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Impact of Increased Genotype or Species Diversity in Short Rotation Coppice on Biomass Production and Wood Characteristics

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Abstract
Short rotation coppice (SRC) plantations are predominantly established as monocultures. Reasons include simplicity and thus efficiency in planting, homogeneous growth, and a desire to maximize yields by selecting top-performing species. However, pests and disease outbreaks generally cause much greater damage to monocultures than to mixed plantations, thus affecting yields as well as other ecosystem services. Mixed SRC with varying genotypes or even species have the potential to positively affect biodiversity and ecosystem services, however, little is known about the quantity and quality of woody biomass from mixed SRC in respect to its use for energy generation. Therefore, we tested how volume, calorific value, and ash content of woody biomass are influenced by (1) diversity in genotypes in a *Salix* SRC, and (2) diversity of species in a *Salix*, *Robinia*, *Paulownia*, and *Populus* SRC. Results show that increasing the number of genotypes or species in a SRC plantation does not negatively affect woody biomass, calorific value, or ash content of wood chips. On average, the plots with mixed genotypes or tree species produced more biomass compared with monocultures of the component species. We found evidence of overyielding in mixtures of poplar and robinia. Our findings are relevant for managers planning new SRC plantations and indicated that mixtures of specific tree species or genotypes should be considered. Therefore, we argue that "high-diversity SRC" plantations represent a valuable alternative to conventional SRC for sustainable bioenergy production.

Keywords SRC · Biomass · Ash content · Calorific value · Complementarity · TreeDivNet

Introduction

Driven by concerns about global warming and striving for energy independence, the European Union supports a transition to a low-carbon energy economy and has set a 27% target for the overall share of energy from renewable sources by 2030 [1]. Among these sources, woody biomass from sustainably managed resources plays an important role in displacing fossil fuels [2, 3], due to its ability to capture carbon, store energy, provide base load capacity to the power grid and due to other environmental benefits such as higher retention of nitrogen [4].

Currently, woody biomass with an annual gross calorific value of about 56 EJ is used worldwide [5]. As both human population and living standards continue to rise, demand for fast-growing woody biomass is expected to grow. However, the woody biomass potential from forests is limited due to competing land uses, varying site qualities, technical constraints, ecological restrictions, and the sustainability principles of forest management. Thus, sources of woody biomass other than forests are needed in order to help meeting the demand. Crops of fast-growing tree species cultivated in short rotation coppices (SRC) plantations are an alternative to supply the energy demand and also to ease the competition between energy and material uses of wood. SRC plantations with fast-growing trees are able to produce high amounts of biomass on a relative short period of time [6–8]. Further, if such systems are used for energetic purposes, the total greenhouse gas (GHG) emissions can be reduced by up to 90% compared with coal combustion [9].

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Generally, SRC plantations are established as monocultures of a few selected rapidly growing species, such as willows (*Salix sp.*), poplars (*Populus sp.*), eucalypts (*Eucalyptus sp.*), and also paulownia (*Paulownia tomentosa*) and robinia (*Robinia pseudoacacia*). While the choice of these highly productive species is driven by a goal of maximizing yields, monoculture yields can be strongly affected by disease outbreaks [10–12]. Mixed cultures have been suggested as a non-chemical strategy for pest management [13]. Further motivations for increasing tree species richness into SRC include the support of biodiversity (e.g., in growth-related phenological, functional, and morphological traits, or in the associated diversity of arthropods, birds or mammals), and the provision of additional ecosystem services (e.g., carbon sequestration, erosion control) [14, 15]. At the genotype level, studies have shown that increasing genetic richness could have either positive or at least no negative effects on productivity [16, 17]. Also at the species level, biomass production tends to increase with increasing species richness and trait dissimilarity [18–21], often due to selection or complementarity effects [22, 23]. Thus, there is a potential to design site-specific mixtures of SRC plantations in order to promote both high diversity and high biomass production [19].

In addition to the amount of wood, the quality of the wood fuel is important, too. From a biomass to energy perspective, most important measures of wood quality are the calorific value and the ash content. Both depend on the chemical composition of the wood chips. High ash contents (in combination with low moisture contents) may lead to slagging behavior during combustion and should be avoided. In contrast, high calorific values are targeted because they are the basis for the payments. Further, from an environmental perspective, a higher calorific value of the wood chips leads to increased efficiency in energy production. Wood density mainly determines the calorific value of tree biomass, while its ash content is determined by (i) the chemical composition and (ii) wood/ bark ratio; the lower the ash content, the higher the diameter, e.g., [24, 25]. Wood density is affected by the light environment in angiosperms [26], and could thus be influenced by lower intraspecific competition for light and higher canopy packing in tree mixtures, as shown for natural forests [27]. Changes of chemical constituents relevant for biomass combustion with increasing plant diversity due to soil nutrient complementarity have also been reported before [28].

In this study, we address several hypotheses related to woody biomass production in SRC. First, we hypothesize that biomass yield increases if SRC plantations are established with increasing number of either different *Salix* sp. genotypes or of different tree species, because increasing the number of genotypes or species will contribute to complementarity in resource use and therefore, to an increase in biomass. Second, we hypothesize a positive effect of genetic richness and species richness on (i) the calorific value, due to higher wood density with lower competition for light, and (ii) the ash content, since we expect that due to our initially hypothesized complementarity in resource use, stem diameter will be higher and thus ash content lower.

Third, we aim to disentangle the diversity effects in these two SRC plantations designs, hypothesizing that complementarity effects should be the driving force of any positive effects of increasing the number of genotypes or species in biomass. Furthermore, we expect that diversity effects will be positive and greater at the plantation with mixed tree species than at the one with mixed genotypes, because trait differences are larger between species than between genotypes.

