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Early effects of two planting densities on growth dynamics and water-use efficiency in *Robinia pseudoacacia* (L.) and *Populus deltoides* (Bartr. ex Marsh.) × *P. nigra* (L.) short rotation plantations

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Abstract

- **Key message** Black locust is an interesting option for biomass production at sites prone to water shortage because the species combines water-use efficiency and a biomass yield largely superior to that of poplars under the conditions of the study.
- **Context** Black locust (*Robinia pseudoacacia* L.) is an interesting tree species for woody biomass production. However, its potential for this purpose has been much less studied and characterized than that for species from the Salicaceae family (i.e., poplar and willow).
- **Aims** The objective of our study was to evaluate the potential of black locust for biomass production as compared to that of poplar.
- **Methods** We estimated biomass production, growth habit, and efficiency of water use of two provenances of black locust (1) compared to those of poplar (*Populus deltoides* Bartr. ex Marsh. × *P. nigra* L.), (2) at two planting densities, and (3) 2 and 4 years after planting.

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Contribution of the co-authors

J. Toillon: methodology, investigation; P. Priault: investigation, writing—review and editing; E. Dallé: methodology, resources; G. Bodineau: methodology, resources; J.C. Bastien: project administration, funding acquisition; F. Brignolas: investigation, supervision; N. Marron: investigation, data curation, writing—original draft, writing—review and editing

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- **Results** Black locust had a very different growth habit, much higher biomass production, and larger water-use efficiency than poplar. These differences were exacerbated during the driest year of the experiment. However, black locust responded very badly to harvesting.
- **Conclusion** Black locust was more productive and more efficient in terms of water use than poplar, especially during the driest year of the experiment.

Keywords Biomass production · Water-use efficiency · Nitrogen removal · Black locust · Poplar

1 Introduction

As a renewable energy resource, woody biomass has a role to play in reducing worldwide fossil fuel consumption. Large amounts of woody biomass can be produced with short rotation tree plantations (Dallemand et al. 2008; Raslavicius et al. 2015). The choice of species/cultivar and of production system must be adapted to the specific site conditions (Grünwald et al. 2009; Toillon et al. 2013b; Marron et al. 2018). Woody species suitable for short rotation plantations must have certain common properties including a high initial growth rate, easy vegetative propagation, and formation of coppice sprouts or suckers after harvest. Species in the genera *Salix* spp. L. and *Populus* spp. L. are widely used for this purpose under temperate latitudes. In warmer climates, common short rotation species include genera such as eucalyptus (*Eucalyptus* spp. L'Hér.) and paulownia (*Paulownia* spp. Siebold & Zuccarini).

Black locust (*Robinia pseudoacacia* L.) also prefers warmer climatic zones, although it is also cultivated in temperate climates (Stolarski et al. 2013). Black locust originates from the Eastern United States (Böhm et al. 2011). It has an extensive root system and is therefore widely used for land protection and soil erosion control (Zhou and Shangguan 2005). Black locust is a light-demanding pioneer species capable of tolerating a wide range of edaphic conditions; it is comparatively drought resistant (more than the Salicaceae) and belongs to the small group of atmospheric nitrogen-fixing trees native to the temperate regions (Quinn et al. 2015). Its ability to grow on bare soils under extreme conditions, its fast growth, considerable resprouting ability after cutting, and its excellent energy production properties including high calorific potential, high wood density, and dry matter production have proven to be particularly appropriate for the production of woody biomass for bioenergy, particularly in areas with shallow soils and/or dry conditions (Rédei et al. 2008; Böhm et al. 2011; Rédei et al. 2011; Straker et al. 2015). Black locust is one of the most widely planted woody species in the world. However, it is also listed among the 40 most invasive woody angiosperms, globally highlighting the need for surveillance and monitoring of black locusts stands including a better knowledge and sharing of management practices (Sadlo et al. 2017; Vitkova et al. 2017). In addition to its potentially invasive nature and the consequences on biodiversity, the

cultivation of black locust under intensive regimes can also cause practical problems such as difficulties for harvesting operations because resprouting can occur from the roots in a random way (Vítková et al. 2017).

