other genotypes due to niche differentiation.

2 MATERIALS AND METHODS

2.1 Experimental design

Three field trials were established on arable land in Uppsala, Central Sweden (59°49’ N 17°39’ E), Rostock, Northern Germany (54°02’ N 12°05’ E), and Freiburg, Southern Germany (48°01’ N 7°49’ E) in May 2014 (hereafter Uppsala, Rostock and Freiburg). The three sites together comprise the ECOLINK-Salix project, the goal of which is to investigate the relationship between genotype diversity, genotype identity, productivity and ecosystem function. ECOLINK-Salix is also part of a larger global tree diversity network (TreeDivNet), which aims at exploring the relationships between tree species or genotype diversity and ecosystem function (Verheyen et al., 2016).

Cuttings of four Salix genotypes, all of them grown commercially (for detailed genotype specifications, see Weih & Nordh, 2002), were obtained from the same stock. All four genotypes were planted in Uppsala and Freiburg: “Björn” (Salix schwerinii E. Wolf. × S. viminalis L.), “Jorr” (S. viminalis), “Loden” (S. dasyclados Wimm.) and “Tora” (S. schwerinii × S. viminalis). The design for Uppsala and Freiburg consisted of all monocultures and various mixtures of the four genotypes (two, three and four

![Figure 1 Schematic overview of some important genotype characteristics: The mean shoot height, diameter and leaf area ratio of the four Salix genotypes (“Björn,” “Jorr,” “Loden” and “Tora”) according to previously published data from pot-grown plants (Weih & Nordh, 2002) are shown. Typical genotype-specific shoot heights are illustrated by the different heights of the schematic trees in the figure. The numbers in the lower part of the figure indicate normalized shoot diameters (individual diameter divided by the maximum value of the four genotypes), and the numbers in the upper part indicate normalized figures for the genotype’s leaf area ratios.](image-url)
mixtures) planted in a randomized block design with three blocks (total number of plots \( n = 45 \); Figure 2). In Rostock, space and funding restrictions strongly compromised trial size, and only the two genotypes “Loden” and “Tora” and the mixture could be planted (but in all other aspects, the design was the same). While two-genotype mixtures were planted in a checkerboard pattern, in the three- and four-genotype mixtures planting positions were randomized, with the constraint that individuals of the same genotype should not be directly adjacent to each other within rows. In addition, for each block, the procedure was repeated (Figure 2; “Plot design”). Plots measured 9.6 m × 9.6 m in size and contained 12 rows with 12 plants in each row with an offset every second row, resulting in a hexagonal planting pattern with equal distances of 0.8 m between individuals (Figure 2). This spacing corresponds to approximately 15,600 plants ha\(^{-1}\). The total field size in Uppsala and Freiburg was 4,150 m\(^2\) and was 830 m\(^2\) in Rostock (for further details on the Freiburg site, see Müller, Klein, Scherer-Lorenzen, Nock, & Staab, 2018).

2.2 | Experiment establishment

The preparation of the field trials started in early autumn 2013 by either spraying with Roundup (glyphosate; 4 L ha\(^{-1}\)) to kill perennial weeds (in Uppsala and Rostock) and/or plowing (in Freiburg, Rostock and Uppsala). In spring 2014, just before planting, the site was cultivated with a rotavator. The trials were then manually planted using c. 18 cm long stem cuttings that had been soaked in water for 2 days. The cuttings were inserted into the soil, so that the top of the cutting was even with the surrounding soil.

In early summer 2014, we weeded occasionally using handheld tools and targeting the most weed-infested spots. In 2015 and 2016, weeds were suppressed by mowing between rows when needed using a lawn mower. No fertilizer was applied during the first cutting cycle.

Soil characteristics and climatic conditions during the growing period and during a 30 year period between the three field sites are given in Table 1.