Materials and Methods

Site Description

Two experimental SRC plantations were established on former grassland used for sheep grazing in Freiburg, Germany (48° 02′ N 7° 82′ E; 240 m above sea level). The first, planted in May 2014, was established with four different willow genotypes, namely Björn (*Salix schwerinii* E. Wolf. × *S. viminalis* L.), Jorr (*S. viminalis*), Loden (*S. dasyclados* Wimm.), and Tora (*S. schwerinii* × *S. viminalis*) (hereafter mixed genotypes SRC). This experiment is one replicate within the large multi-site project “ECOLINK-Salix Sweden-Germany”. The second, named HighDiv-SRC, was planted in March 2015, and was established with four species of different genera, namely poplar (*Populus maximowiczii* × *trichocarpa*), paulownia (*Paulownia tomentosa*), robinia (*Robinia pseudoacacia*), and willow (*Salix schwerinii* × *viminalis* “Tora”) (hereafter mixed species SRC). The soil of both trials is a shallow (~ 40 cm) Cambisol which is a high skeletal fraction. Both SRC trials were mechanically treated (mown) to avoid strong weed competition once each summer. However, no herbicide or fertilizer was used. Both SRC plantations are part of the global network “TreeDivNet” and aim to explore the relationships between tree species or genotype diversity and ecosystem function [14, 29].

Experimental Design

Both experiments consist of 45 plots. Trees were planted at 80 cm distance to each other resulting in a density of 15,600 trees ha^{-1}. Each plot of 92.16 m^2 had 144 trees and was divided in 9 subplots. Data were collected from 40 trees taken from the three middle subplots with exception of the outer tree rows (shaded area in Fig. 1 b). The designs utilized all possible combinations (monocultures and mixtures of either two, three, or four genotypes/ species) in three randomized blocks (see Fig. 1 a). Trees were harvested, from the sampling area marked in red (see Fig. 1 b) after the first 3-year rotation cycle.

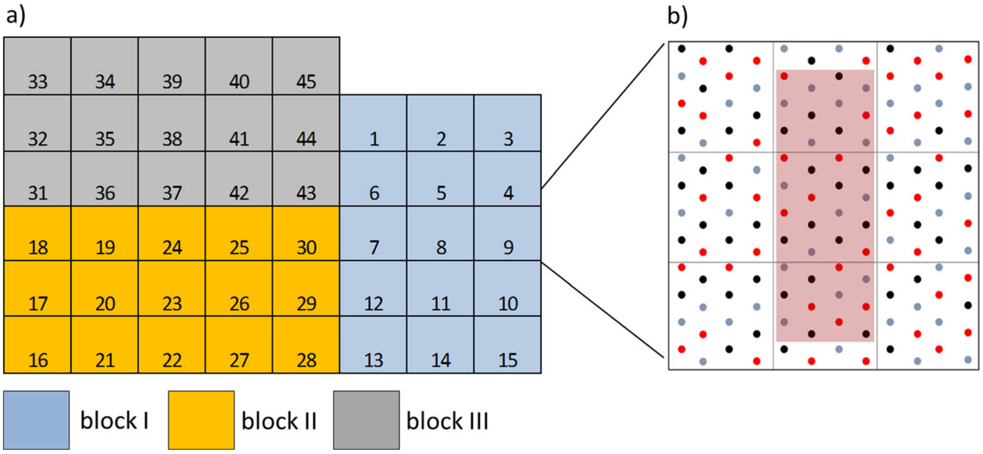

Fig. 1 **a** Randomized block design with 15 plots in three replicates (blocks I, II, and III) applied in both experimental plantations and **b** plot with sampling area colored in red. Colors in **b** represent different genotypes or species in a three-genotype/species mixture

The mean precipitation during the growing season (March to October) was 575 mm at the mixed genotypes SRC and 538 mm at the mixed species SRC for the 3-year rotation cycle. The mean temperature from March to October was 14.9 °C at the mixed genotypes SRC and 12.1° at the mixed species SRC. A more detailed description of the mixed genotypes SRC experimental design has been published by Hoeber et al [17] and Müller et al. [30]. The same randomized block design and planting scheme was used in the mixed species SRC plantation.

In the mixed genotypes SRC, trees in 6 out of 45 plots did not survive (plots no. 16, 17, 18, 31, 32, 33) (see Table 1 for detailed number of plots per mixture) and thus, could not be included in the analysis (resulting $N = 39$). These six plots were located at the eastern end of the plantation on shallow soils of ca. 40 cm above a gravel layer (not the total soil depth). In the mixed species SRC, Paulownia died shortly after planting, likely as a result of adverse climatic conditions at the time of planting in combination with strong competition by grasses, since herbicide was not applied and Paulownia was the species that suffered most from this competition. As the mortality occurred at a very early stage after planting, it was clearly not caused by the neighboring trees and was not related to tree diversity. To avoid a confounding effect of different planting densities per plot and also considering that remaining trees have a growing advantage, we decided to exclude all plots in which Paulownia was planted from the analysis (resulting $N = 20$).

Sampling

Aboveground woody biomass was harvested in winter 2016 (at the mixed genotypes SRC) and 2017 (at the mixed species SRC). To minimize edge effects in further analyses, only trees within the sampling area of the plots were used for analyses (shaded area in Fig. 1 b). All shoots of each tree located in the sampling area (i.e., 40 trees per plot) were cut at 10 cm above ground. Thereby, shoots were considered when they exceeded a minimum length of 50 cm from the ground. Shoots were carried to the field's edge, where their weight and diameter at breast height (DBH) were measured and tree numbers and genotypes/species were recorded for each of the shoots. The total sampling area of each plot was chipped on-site separately per genotype/species. For chipping, a 5.8-kW hand-fed mobile chipper was used (Model Viking GB 460C, Waiblingen, Germany).