Besides carefully selecting the plant material, plantations for woody biomass production can also be adapted by changing planting density and rotation length. In temperate latitudes, two coppice systems are typical for both poplar and black locust (Dallemand et al. 2008): (1) short rotation forestry (SRF), with planting densities ranging from 1000 to 2000 trees per hectare and rotation lengths between 6 and 8 years, and (2) short rotation coppice (SRC) with higher planting densities (6000–15,000 trees per ha) but shorter rotation lengths (typically from 2 to 4 years). In both of these silvicultural systems, black locust biomass yields ranging from 1.3 to 14 t ha⁻¹ year⁻¹ can be expected, depending on plantation age, site conditions, rotation interval, and planting layout. In comparative studies, black locust is one of the most productive species (Geyer 1989; Grünwald et al. 2009; Kanzler et al. 2015; Huber et al. 2018).

To screen candidate species and genotypes for biomass production, it is important to identify tree species that are efficient in balancing water loss and carbon uptake, especially under marginal site conditions (i.e., poor, dry, shallow soils) based on physiological variables associated with growth and water use (Wang et al. 2013; Mantovani et al. 2015). Water-use efficiency (WUE, at tree level, the amount of plant biomass produced per unit of water used, often estimated through leaf carbon isotope discrimination, $\Delta^{13}\text{C}$) has therefore emerged as a relevant criterion to be accounted for in tree selection, in conjunction with other common criteria already in use such as disease resistance, productivity, and wood quality (e.g., Monclus et al. 2005; Lopez-Sampson et al. 2017; Suárez-Vidal et al. 2021). Along the same lines, it has been shown that, in large-scale agricultural production systems, using species or genotypes with high nitrogen-use efficiency, and hence lower nitrogen removal for a given carbon gain, maximizes biomass production from both an economic and a sustainability perspective (Adegbidi et al. 2001). Black locust, thanks to its ability to symbiotically fix atmospheric nitrogen, is likely to be well adapted to poor environments, and issues related to excess nitrogen removal during harvest are less pregnant than for non-fixing species such as poplar and willow.

The potential for biomass production of species from the Salicaceae family (including the *Populus* and *Salix* genera) in relation to their resource use has been extensively described in the literature (e.g., Dillen et al. 2011; Toillon et al. 2013a). Data on the black locust are much rarer than those for the Salicaceae, and comparisons between planting densities are even rarer. Though black locust has been studied for a long time in some parts of the world (e.g., Central Europe), this has been mainly in terms of its economic value rather than its ecology (Vitkova et al. 2017). In Europe, lignocellulosic short rotation crops such as poplar and willow are hardly profitable in most countries especially on low-quality lands (Panoutsou and Alexopoulou 2020). To make these plantations economically feasible, average threshold yields of 10 to 12 t ha⁻¹ year⁻¹ have been cited (Heath et al. 1994; Grünewald et al. 2009) while more recently, lignocellulosic crop yields of 5 to 6.5 t ha⁻¹ year⁻¹, depending on land quality, have been cited as required to breakeven total production costs and gross sales income (Panoutsou and Alexopoulou 2020). However, yields of short rotation plantations vary widely depending on the nature of the plant material, the site conditions, and production system. Commonly observed yields in Europe are around 6–10 t ha⁻¹ year⁻¹ when neither fertilization nor irrigation is applied (Bullard et al. 2002; Scholz and Ellerbrock 2002). Short rotation plantations can be problematic because of soil impoverishment, especially when rotations are frequent and cause a net removal of nutrients from the soil. In this regard, industrial fertilizers (e.g., nitrates) are expensive to produce in terms of energy use and these energy costs will reduce the benefits of woody biomass in reducing fossil fuel consumption (Dallemand et al. 2008).

The objectives of our study were to evaluate the potential of black locust for biomass production as compared to that of poplar, (1) by estimating whether planting density (SRF vs. SRC) influences growth and physiology, notably water-use efficiency (estimated through carbon isotopic discrimination of wood and leaves) for the two species, (2) by comparing biomass production and nitrogen quantities removed during harvest for the two species in a SRC plantation, and finally (3) by assessing how leaf traits and growth performance evolved during the second rotation in a SRC plantation (4 years after planting) as compared to the first rotation (2 years after planting).