2.3 | Biomass assessment

During the winter of 2016/2017 (three growing seasons after planting), all individual shoots within the measurement area of \( 8.0 \times 3.2 \) m = 26.24 m\(^2\) (Figure 2, red-colored area in the plot design) were cut 10 cm above ground and weighed (fresh weight) to the nearest 10 g. The assessments per measurement area were later upscaled to one hectare for comparison with other studies. A stratified sampling of 30 shoots per genotype was performed among the plants outside the measurement area of all monoculture communities (plots) to determine the relationship between shoot fresh and dry weight (shoot biomass). The fresh weight of each shoot was recorded, and the shoot biomass was determined after oven-drying each sample at 70°C for 96 hr. The stratified sampling was only performed in the monoculture communities (plots) because allometric relationships in the mixed communities (plots) were not found to differ from the monoculture communities (plots) (pilot study, unpublished data).

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**FIGURE 2** Left: The randomized block design of the field trials in Uppsala and Freiburg, with three blocks (I to III) and communities (plots) of various genotype monocultures and mixtures consisting of up to four *Salix* genotypes (A = “Björn,” B = “Jorr,” C = “Loden,” D = “Tora”). Each block included 15 communities (plots) (in total 45 plots) with a size of 9.6 m × 9.6 m. Right: Example of a single community (plot) consisting of nine subplots and including three genotypes, illustrating the randomized planting pattern (different colors indicate different genotypes) and the displaced row (system); the red area indicates the measurement area of 8.0 × 3.2 m in which plants were sampled destructively (see Material and Methods).
In only five communities (plots) in Freiburg, the biomass could not be measured as there were no living trees taller than 50 cm in the sampling area. This lower growth was primarily driven by higher skeletal fraction compared to the remaining plots (Zur Loye, 2015).

To compare the individual genotype characteristics used in Figure 1 with the corresponding genotype characteristics in our field study, we compiled the corresponding data from the field trial in Uppsala. Thus, 12 plants (per genotype) in each monoculture community (plot) were selected for assessment of leaf area and leaf biomass (three replicated plots, 36 plants per genotype in total), and the specific leaf area (SLA) was calculated as the leaf area per leaf biomass. In each monoculture community (plot), all shoot diameters at 50 cm above ground were measured for all individual plants, that is 144 plants per genotype and monoculture plot. To determine the mean height of all 144 individual plants in the monoculture communities (plots), a (power law) relationship between height and diameter was determined by measuring 30 shoots per genotype in height and diameter.

### 2.4 Diversity effects

We calculated the diversity effects using the additive partitioning equation from Loreau and Hector (2001), replacing species by genotype (Equation 1). We used the biomass measured in the sampling area (n = ~40 individuals per plot; Figure 2) and the proportion of surviving individuals of each genotype within the sampling area in each community (plot). In Equation 1, the net biodiversity effect is defined as the additive partitioning of two biodiversity effects: (1) the complementarity effect, which is measured by \( N \Delta R Y M \), and (2) the selection effect, which is captured by \( N \text{cov}(\Delta R Y, M) \).

The net effect measures the deviation from the mixture yield from its expected yield based on the yield in monocultures and the proportion of each genotype in each mixture. We calculated the complementarity effect, selection effect and net effect for each two-, three- and four-mixture communities (plots) at each site.

\[
\Delta Y = Y_o - Y_E = \sum_i RY_{o,i}M_i - \sum_i \Delta RY_{E,i}M_i = \sum_i \Delta RY_iM_i = N\Delta R Y M + N \text{cov}(\Delta R Y, M)
\]

\( \Delta Y \) = net biodiversity effect

\( Y_o \) = observed yield of genotype \( i \) in the mixture

\( Y_E \) = expected yield of genotype \( i \) in the mixture

\( RY_{o,i} \) = observed relative yield of genotype \( i \) in the mixture

\( RY_{E,i} \) = expected relative yield of genotype \( i \) in the mixture

\( M_i \) = yield of genotype \( i \) in the monoculture

\( \Delta RY_i \) = \( RY_{o,i} - RY_{E,i} \) = deviation from expected relative yield of genotype \( i \) in the mixture

\( N \) = number of genotypes in mixtures

### 2.5 Data analysis

We summed shoot biomass of all genotypes of the sampling area to refer to shoot standing biomass per area, hereafter community (plot) shoot biomass (Mg ha\(^{-1}\)). Genotype shoot biomass per plant (g plant\(^{-1}\)) is the community (plot) mean individual plant shoot biomass of a specific genotype when grown either in monoculture or together with other genotypes.