Analysis of Physical Wood Characteristics

The wood chips were weighed in the field (accuracy 0.01 g) and oven dried at 103 °C to a constant mass in order to determine wood moisture content (MC) according to DIN 52183 [31]. The MC was reported in percent. For each plot, a 300 g mass-based sample of wood chips was produced, whereby genotypes/species were mixed accordingly to their contribution to the total biomass.

To determine the ash content, wood chips were further pulverized using a mill (Retsch Schneidmühle SM 200 by Retsch, Haan, Germany) to reach the required particle size ≤ 1 mm. For each plot, three samples of 0.3–0.5 g pulverized material were ashed in a muffle furnace, which was heated up slowly, kept the aimed temperature of 550 ± 10 °C for one hour and then cooled down. The ash content (Ad) was measured according to DIN EN 14775 [32] and was reported in percent.

The gross calorific value ($H_{o,v}$) was determined by combusting three pellets of 1.0–1.5 g material using a bomb calorimeter according to DIN 51900-2 [33] and was reported in MJ kg^{-1}.

A one-way analysis of variance (ANOVA) was performed to compare mean ash content between both SRC plantations (the genetic divers and the species divers) followed by a TukeyHSD test to compare ash content of monocultures, 2 and 3 mixtures of genotypes and monocultures, 2 and 3 mixtures of species.

Table 1 Mean ash content (%) and gross calorific value (MJ kg^{-1}) and standard deviation (SD) of the mixed genotypes and species SRC, determined after harvest, N for each mixture is indicated in brackets e.g. ($n = 3$)

SRC	Mixture	Ash content (SD)	Calorific value (SD)	Moisture content (SD)
	Unit	%	MJ kg^{-1}	%
Mixed genotype SRC	Mono (B) ($n = 3$)	1.5 (± 0.21)	16.2 (±0.43)	48.8 (±7.71)
	Mono (T) ($n = 3$)	1.6 (±0.19)	16.2 (±0.29)	39.2 (±19.68)
	Mono (J) ($n = 3$)	1.6 (±0.34)	16.2 (±0.47)	35.4 (±30.67)
	Mono (L) ($n = 2$)	1.9 (±0.18)	16.2 (±0.32)	35.9 (±11.99)
	Average mono	1.7 (±0.19)	16.2 (±0.14)	39.8 (±17.51)
	2 Mix (B/J) ($n = 3$)	1.6 (±0.12)	16.6 (±0.25)	42.5 (±17.30)
	2 Mix (J/L) ($n = 1$)	1.7 (±0.00)	16.9 (±0.00)	52.7 (±0.00)
	2 Mix (B/L) ($n = 3$)	1.8 (±0.50)	16.6 (±0.50)	53.5 (±1.21)
	2 Mix (J/T) ($n = 3$)	1.6 (±0.07)	16.6 (±0.07)	54.2 (±0.02)
	2 Mix (B/T) ($n = 2$)	1.6 (±0.30)	16.6 (±0.29)	35.1 (±3.86)
	2 Mix (L/T) ($n = 3$)	1.7 (±0.04)	16.6 (±0.47)	38.9 (±13.28)
	Average 2 mix	1.7 (±0.08)	16.6 (±0.11)	46.2 (±5.95)
	3 Mix (B/J/T) ($n = 2$)	1.5 (±0.31)	16.9 (±0.22)	39.9 (±20.22)
	3 Mix (B/L/T) ($n = 3$)	1.8 (±0.19)	16.2 (±0.11)	35.8 (±14.46)
	3 mix (B/J/L) ($n = 3$)	1.7 (±0.20)	16.9 (±0.61)	48.4 (±8.82)
	3 mix (J/L/T) ($n = 2$)	1.9 (±0.21)	16.6 (±0.72)	54.2 (±0.00)
	Average 3 mix	1.7 (±0.17)	16.6 (±0.36)	44.6 (±10.88)
	4 Mix (B/J/L/T) ($n = 3$)	1.9 (±0.13)	17.3 (±0.22)	35.4 (±7.81)
Mixed species SRC	Mono (Pop) ($n = 3$)	2.2 (±0.58)	16.2 (±0.72)	51.5 (±0.00)
	Mono (Ro) ($n = 3$)	2.7 (±0.35)	16.2 (±0.14)	42.0 (±0.00)
	Mono (Sa) ($n = 3$)	2.7 (±0.16)	16.9 (±0.36)	49.6 (±0.00)
	Average mono	2.5 (±0.27)	16.6 (±0.43)	47.7 (±0.00)
	2 Mix (Pop/Sa) ($n = 3$)	2.1 (±0.32)	16.2 (±0.22)	51.1 (±0.09)
	2 Mix (Ro/Pop) ($n = 3$)	2.2 (±0.32)	16.6 (±0.72)	44.6 (±2.09)
	2 Mix (Sa/Ro) ($n = 3$)	2.8 (±0.57)	16.6 (±0.18)	42.5 (±0.34)
	Average 2 mix	2.4 (±0.37)	16.6 (±0.18)	46.1 (±0.84)
	3 Mix (Sa/Ro/Pop) ($n = 3$)	2.7 (±0.00)	16.6 (±0.00)	44.0 (±0.75)

B, Björn; *T* Tora; *J*, Jorr; *L*, Loden; *Pop*, *Populus*; *Ro*, *Robinia*; *Sa*, *Salix*; *DBH*, diameter at breast height; *mm*, millimeter; *Mg*, megagramm; *dm*, dry matter; *ha*, hectare; *MJ*, mega joule

Biomass Assessment

For each monoculture plot, 30 trees of each genotype/species were sampled to determine fresh to dry weight relationships. Allometric equations to determine the relationships between shoot fresh weights and shoot dry biomass were developed for each genotype and species according to [34–37]. Equation 1 was used for the genotype/species-specific linear regression in order to calculate the amount of biomass for each individual tree on the sampling area.