2 Materials and methods

2.1 Study site

The study was carried out in Northern France at Guéméné-Penfao (Loire-Atlantique). The site is characterized by an oceanic climate with mild annual temperatures. The study site is located in an area defined as a habitat with medium to mid-high suitability/survivability potential for black locust in the

European Atlas of forest tree species by Sitzia et al. (2016) or with high suitability in terms of climate by Li et al. (2014). Meteorological data were obtained from the closest meteorological station (Le Rheu, INRAE Rennes). Volumetric soil water content (SWC, %) was monitored with a water content reflectometer (model CS616, TDR type, Campbell Scientific, Logan, UT, USA) at 20 cm in depth. The values provided by two probes per species and per silvicultural system were averaged. Before planting, 20 soil samples were collected at depths of 0–20 and 20–40 cm (ten samples per depth, distributed on a 50-m grid), each sample being a composite of 16 subsamples. In 2009, the Service Unit 10 from the Soil Analysis Laboratory of Arras (INRAE Lille, France) determined soil texture (% sand/% silt/% clay), composition (organic matter (g kg⁻¹), organic carbon content (C, g kg⁻¹), nitrogen content (N, g kg⁻¹), and pH. No significant differences were found between the two silvicultural systems (Appendix Fig. 5); mean values are presented in Table 1. The soil was a loamy type, with organic matter, organic carbon, and total nitrogen contents of 40, 23, and 1.7 g kg⁻¹, respectively, for the top layer (0 to 20 cm in depth), and 24, 14, and 1.1 g kg⁻¹, respectively, for the deeper layer (20 and 40 cm in depth) (Table 1).

2.2 Experimental design and plant material

The plantation was established in April 2009 by planting 25-cm-long woody-stem cuttings of poplar (*Populus deltoides* × *P. nigra*, clone ‘Dorskamp’) and 1-year-old rooted seedlings

Table 1 (A) Pedoclimatic conditions: TAP, total annual precipitation; TSP, total summer precipitation (from May to August); MAT, mean annual temperature; MST, mean summer temperature; mean summer soil water content at 20 cm in depth in the different silvicultural systems, between 2009 and 2012. (B) Soil texture, composition, and pH for the 0–20- and 0–40-cm-deep layers at Guéméné-Penfao

A	2009	2010	2011	2012
<i>Climate</i>				
TAP (mm)	764	599	608	809
TSP (mm)	223	148	286	219
MAT (°C)	11.5	10.8	12.5	11.5
MST (°C)	16.7	16.7	16.2	16.4
<i>Mean summer soil water content (%)</i>				
Black locust SRC		19.9 ± 2.1	17.6 ± 2.3	24.6 ± 1.9
Poplar SRC		17.5 ± 1.9	18.2 ± 3.1	26.8 ± 0.2
Black locust SRF		16.8 ± 1.9	14.8 ± 0.1	21.8 ± 0.9
Poplar SRF		14.1 ± 0.4	14.1 ± 0.2	21.3 ± 2.3
B				
Soil layer				
0–20 cm				
20–40 cm				
<i>Texture (g kg⁻¹)</i>				
Clay	200.0 ± 8.9		204.9 ± 7.3	
Silt	212.9 ± 4.8		211.4 ± 5.3	
Sand	187.1 ± 10.0		186.2 ± 9.3	
<i>Composition (g kg⁻¹)</i>				
Organic C	23.0 ± 1.4		14.0 ± 0.8	
Total N	1.7 ± 0.1		1.1 ± 0.1	
Organic matter	39.8 ± 2.4		24.3 ± 1.4	
pH	6.8 ± 0.1		6.6 ± 0.1	

of black locust (*Robinia pseudoacacia*, provenances ‘Nagybudmerii’ and ‘Nyirseg’). Both the poplar and black locust were planted at two densities: (1) under a short rotation forestry (SRF) system in single rows with 2 m between trees and 3.5 m between rows (1428 trees ha⁻¹; about 0.38 ha per species and provenance), and (2) under a short rotation coppice (SRC) system with a double-row planting scheme alternating distances of 0.75 m and 2 m between the rows and with 1 m between trees within the rows (7272 trees ha⁻¹; about 0.25 ha per species and provenance). Neither fertilization nor irrigation was applied. Herbicide was used just after planting in order to control weeds (3.5 L ha⁻¹ GARDENET Paysage, Dow AgroScience SAS, Mougins, France). To reduce border effects, one border row for the SRF and two border rows for the SRC around each plot were excluded from the measurements (Appendix Fig. 5).