All statistical analyses were conducted in R (version 3.3.3; R Core Team 2017).

Shoot biomass was determined by relating genotype-specific shoot fresh weight and dry weight (shoot biomass) from the stratified sampling. Using the resulting genotype-specific linear regression (shoot biomass = \( a + b \times \) shoot...
fresh weight), shoot biomass per individual plant was calculated. A linear model was used to test the effect of shoot fresh weight, genotype and site on shoot biomass. Shoot biomass was used as a proxy describing productivity of specific genotypes.

We performed a restricted maximum-likelihood mixed-effects model (REML) to test whether community shoot biomass increased with genetic richness, with genetic richness defined as a fixed-effects variable [lmerTest package: “lmer” by Kuznetsova, Brockhoff, and Christensen (2017)]. Site, mixture combination and block were included as random-effects variables, with block nested within site, to account for the amount of residual variance that they explained (Schmid, Baruffol, Wang, & Niklaus, 2017; Schmid et al., 2002). To explain the variance of the fixed factors, the marginal $R^2$ was obtained. In addition, the conditional $R^2$ was obtained to explain the variance by both fixed and random factors [MuMIn package by Bartón (2010)].

To assess whether the complementarity effect, selection effect and net diversity effect were significantly different from zero, two-sided one-sample Student’s $t$-test was performed for each genetic richness level separately (two, three and four mixtures) at each site.

For the analyses at the genotype level, a Bayesian ANOVA-like mixed model was used to calculate the probability and range of credible values that adding a specific Salix genotype to a community with other Salix genotypes would have on average shoot biomass per plant in that community. Here, the model parameters allowed the shoot biomass for any combination of Salix genotypes in a community to be estimated (Supporting Information Supplement a). From this model, we derived biomass estimates for the different community genotype combinations. This allowed us to then compare the estimated differences for all possible community combinations with and without a specific genotype. Because outputs from Bayesian models are posterior probability distributions, all variables derived from these outputs are also probability distributions. This means that we could subtract the estimated biomass for each community from its equivalent with a specific genotype added to find the magnitude and direction of an effect of adding that genotype to the community. By taking the mean of all of these differences, we derived the probability and range of estimated effect that the addition of a specific genotype to a general plant community favors an increase in the plot-level community shoot biomass per plant (see Supporting Information Supplement a). Parameters and derived variables where the posterior distribution largely overlaps zero were considered relatively unimportant or having little effect (Hobbs & Hooten, 2015). All Bayesian models were implemented in JAGS (Plummer, 2003) via the “rjags” package in R. Model convergence was checked by visual inspection of trace plots and using the Gelman and Rubin diagnostic (all estimated parameters <1.1; Gelman & Rubin, 1992). Model validity was assessed using posterior predictive checks and Bayesian “$p$” values (Hobbs & Hooten, 2015). Priors, for example previous estimated values, were weakly informative and centered on expected values from our field studies to speed model convergence (McElreath, 2015; see Supporting Information).

We used a Bayesian hierarchical linear model to calculate the probability and range of credible values of genotype-specific shoot biomass for plants grown in monoculture versus those grown in a crop mixture (two, three and four). For this, the model included parameters for the number of additional genotypes present in the mixture, so we could compare shoot biomass per plant for each genotype when grown in monoculture versus increasing levels of cropping mixtures (Supporting Information Supplement b).