Shoot biomass (Eq. 1):

$$\text{shoot dry biomass} = \text{a} + \text{b}^{*}\text{shoot fresh weight} \qquad (1)$$

aintercept estimate;bslope estimate, from the regression.

We fit a restricted maximum likelihood mixed effects model (REML) to test if plot shoot biomass increased with genetic or species richness (diversity), where diversity was set as a fixed effect and mixture and block were considered as random effects (lme4 package: 'lmer') [38] to account for the amount of residual variance that they explained [39, 40]. In order 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 [41]).

Diversity Effect Analysis

In order to test our hypothesis that diversity effects should be positive and greater in mixtures with different tree species than in mixtures with different genotypes, we used the additive partitioning equation from Loreau and Hector [23] (Eq. 2). We used the proportion of surviving individuals of each species within the sampling area in each plot to calculate the expected yield. In Eq. 2, the net biodiversity effect is defined as the additive partitioning of two biodiversity effects (1) the complementarity effect which is measured by $N\Delta\overline{RY}\,\overline{M}$ and (2) the selection effect, which is captured by $N\,\mathrm{cov}(\Delta RY, M)$. 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 species in each mixture. We calculated the complementarity effect, selection effect and net effect for all mixture plots. We calculated these diversity effects for the biomass produced and the ash content.

Net biodiversity effect (Eq. 2):

$$\begin{aligned}\Delta Y = Y_O - Y_E = \sum_i RY_{O,j}M_i - \sum_i \Delta RY_{E,j}M_i = \sum_i \Delta RY_i M_i \\ = N\overline{\Delta \mathrm{RY} M} + N\,cov(\Delta RY, M)\end{aligned} \tag{2}$$

ΔY	net biodiversity effect;
Y_O	observed yield of genotype/species i on the mixture;
Y_E	expected yield of genotype/species i on the mixture;
$RY_{O,j} Y_{O,j}/M_i$	observed relative yield of genotype/species i in the mixture;
$RY_{E,j}$	expected relative yield of genotype/species i in the mixture;
M_i	yield of genotype/species i in the monoculture;
$\Delta RY_i\ RY_{O,j} - RY_{E,j}$	deviation from expected relative yield of genotype/species i in mixture;
N	number of genotype/species in mixtures.

In order to assess whether the complementarity effect, selection effect and net diversity effect were significant, a two-sided one sample Student's *t* test was performed for each genetic/species richness level separately (2, 3, and 4 mixtures). All abovementioned statistical analyses were conducted in *R* (Version 3.3.3 [42]).

Results

Biomass

The mean plant survival rate per plot was 88% in the mixed genotypes SRC, and 83% in the mixed species SRC. In the mixed genotypes SRC, the amount of biomass was between 3.5 $\mathrm{Mg_{dm}\ ha^{-1}}$ (4 genotypes) and 7.6 $\mathrm{Mg_{dm}\ ha^{-1}}$ (3 genotypes) on average (Table 2, Fig. 2). The amount of shoots per tree was between 1.7 (monocultures) and 2.0 (3 genotypes) on average and the DBH was between 10.7 mm (4 genotypes) and 14.7 mm (3 genotypes) on average. All characteristics were slightly lower in the mixed species SRC (Table 2, Fig. 2): the amount of biomass varied between 3.0 $\mathrm{Mg_{dm}\ ha^{-1}}$ (monocultures) and 4.7 $\mathrm{Mg_{dm}\ ha^{-1}}$ (2 species), the amount of shoots per tree was 1.3 on average in all cases and the DBH was between 9.7 mm (monocultures) and 13.7 mm (2 species) on average (Table 2, Fig. 2). Probably because of adverse growing conditions in the first year (2015).

We found no effect of genetic richness nor species richness on the amount of biomass produced per hectare ($p > 0.05$, Table 3). The marginal R^2 value of 0.078, which describes the proportion of variance explained by species richness on biomass alone, was small indicating a poor explanatory power of species richness alone. Similarly, the marginal R^2 for genetic richness was < 0.001 (Table 3).

Physical Wood Characteristics

The average ash content of the mixed genotypes SRC was 1.7% in the plots established with monocultures and also in the plots with 2 and 3 genotypes; and 1.9% within the plot with 4 genotypes (Table 4). In the mixed species SRC, the average ash content was significantly higher ($p < 0.01$): 2.5%, 2.4%, and 2.7% in the plots with monocultures; 2 species and 3 species, respectively (Table 4). The calorific value of the mixed genotypes SRC was on average 16.2 MJ $\mathrm{kg^{-1}}$ in the monocultures, 16.6 MJ $\mathrm{kg^{-1}}$ in the plots with 2 and 3 genotypes, and 17.3 MJ $\mathrm{kg^{-1}}$ in the plot with 4 genotypes (Table 4). In the mixed species SRC, the average calorific value was 16.6 MJ $\mathrm{kg^{-1}}$ in all cases (Table 4).

Species richness had no effect on the calorific value. However, genetic richness had a positive and significant effect on the calorific value ($p < 0.01$, Table 3). The marginal R^2 was 0.009 for species richness. On the contrary, the marginal R^2 for the effect of genetic richness on calorific value was much higher, 0.299.

Neither genetic nor species richness had an effect on ash content. The explanatory power of both genetic richness and species richness on the ash content was very low as showed by their marginal R^2 of 0.04 and 0.02, respectively (Table 3).