2.3 Climate and soil conditions

Total annual precipitation was 764 mm in 2009, 599 mm in 2010, 608 mm in 2011, and 809 mm in 2012 (Table 1). Total summer precipitation (May to August) was 223 mm in 2009, 148 mm in 2010, 286 mm in 2011, and 219 mm in 2012. Temperatures between 2009 and 2012 were quite stable, averaging 11.6°C, while the mean summer temperature was around 16.5°C irrespective of the year. Summer soil water content (SWC) at 20 cm deep averaged 17.1% in 2010, 16.2% in 2011, and 23.1% in 2012. The SWC was higher in the SRC than in the SRF. During the growth year with phenology monitoring (2010), soil water content fluctuated considerably (Fig. 1A). The soil was very dry during the summer, with values between 20 and 10% from day 180 (end of June) until day 275 (beginning of October), irrespective of species and planting density. The lowest SWC values were reached around day 240 (end of August), with the poplar SRF plantation being the driest.

2.4 Sampling

For 150 trees under SRF (3 plots of 50 trees; see Appendix Fig. 5) and 400 trees under SRC (4 plots of 100 trees) per species and per provenance, stem height was measured at the end of each growing season, from 2009 to 2012; stem circumference and tree biomass were measured at the end of years 2010 and 2012. Tree survival was also estimated in these plots (Appendix Fig. 5). In addition, 20 individuals per planting density for poplar and 10 individuals per provenance and per planting density for black locust were randomly selected in the previously defined plots to monitor tree growth and phenology and to provide wood and leaf samples in 2010 and 2012. Because the two black locust provenances were not significantly different for any of the measured parameters (see

Appendix Table 5), the 20 selected individuals were averaged ($n = 20$). The measurement schedule is presented in Fig. 2.

2.5 Measurements

2.5.1 Tree dimensions

At the end of each growing season, the height of the dominant stem (height, cm) was measured to the nearest centimeter with a graduated pole. At the end of the growing season in 2010 and 2012, stem circumference (Circ., mm) was measured 20 cm aboveground to the nearest millimeter with a tape measure.

2.5.2 Phenology

Phenology was characterized by the bud burst and bud set dates in 2010. From the beginning of March, the top of the main stem was observed weekly and the bud burst date (day of year, DOY) was set when the apical bud was completely open with the leaves still clustered together (Castellani et al. 1967). At the end of the growing season, the date of bud set (DOY) was recorded when the apical bud was closed and reddish-brown (Rohde et al. 2011). Growing season length (GSL, days) was then calculated as the difference between bud set and bud burst dates (DOY).

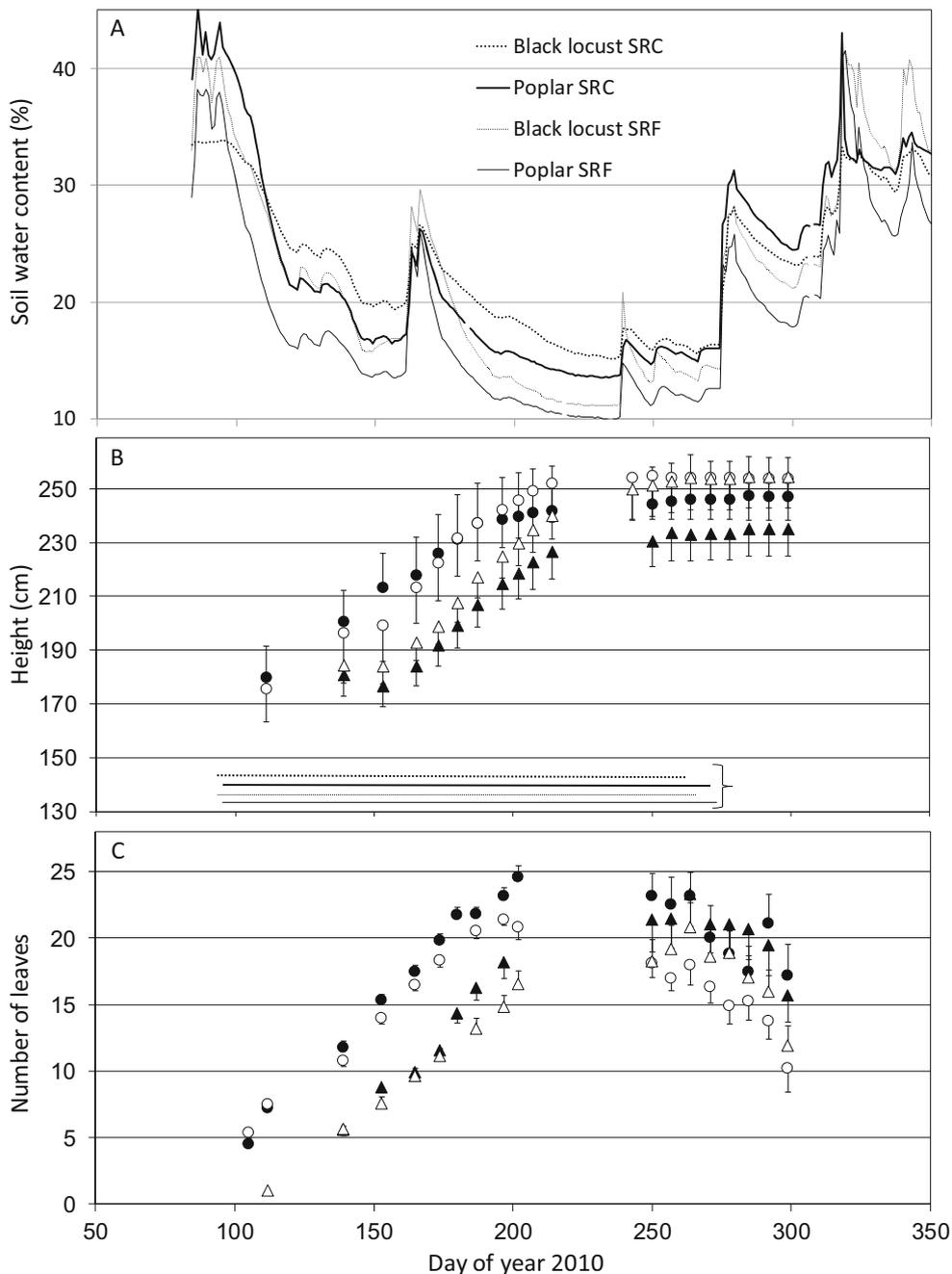
2.5.3 Growth dynamics and tree architecture