## 3 RESULTS

In most of the communities (plots), canopies were closed during the summer prior to the shoot harvest, which was indicated by leaf area index (LAI) figures ranging from <1 to about 4.5 recorded in Uppsala and Freiburg in August 2016 (mean LAI ± SD was 1.8 ± 0.8 for Freiburg and 1.0 ± 0.3 for Uppsala, respectively, data not shown). Genotype-specific regression analysis between shoot fresh and dry weights of the separately sampled shoots revealed reliable equations (Table 2) that could be used to convert the fresh weights of the shoots sampled within the measurement area (Figure 2) into shoot biomass used in all further analysis.

### 3.1 Effect of genotype diversity on shoot biomass productivity

In Freiburg and Uppsala trials, the plant survival rate per community (plot) ranged from 70% to 100%, with mean survival rates of 88% in Freiburg, 97% in Uppsala and 100% in Rostock (data not shown). In the sites accommodating all four genotypes, the mean shoot biomass per community (plot) ranged from about 1.9–15.2 Mg ha$^{-1}$ in Freiburg and 2.8–9.2 Mg ha$^{-1}$ in Uppsala. In Rostock, where only two genotypes were represented, the mean shoot biomass per community (plot) varied between 4.6 and 15.8 Mg ha$^{-1}$. Mean shoot biomass across all communities (plots) was greatest in Rostock (8.7 Mg ha$^{-1}$), lower in Freiburg (6.9 Mg ha$^{-1}$) and lowest in Uppsala (5.7 Mg ha$^{-1}$; see Figure S1).

Across all sites, community (plot) shoot biomass did not increase with genetic richness on the plot ($p = 0.79$, Table 3, Figure 3). Of all random-effects variables, site accounted for the biggest amount of model variance. The
**TABLE 2** Linear regression model between shoot biomass and shoot fresh weight (FW) to analyze the effect of fresh weight and four *Salix* genotypes (“Björn,” “Jorr,” “Loden,” “Tora”) grown in three field sites (Uppsala, Rostock and Freiburg) for 3 years (first rotation) on biomass. Exact p-values are given at p < 0.05; n.s. indicates no significance. Linear regressions (LiRe) between fresh weight and dry weight of a selected number of shoots were used to obtain dry weights per genotype.

| Variables       | Freiburg | Rostock | Uppsala |
|-----------------|----------|---------|---------|
| Intercept (“Björn”) | n.s.     | –       | n.s.    |
| “Jorr”          | n.s.     | –       | n.s.    |
| “Loden”         | n.s.     | n.s.    | n.s.    |
| “Tora”          | n.s.     | n.s.    | n.s.    |
| “Jorr” × FW     | n.s.     | –       | 0.00205 |
| “Loden” × FW    | n.s.     | –       | n.s.    |
| “Tora” × FW     | n.s.     | 0.00215 | <2.00e-16 |

LiRe “Björn” \( \hat{y} = -3.791 + 0.4543^* x \) \( \hat{y} = 40.9858 + 0.5385^* x \)

LiRe “Jorr” \( \hat{y} = 35.622 + 0.4097^* x \) \( \hat{y} = 31.18135 + 0.58966^* x \)

LiRe “Loden” \( \hat{y} = 0.0448 + 0.4879^* x \) \( \hat{y} = -0.0898 + 0.5187^* x \) \( \hat{y} = 41.71393 + 0.56178^* x \)

LiRe “Tora” \( \hat{y} = -0.6698 + 0.4357^* x \) \( \hat{y} = 4.3929 + 0.481^* x \) \( \hat{y} = 17.189059 + 0.507281^* x \)

**TABLE 3** Summary of restricted maximum-likelihood mixed-effects model on the effect of genetic richness (fixed-effects variable), block nested in site, site and mixture (as random-effects variables) on plot-level community shoot biomass. Reporting fixed and random effects separately. Marginal \( R^2 (R^2 \text{marg}) \) and conditional \( R^2 (R^2 \text{cond}) \) are also reported.