Additive Partitioning of Diversity Effects

The effect size of complementarity, selection and net effect varied among the genetic and the species richness SRC and were of considerable difference for biomass and for ash content (Fig. 3). Most diversity effects in the mixed species SRC were not different from zero, indicating no higher biomass or ash content in mixtures compared with what would be expected based on performance in monocultures. Exceptions were a negative complementarity effect on biomass for the four genotype mixtures ($p < 0.05$), and a positive net effect for ash content at the 2-species level ($p < 0.05$) (Fig. 3).

In a detailed analysis of the biomass in the two species mixtures SRC, we found that the observed biomass of poplar in a poplar-willow mixture was higher than the expected based on the monoculture biomass production (Fig. 4). However,

Table 2 Mean biomass, shoots per tree, and average diameter at beast height (DBH) and standard deviation (SD) of the mixed genotypes and species SRC

SRC	Mixture Unit	Biomass (SD) mg$_{dm}$ ha^{-1}	Shoots (SD) Shoots/tree	DBH (SD) mm
Mixed genotype SRC	Mono (B)	5.6 (± 0.74)	1.4 (± 0.23)	14.6 (± 0.81)
	Mono (T)	5.9 (± 1.6)	1.4 (± 0.16)	15.2 (± 2.44)
	Mono (J)	6.6 (± 0.43)	1.4 (± 0.14)	15.1 (± 1.51)
	Mono (L)	7.2 (± 1.03)	2.7 (± 0.44)	13.3 (± 2.25)
	Average mono	6.3 (± 0.31)	1.7 (± 0.67)	14.5 (± 1.69)
	2 Mix (B/J)	5.0 (± 0.40)	1.7 (± 0.11)	13.5 (± 0.83)
	2 Mix (J/L)	8.5 (± 0.00)	1.5 (± 0.00)	17.5 (± 0.00)
	2 Mix (B/L)	4.9 (± 1.03)	2.1 (± 0.60)	12.1 (± 1.35)
	2 Mix (J/T)	5.1 (± 1.86)	1.6 (± 0.20)	13.5 (± 4.85)
	2 Mix (B/T)	4.4 (± 1.77)	1.6 (± 0.17)	12.0 (± 4.94)
	2 Mix (L/T)	8.0 (± 0.41)	2.1 (± 0.30)	14.5 (± 0.97)
	Average 2 mix	5.6 (± 0.66)	1.8 (± 0.38)	13.5 (± 2.78)
	3 Mix (B/J/T)	6.8 (± 0.55)	1.6 (± 0.27)	14.7 (± 2.59)
	3 Mix (B/L/T)	7.8 (± 0.33)	2.3 (± 0.02)	14.0 (± 1.34)
	3 Mix (B/J/L)	7.7 (± 0.72)	2.1 (± 0.26)	14.6 (± 1.82)
	3 Mix (J/L/T)	8.0 (± 2.16)	1.7 (± 0.69)	16.0 (± 4.13)
	Average 3 mix	7.6 (± 0.23)	2.0 (± 0.43)	14.7 (± 2.09)
	4 Mix (B/J/L/T)	3.5 (± 0.61)	1.8 (± 0.78)	10.7 (± 2.40)
Mixed species SRC	Mono (Pop)	2.3 (± 1.75)	1.2 (± 0.21)	9.9 (± 4.14)
	Mono (Ro)	5.2 (± 3.09)	1.1 (± 0.06)	12.3 (± 4.14)
	Mono (Sa)	1.6 (± 0.64)	1.6 (± 0.31)	7.3 (± 1.76)
	Average mono	3.0 (± 2.44)	1.3 (± 0.30)	9.7 (± 3.83)
	2 Mix (Pop/Sa)	4.5 (± 3.14)	1.5 (± 0.16)	13.3 (± 4.72)
	2 Mix (Ro/Pop)	6.7 (± 1.85)	1.7 (± 0.08)	18.0 (± 3.11)
	2 Mix (Sa/Ro)	3.0 (± 1.94)	1.2 (± 0.10)	9.9 (± 3.89)
	Average 2 mix	4.7 (± 2.61)	1.3 (± 0.20)	13.7 (± 4.90)
	3 Mix (Sa/Ro/Pop)	3.4 (± 3.80)	1.3 (± 0.22)	10.5 (± 2.46)

B, Björn; *T*, Tora; *J*, Jorr; *L*, Loden; *Pop*, *Populus*; *Ro*, *Robinia*; *Sa*, *Salix*; *DBH*, diameter at breast height; *mm*, millimeter; *Mg*, megagramm; *dm*, dry matter; *ha*, hectare

willows did not benefit as poplar did in that mixture. The observed biomass of robinia (Ro) when in the mixture robinia-poplar (Ro-Pop) was higher than the expected based on the biomass of robinia (Ro) in monoculture, but poplar (Pop) biomass in that mixture was not significantly greater than the expected. In the mixture robinia-willow (Ro-Sa),