Before bud burst in 2010, the number of sylleptic branches was counted. From the end of March (day 88) until the end of October (day 299), the height of the dominant stem was monitored, and the number of leaves on the dominant stem was counted every 2 weeks. Stem height increase rate (dHt/dt , cm day⁻¹) and leaf increment rate (dnl/dt , day⁻¹) were computed as the slopes of the relationship between time and stem height or number of leaves, respectively, during the linear phase of growth, from day 100 to day 188.

2.5.4 Leaf collection

At the end of July 2010 and 2012, a fully illuminated mature leaf was collected from the main stem of each tree. Individual leaf area (LA, cm²) was immediately determined with a leaf area meter (Li-Cor, Li-3000A, Lincoln, Nebraska, USA). The leaves were then oven-dried at 60°C for at least 48 h and then weighed. Specific leaf area (SLA, cm² g⁻¹) was calculated as the ratio between the LA and the leaf dry mass. The same samples were then used to determine foliar carbon and nitrogen contents and carbon isotopic composition.

Fig. 1 Timeline of soil water content (%), stem height (cm) and growing season length (B), and number of leaves (C) during the 2010 growing season at Guémené-Penfao for poplars (circles and continuous lines) and black locusts (triangles and dotted lines) grown under SRC (open symbols) and SRF (closed symbols). Circles/triangles represent means (\pm SE): $n = 20$.



2.5.5 Aboveground biomass production and wood collection

The poplar and black locust trees under the SRC system were cut back to 5 cm aboveground in December 2010 and 2012 (because of the longer rotation length, tree biomass was not estimated for the SRF system). Total aboveground fresh weight was measured. In 2010 only, 20-cm-long samples were taken from the stem of each tree at 1 m aboveground. To determine the dry/fresh weight ratio, all of these samples were weighed before and after being oven-dried at 60°C for 2 weeks. The dry/fresh weight ratio was then used to compute the total shoot dry biomass per tree (Biomass, g) as:

$$\text{Biomass} = \text{dry/fresh mass ratio (from samples taken)} \times \text{total individual fresh mass}$$

Biomass yield ($\text{t ha}^{-1} \text{ year}^{-1}$) was then calculated as:

$$\text{Yield} = (\text{Biomass} \times \text{number of stools per hectare} \times \text{tree survival}) / \text{number of growth years}$$

Twenty of these dry samples per species were then used to determine wood carbon and nitrogen contents and carbon isotopic composition.