| Fixed effects | Estimate | SE  | T value | p>||\( t \)\> | \( R^2 \text{marg} \) |
|---------------|----------|-----|---------|---|-----------------|-----------------|-----------------|
| Genetic richness | 0.07297 | 0.27561 | 0.265 | 0.7919 | 0.00046 |

| Random effects | Variance | SD  | \( R^2 \text{cond} \) |
|----------------|----------|-----|---------------------|
| Mixture        | 1.250e-14 | 1.118e-07 | 0.41 |
| Block: site    | 5.342e-01 | 7.309e-01 |
| Site           | 3.298     | 1.816 |
| Residuals      | 5.420     | 2.328 |

conditional \( R^2 \), which describes the proportion of variance explained by both the fixed and random variables, was 0.41. With a value of 0.00046, the marginal \( R^2 \), which describes the proportion of variance explained by genetic richness alone, was very small. This is further evidence for the poor explanatory power that can be allocated to the genetic richness.

The importance of net diversity effects, complementarity effects and selection effects varied across the experimental sites (Figure 4). Complementary effects were mostly positive, however, only statistically significant in the two-genotype mixtures in Uppsala (\( p < 0.05 \)). We also found a significant, negative complementarity effect in the four-genotype mixtures in Freiburg (\( p < 0.05 \)). All selection effects were negative but only significantly different from zero in the two- and three-genotype mixtures in Uppsala.

**FIGURE 3** Mean community (plot) shoot biomass (Mg ha\(^{-1}\)) including standard error with increasing genetic richness (i.e., plots with one to four genotypes) for the Salix trials in Freiburg, Uppsala and Rostock.
(\(p < 0.05\) and \(p < 0.01\), respectively). Net diversity effects were not significantly different from zero.

### 3.2 Influence of presence or absence of individual genotypes on mixed community productivity

The probabilities for individual genotypes to increase community (plot) productivity varied between the locations and genotypes investigated here (Figure 5). For example, the probability for “Björn” to exert a positive effect on the community (plot) shoot biomass was 0.22 in Freiburg and 0.32 in Uppsala. This indicates that “Björn” had mostly a negative effect (probabilities of negative effect = 0.77 and 0.68; where a probability of 0.5 indicates no effect) on the community (plot) shoot biomass on both sites. Besides the generally greater variation within genotypes observed in the Freiburg data compared to Uppsala data, probability patterns for the individual genotypes to increase community (plot) productivity were similar (in terms of both magnitude and direction) in the data from the two locations (Figure 5). Thus, the addition of “Jorr” is very likely to exert a positive effect on the community (plot) shoot biomass production (with probabilities of 0.96 and 0.99; Figure 5). Also, the genotype “Loden” is likely to positively affect community (plot) productivity, but at a lower probability level compared to “Jorr” (probabilities of positive effect between 0.85 and 0.82), whereas the presence of “Tora” is likely to reduce community (plot) productivity, at a similar probability compared to the positive effect of “Loden” (probabilities of negative effect for “Loden” between 0.88 and 0.82).