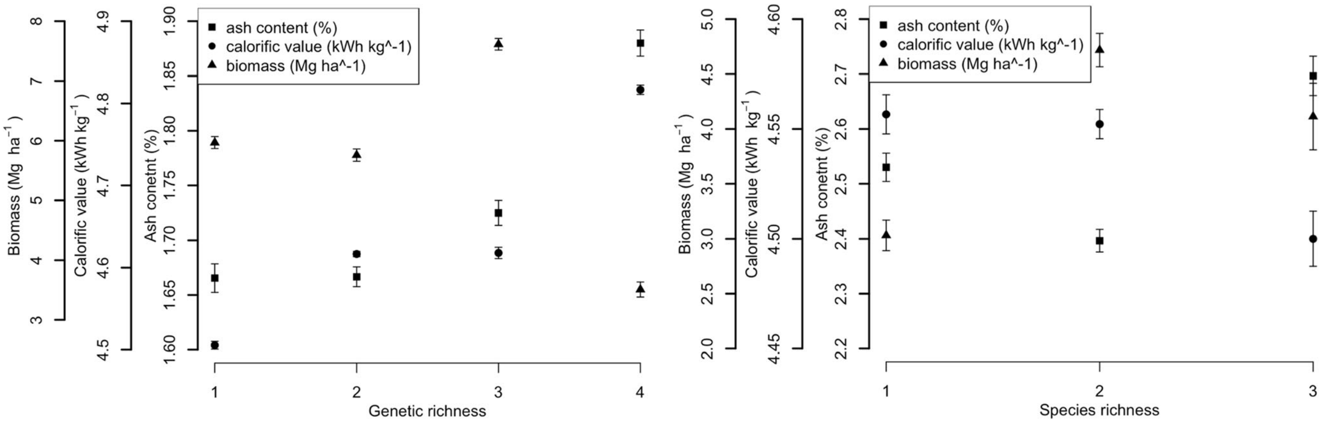

Fig. 2 Mean aboveground woody biomass (Mg ha^{-1}), calorific value (MJ kg^{-1}), and ash content (%) with increasing **a** genetic (i.e., plots with one to four genotypes) and **b** species (i.e., plots with one to three species) richness in each of the short rotation coppice plantations (whiskers show standard errors)

Table 3 Summary of restricted maximum likelihood mixed effects models for the effect of genetic and species richness, as fixed-effect variables, on above ground biomass (Mg ha^{-1}), calorific value (MJ kg^{-1}), and ash content (%) of each mixture plot for both the mixed genotypes SRC and mixed species SRC; block and mixtures as random effect variables. Parameter estimate values and (standard error) are reported. Variance values indicate the variance of the random variables (mixture and block) in the model with either genetic richness or species richness as fixed effect variable. Marginal R^2 values for each model are reported

Response variable	Biomass (Mg ha^{-1})		Calorific value (MJ kg^{-1})		Ash content (%)	
Fixed effect	Est. (SD)	*T* value	Est. (SD)	*T* value	Est. (SD)	*T* value
Genetic rich.	0.041 (0.451)	0.09 n.s.	0.077 (0.021)	3.75 **	0.053 (0.041)	1.29 n.s.
Species rich.	0.827 (0.966)	0.86 n.s.	− 0.022 (0.045)	− 0.49 n.s.	0.029 (0.183)	0.16 n.s.
Random effects	Variance (SD)		Variance (SD)		Variance (SD)	
Mixture						
Genetic rich.	0.421 (0.648)		1e^{-3}		0.0 (0.0)	
Species rich.	1.785 (1.336)		2e^{-3}		8e^{-3} (2.867e^{-1})	
Block						
Genetic rich.	0.0 (0.0)		1e^{-4}		0.0 (0.0)	
Species rich.	1.299 (1.140)		3e^{-3}		< 0.001 2(< 0.001)	
	Marg. R^2	Cond. R^2	Marginal R^2	Cond. R^2	Marginal R^2	Cond. R^2
Genetic rich.	2.4e^{-4}	0.069	0.299	0.375	0.04	0.041
Species rich.	0.078	0.447	0.009	0.313	0.02	0.456

n.s., not significant; ** = $p < 0.01$

neither of the two species showed higher biomass production compared with their respective monocultures (Fig. 4).

Discussion

In the literature, there are some studies reporting results for a variety of different genotypes and/or species, but these studies differ from our study because trees were not grown as a mixed SRC [e.g., 43, 44, 45, 46]. In a few cases, trees were grown in a design comparable to that employed here, with pure and mixed stands, but results were reported per genotype and/or species only, and potential effects of diversity on responses were not considered [e.g., 47, 48, 49, 50, 51, 52]. Some studies focused on different genotypes and/or species, but the scope of the study was another one [53, 54].

Results demonstrated that the biomass production was low in both plantations: the average biomass production was between 5.7 $\mathrm{Mg_{dm}}$ ha^{-1} (plots with mixed SRC) and 4.9 $\mathrm{Mg_{dm}}$ ha^{-1} (plots with monoculture SRC). When sorting by genotypes/species, the amount of biomass was significantly higher in plots with mixed genotypes SRC compared with mixed species SRC. One explanation might be, since the time of establishment of the mixed genotypes SRC and mixed species SRC differed by 1 year and growing conditions were dry in 2015 (when the mixed genotypes SRC was already accessing deeper soil layers with more moisture), the mixed species SRC had shorter total growing period compared with the mixed genotype SRC. However, it is well known that yields are low in the first rotation cycle and thereafter increase and our findings were comparable with that reported in other studies when considering the first rotation cycle only [55]. Further, no herbicides, fertilizer, or any other soil treatments were applied and weeding was mechanically performed only once a year. Nevertheless, we recommend extending the rotation cycles in order to be less vulnerable to extreme weather conditions and to increase the biomass output per hectare and harvest and thus, to enhance the diversity effects [56, 57]. In

Table 4 Summary of the above ground biomass production and wood quality for each richness level at both SRC trial (mixed genotypes SRC and mixed species SRC). Mean aboveground woody biomass (Mg ha^{-1}), calorific value (MJ kg^{-1}), and ash content (%) with increasing (a) genetic (i.e., plots with one to four genotypes) and (b) species (i.e., plots with one to three species) and standard deviation (SD)