### 3.3 Productivity of individual genotypes in response to pure vs. mixed culture

When grown in pure culture, the four genotypes differed markedly from each other (Supporting Information Table S2). The productivity response of individual genotypes to cultivation in mixture (Figure 6) was different from the effects of the same individual genotypes on community (plot) productivity (Figure 5). The shoot biomass of individual genotypes varied greatly between cultivation in monoculture and mixed communities (plots) (Figure 6; Table 4). The positive values (Figure 6 and Figure S2) indicate a higher genotype-specific shoot biomass when the corresponding genotype was grown in mixture compared to the monoculture, whereas negative values indicate a lower genotype-specific shoot biomass in the mixture compared to the monoculture. Individual genotype responses to pure vs. mixed culture partly varied between the experimental sites. Thus, for “Björn,” the genotype-specific shoot biomass in the mixtures was either lower (Freiburg data, probability of negative effect = 0.90) or higher (Uppsala data, probability of positive effects = 0.83) compared to its biomass achieved in monoculture. In addition, the effect of mixed culture on genotype performance was not consistent across the types of mixtures (e.g., mixtures of two, three or four genotypes). For example, in Freiburg, “Loden” showed a negative genotype-specific shoot biomass in the mixture with four genotypes (probabilities of negative effect between 0.98 and 0.96) compared to the monoculture, whereas the same genotype showed a positive genotype-specific shoot biomass when grown in the mixture with three genotypes (probability = 1). Based on the data from Freiburg and Uppsala (including all genotypes and genotype mixtures), “Tora” is very likely to perform better in all the mixtures with two and three genotypes compared to the corresponding monocultures (probabilities of positive effects between 0.96 and 0.99), whereas the data from Rostock (including only the genotypes “Tora” and “Loden”) suggest a poorer performance of “Tora” in the mixture with “Loden” than its monoculture (probability of negative effect = 0.93). Compared to its monoculture, “Loden” is predicted to perform better in its mixture with “Tora” based on the data from Freiburg, but not from Uppsala (Figure 7, Supporting Information Table S1).
DISCUSSION

Plantations of willows (Salix spp.) are a promising source of lignocellulosic biomass in many regions worldwide. Contrary to the current practice of growing plantations with single genotypes, it seems that genetically more diverse production systems including a wide range of traits are able to more efficiently utilize the niche space of the production system, thus reducing resource losses and enhancing environmental performance (Weih, Hoeber, Beyer, & Fransson, 2014). Exploiting this diversity-driven improvement of resource-use efficiency and environmental performance could be a useful strategy in the design of novel and more sustainable production systems for lignocellulosic biomass. The results from this study provide insights into the complex interactions between multiple genotypes of Salix spp. and their effects on productivity. In general, the biomass yield levels in this study were low but similar to those of other nonfertilized willow trials (Weih & Nordh, 2005). The nonfertilized conditions applied here are motivated by the frequent recommendations to establish willow short-rotation coppice on marginal sites with low soil quality, to avoid competition with food and feed production land (Knur, Murn, & Murach, 2008). In addition, there is evidence that diversity effects on productivity are more pronounced in low-resource conditions favoring diversity by providing a wider range of niches compared to high-resource conditions (Wedin & Tilman, 1996). In our study, canopy closure occurred only in the final year before harvest, but resource competition in terms of, for example, reduction of soil resource availability by neighboring plants (Craine & Dybzinski, 2013) may have occurred during at least two growing seasons. Nevertheless, increasing diversity of genotypes did not have significant effect on community productivity in this study, indicating that mixtures performed similar to the monocultures (at plot level) during the first cutting cycle. However, there were positive and negative effects on community and genotype productivity (both at plot level) when examining the individual genotype-specific relationships, indicating the importance of genotype identity for the productivity of the whole community and also the performance of individual genotypes when grown in different mixture combinations.

This is one of the first studies to systematically evaluate the effects of genotype identity and diversity for a commercially used biomass crop across different sites and using commercially bred plant material. Although we were unable to establish the full experimental design at all locations, because the trial at Rostock only accommodated two genotypes and their mixture, the results obtained are relevant for many locations with similar climatic and soil conditions. In addition to the exploration of diversity–productivity patterns in young willow stands, hypotheses were developed and tested beyond the pure description of diversity effects on productivity (Cardinale et al., 2011) and targeting, in a first attempt, the potential mechanisms behind the frequently described effects of diversity on diversity–productivity patterns in young willow stands, hypotheses were developed and tested beyond the pure description of diversity effects on productivity (Cardinale et al., 2011) and targeting, in a first attempt, the potential mechanisms behind the frequently described effects of diversity on
These hypotheses were developed based on the characterization of the relevant genotypes obtained from a previous study (Figure 1) and explored by applying appropriate statistics (here Bayesian statistics). Using a Bayesian approach, it was possible to assign probabilities to specific hypotheses related to individual genotypes enhancing community performance and hence the importance of genotype identity for community productivity. The methodology used here also appears promising for the exploration of similar hypotheses using different crops or production systems.

In general, the mean biomass production at our three sites is similar to the biomass production reported in other mixed willow clone short-rotation coppice plantations (Dillen et al., 2016; McCracken et al., 2011) where values between 5 and 10 Mg ha\(^{-1}\) were found. Specifically, our first hypothesis was that community shoot biomass in the plantations increases with increasing genetic richness. The data from our study provides no convincing evidence in support of this hypothesis, as we did not find any effect of increasing genetic richness on community shoot biomass, and hence, no positive net biodiversity effect at any of the three sites investigated here. This result is in line with a similar study by Dillen et al. (2016) investigating three \textit{Salix} genotypes growing in monoculture and mixture. The authors found that there were no differences in productivity with increasing genetic richness as well as no significant diversity effects during the first cutting cycle.

We also could not find much evidence in support of our second hypothesis, postulating complementarity effects to drive responses in biomass production. We only found negative selection effects in our study (albeit statistically significant only for some of the mixtures in the Uppsala data, Figure 4), which is similar to the findings reported by other studies (Cardinale et al., 2007; Hooper & Dukes, 2004). The observed negative selection effects arise due to the presence of a less productive genotype dominating the
From both an ecological and an agronomical perspective, it is interesting to identify whether the presence of a specific genotype is likely to have a positive, neutral or negative effect on the community productivity. Here, we found that all genotypes consistently showed the same pattern across the two locations with the full design (i.e., Uppsala and Freiburg) when analyzing the probability of individual genotypes to increase community productivity (Figure 5). Thus, the presence of the genotypes “Jørn” or “Loden” in mixtures involves a high likelihood to increase community productivity, while the presence of “Tora” or “Björn” is associated with an increased risk of a negative impact on community productivity. The potentially negative impact of “Tora” and “Björn” on community productivity could be associated with the greater height of these two genotypes compared to the other two genotypes (Supporting Information Table S2). The greater shoot growth performance could enable these genotypes to outgrow the other genotypes when grown in mixtures, lowering the mean growth of the entire community and decreasing community productivity. On the one hand, despite its increased growth in mixture than in monoculture, “Tora” is apparently unable to compensate for the corresponding loss of community productivity caused by its presence (Figure 6). On the other hand, the positive impact of “Jørn” on community productivity could be linked to its morphological and phenological traits such as low height and leaf area (Figure 1) (Weih & Nordh, 2005), providing much space (e.g., light) for other genotypes to grow better. The positive effect of the presence of “Loden” on community productivity could be due to enhanced canopy stratification (“Loden” has generally a lower height growth but greater leaf area than the other genotypes (Weih & Nordh, 2002, 2005)), presumably resulting in the presence of an extended second canopy layer when grown in mixture with other genotypes. In our study, light levels were lower below the canopies of pure “Loden” plots compared with the plots in which “Loden” was mixed with other genotypes (PAR 75 μmol m⁻² s⁻¹ in pure plots vs. 104 μmol m⁻² s⁻¹ in mixed plots, data from Uppsala, not shown). Hence, we
speculate that this genotype could be able to capture light that penetrates the upper canopy made up by other genotypes, which then would profit from the absence of a highly growing competitor. Such a canopy stratification by plants with different traits has been shown to result in complementarity resource use (Kelty, 2006). These examples suggest that aboveground niche differentiation has occurred in these communities, although it has so far not resulted in any positive net diversity effect.