SRC	Mixture Unit	Biomass (SD) $\mathrm{Mg_{dm}}$ ha^{-1}	Calorific value (SD) MJ kg^{-1}	Ash content (SD) %
Genotypes	Average mono	6.3 (± 0.31)	16.2 (± 0.14)	1.7 (± .19)
	Average 2 mix	5.6 (± 0.66)	16.6 (± 0.11)	1.7 (± 0.08)
	Average 3 mix	7.6 (± 0.23)	16.6 (± 0.36)	1.7 (± 0.17)
	4 Mix	3.5 (± 0.61)	17.3 (± 0.22)	1.9 (± 0.13)
Species	Average mono	3.0 (± 2.44)	16.6 (± 0.43)	2.5 (± 0.27)
	Average 2 mix	4.7 (± 2.61)	16.6 (± 0.18)	2.4 (± 0.37)
	3 Mix	3.4 (± 3.80)	16.6 (± 0.00)	2.7 (± 0.00)

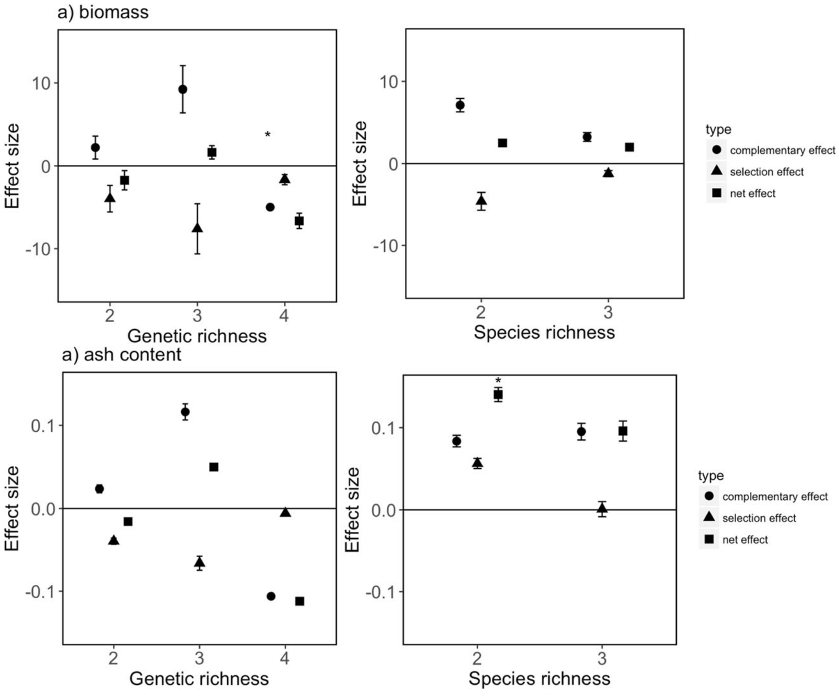

Fig. 3 Complementarity (●), selection (▲) and net effect (■) for the amount of biomass and ash content for the **a** genetic and **b** species richness level. Means and standard errors are shown. Asterisks indicate level of statistical significance by two-sided Student's *t* test (* = $p < 0.05$). A positive complementarity effect indicates that the amount of biomass produced in that mixture is higher than the expected based on the performance of each species (or genotype) in monoculture. A positive selection effect indicates that one high productive species (or genotype) is dominating the yield in the mixtures

addition, previous research suggests that increment is higher in longer rotation cycles. For instance, in the case of poplar, rotation cycles with 5 to 6 years should be favored compared with rotation cycles with 3 years [58, 59]. Further, yield-scaled emissions decrease in longer rotation cycles. Schweier et al. [60] showed that the use of the 7-year compared with the 3-year rotation cycles decreased yield-scaled emissions of a poplar SRC by a factor of 2.2 ± 0.1.

The genotype “Tora” was planted in both experiments analyzed. On the one hand, it was grown as monoculture in the genotypes SRC, where it performed well; and on the other hand it was grown as monoculture in the species SRC (Table 1, Table 2), where it performed less well. In the latter, a lower amount of biomass as well as a smaller DBH was reached. Thus, the bark proportion was less favorable and as a consequence, the ash content and the calorific value were higher. Bark proportion has a direct impact on the quality of wood chips when used for energetic purposes due to high elemental concentrations [24] and that it decreases rapidly with increasing tree diameter [57]. High shares of bark increase the emissions of pollutants during the burning process. Adler et al. [61] recommend harvesting willows SRC when most of the shoots reach a diameter of 20 mm (at 55 cm height); Tullus et al. [24] recommend a DBH of 40 mm for hybrid aspen SRC as reasonable target diameter in order to minimize bark proportion. In Germany, for instance, wood chips used for biofuel are classified by a new standard (ENplus) since 2016. In order to reach top classification (ENplus A1 or ENplus A2), ash content has to be equal or smaller than 1.5%. Thus, from an environmental viewpoint, we recommend extending rotation cycles to increase biomass production.

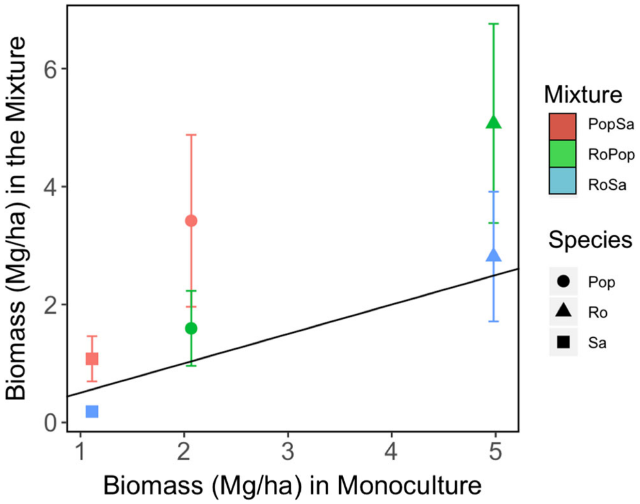

Fig. 4 Mean biomass (Mg ha^{-1}) of each tree species in a two-species mixtures against its expected biomass based on the monoculture production. Slope indicates a 1-to-1 relation taking into account the share of each species in the two-species mixture (whiskers show standard errors). Pop = *Populus*, Ro = *Robinia*, Sa = *Salix*