In this study, the individual genotype performance in mixtures increased, decreased or remained similar compared to their productivity in monoculture, although these responses were in part also site specific. For example, performance of “Björn” and “Tora” showed opposing effects to mixing, although both genotypes were the most productive when grown in monoculture (Figure 1, Supporting Information Table S2). In addition, it is noteworthy that “Björn” and “Tora” are taxonomically very close (full siblings; Barker et al., 1999), but performed here differently when grown in monoculture and mixture. If verified, this pattern indicates that small genetic differences can have large effects on productivity in different contexts (here pure vs. mixed culture). In the future, it would be interesting to explore the specific physiological differences between the two genotypes for causing the contrasting performance especially in mixed culture.

A closer look into the relationship between shoot biomass of “Loden” and “Tora,” the two taxonomically most distinct genotypes (Weihe & Nordh, 2002), revealed a contradicting pattern between the three study sites (Figure 7). In Rostock, “Tora” grew better in monoculture compared to its mixture with “Loden,” whereas in Freiburg and Uppsala, the pattern was reversed. Interestingly, the growth pattern of “Tora” seen in the Rostock site was similar to the pattern observed in a pot study in which both genotypes were grown in monoculture and mixture in sandy soil (Hoeber et al., 2017). For example, in the low-fertilization condition of the study by Hoeber et al. (2017), the nitrogen (N) uptake efficiency of “Tora” increased when grown in the presence of “Loden” and when compared to the monoculture, whereas the opposite pattern was observed in the high-fertilization conditions. Thus, the observed differences in the growth pattern of “Tora” between the three sites are possibly linked to its N economy and the site conditions varying between the three locations investigated here (cf. Table 1), but no data on the plant and soil nutrient conditions in the three sites are yet available.

### 4.1 Implications for management

In this study, a planting design of equally spaced neighbors was used, which was appropriate for exploring the objectives and hypotheses of this study. This planting design is different from the design frequently used in commercial willow plantations, but we believe that the main conclusions from our study should also apply to commercial willow plantations, although this needs to be verified.

No clear evidence for increased productivity with genetic diversity in young willow stands was found in this study, but it is possible that a (positive) diversity effect on productivity will evolve as these plantations grow older. Most importantly, our results also imply that increasing genetic richness has no negative effect on productivity. Increased genetic richness, especially when it does not jeopardize production, has also the potential to positively affect the community’s growth due to a decreased risk for pathogen and disease attacks (e.g., Dawson & McCracken, 1995; White, 1982) and thereby higher pest resistance. Mixing genotypes can also have positive effects on other ecosystem services, such as providing habitat for other organisms. In fact, at the experimental site in Freiburg, it has been shown that an increase in genotype diversity leads to higher diversity and abundance of arthropod species (Müller et al., 2018), thus supporting a higher overall biodiversity.

Our results suggest that farmers should pay attention to the plant material they intend to include in mixed plantations, as we found strong effects of genotype identity on both community productivity and genotype performance in mixtures. For example, we found that two of the four commercial genotypes used here had an overall positive effect on the community, and two genotypes had a rather negative effect on the community productivity. Today, genotype recommendations for use in pure culture are common, and future studies should develop specific recommendations also regarding suitability of commercial willow hybrids for culture in mixed stands. In addition, we have here only evaluated mixed communities in which the community components (i.e., genotypes) were grown in equal proportions. It is possible that unequal proportion of certain community components is a promising tool in the management of mixed plantations, which is yet unexplored.

### 5 CONCLUSION

Increasing genetic richness did not change the productivity of willow plantations during the first cutting cycle. However, we demonstrated that the presence of individual genotypes is likely to increase or decrease biomass production in mixed communities. This points to the potential to design specific genotype mixtures to promote biomass production. The genotype-specific impact on the community biomass production varied site specific. Therefore, an optimized mixture of genotypes has to be selected in local site conditions. Subsequent studies should investigate the mechanistic basis for site-specific differences in the genotype combinations to accelerate genotype selection for site-adapted mixtures.
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