The average ash content was in accordance with other studies [44, 48, 50, 62–64]. Sannigrahi [65] reviewed the compositional characteristics of poplars and reported ash contents ranging from 0.6 to 2.7% (1.9–2% in our case). However, when sorting by genotypes/species, the ash content was significantly higher in the mixed species SRC compared with the mixed genotypes SRC ($p < 0.01$). Because of the low dimensions of shoots and relatively high bark content, respectively ash content, the calorific value may be lower compared with wood chips from woody biomass of higher dimensional wood. The different conditions during the time of establishment might have played a role in the observed differences in ash content among the two SRC.

The average calorific value was slightly lower compared with other studies reporting calorific values being higher than 19 MJ kg^{-1} [43–45, 47, 48, 50]. However, those studies reporting higher calorific values differ in the management and design of the SRC plantation, for instance in the age at which trees were harvested, different planting schemes and densities, higher number of rotation cycles, and had most likely less adverse growing conditions during the growing period (i.e., drought). There was no significant difference between the mixed genotypes SRC compared with the mixed species SRC (both 16.6 MJ kg^{-1} on average).

We found a significant effect of genetic richness on the calorific value. This could be due to canopy stratification in mixtures resulting in the presence of an extended second layer when the genotype "Loden" was present [17]. The resulting canopy stratification would lower competition for light [27], and thus influence wood density which determines the calorific value. We found no significant effect of increasing genetic richness or species richness on the biomass yield, nor ash content or calorific value of the wood chips. These results are in line with the results from other studies [17, 55]. The fact that we did not find any effect on biomass can be attributed to the young age of the plantation, since the data was collected at the first rotation cycle and one can expect that shoot growth is higher after the first rotation cycle [66]. A further explanation for these findings is the low dimensions of shoots and relatively high bark content.

Results from other biodiversity experiments also indicate that diversity effects usually are getting stronger with time, related to the shift from early exponential growth of young plants without much interaction with neighbors, to growth responses at later stages with higher interactions strength due to competition or facilitation [67].

The low biomass reported for the four-genotype mixture SRC is due to one of the plots performing poorly. Yet, we find an effect of genetic richness on the calorific value which adds an argument for using mixed SRC plantations instead of monocultures, since the calorific value is probably the most important characteristic of SRC plantations for energy production.

Although research during the past two decades has shown that biodiversity effects on ecosystems are often caused by complementarity [20], our initial hypothesis postulating positive complementarity effects could not be confirmed. Whereas it is true that for the species-rich plantation almost all diversity effects were positive as hypothesized, only one net diversity effect was significant for the two species mixtures and not for the three species mixtures. The negative selection effects found for biomass in both the genetic and the species rich SRC plantations, are in line with previous studies [68, 69]. These negative selection effects indicate the presence of a less productive genotype, or species, driving biomass production in mixtures. In a previous study [17], the genotype "Tora" was identified to be the one causing negative selection effects since it showed to perform better in mixtures than in monocultures. The potentially negative impact of "Tora" on the community could be associated with its greater height compared with the other genotypes, outgrowing the other genotypes but not being able to compensate for the loss in the community productivity. There was no positive and significant diversity effect on biomass. However, a detailed analysis of the individual mixtures (Fig. 4) showed that some species indeed profited from growing in mixtures compared with their monoculture growth. Considering the fact that almost all species produced equally or even more biomass when occurring in mixture than in monoculture, with the exception of willows when growing with robinia, we can conclude that most species are, at least at this time point, not negatively affected by interspecific competition in mixed communities. Thus, intraspecific competition should be rather higher than interspecific competition. The two species mixtures which showed greater biomass compared with their monocultures were not necessarily those mixtures where robinia was present. We found that poplar seemed to benefit when planted with willow but not with robinia. Therefore, we can assume that this positive and significant net effect is indeed due to some complementarity occurring and not due to the nitrogen fixing ability of robinia. This indicates that some mixtures outperform monocultures, since they show higher biomass production compared to what would be expected based on their performance in monocultures. Although positive complementarity could be due to several causes acting simultaneously [70], in this case, one possible explanation for the higher biomass production compared with the expected could have been, among others, due to canopy stratification by species with different traits, such as height and leaf area, which can result in complementarity in resource use [71]. In this regard, poplars, with higher leaf area could have intercepted more light than willows when those two species were mixed together. Similarly, robinia seemed to perform better than poplars when both were together. Therefore, farmers may use this potential to develop site-specific mixtures, being the mixtures poplar-willow and robinia-poplar interesting ones to consider for SRC plantations.

Conclusion

Our results show that SRC while increasing the number of genotypes or species in a SRC plantation did not have a positive effect in stand-level productivity, or on the physical characteristics of the wood chips it did not impair biomass production and its quality, so that there is no clear advantage of monocultures in this regard. Furthermore, mixed plantations are considered as a non-chemical strategy for pest management and they contribute to increase the overall biodiversity, creating new habitats for associated organisms. For these reasons, we argue that mixed or "high-diversity SRC" plantations should be considered as a valuable alternative to conventional ones for sustainable bioenergy production. Thereby, farmers need to consider that adequate genotypes or tree species combinations according to their site characteristics are chosen.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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