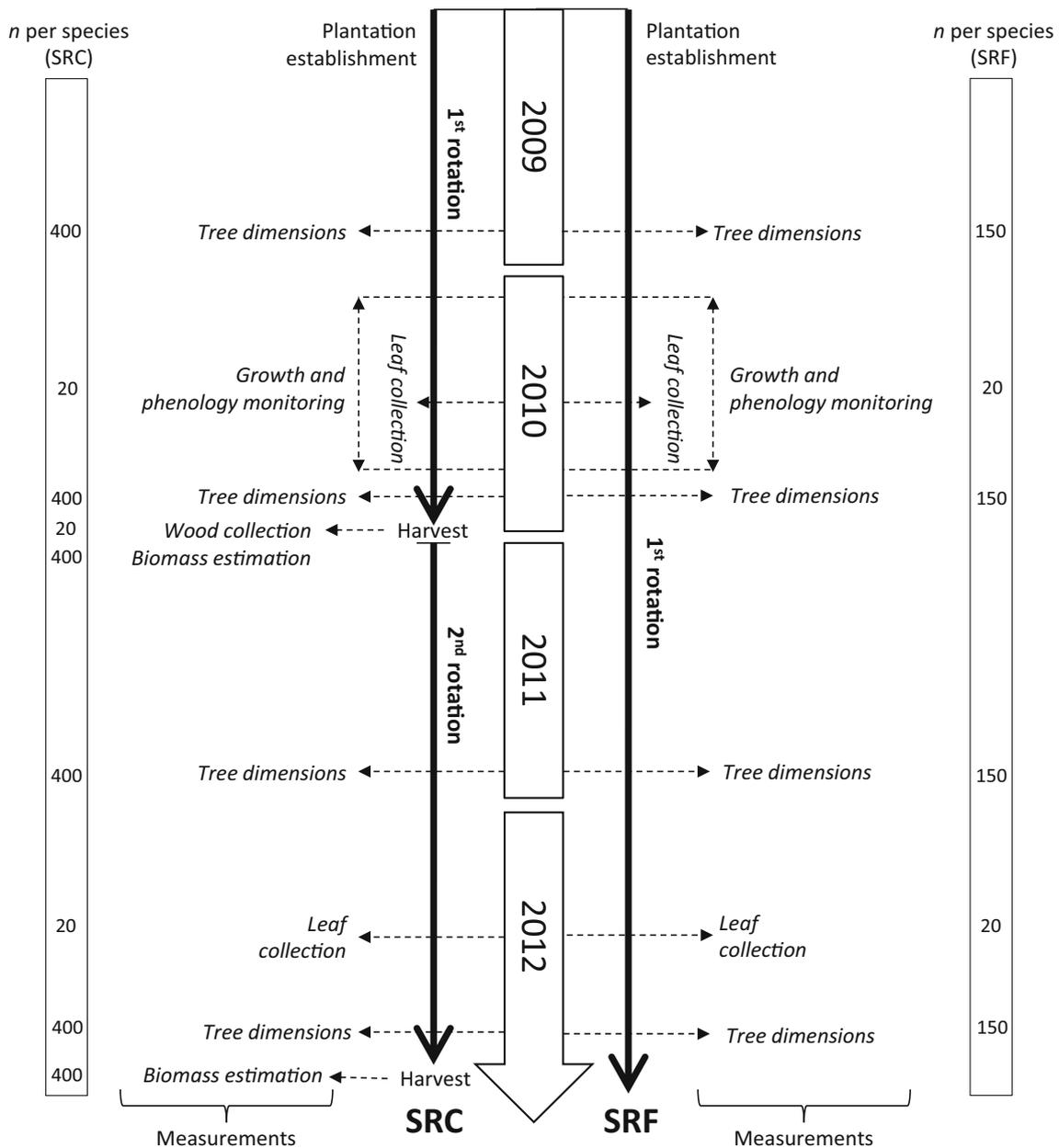


Fig. 2 Chronology of measurements and leaf and wood sampling in the SRF and SRC plantations at Guémené-Penfao between 2009 and 2012. Number of measured trees per species (n) is indicated for each cultural system.

2.5.6 Leaf and wood composition

The dried wood and leaf samples were ground to powder and 1 mg of homogenous powder was analyzed for total carbon and nitrogen contents (C_{leaf} , C_{stem} , N_{leaf} , and N_{stem} , mg g^{-1}) and carbon isotopic composition ($\delta^{13}\text{C}$, ‰) with an elemental analyzer (NCS2500, EA/NA 1110, CE instrument Thermo Quest, Italy) coupled with an isotope ratio mass spectrometer (Delta S, Finnigan MAT, Bremen, Germany). Carbon isotopic composition ($\delta^{13}\text{C}$) was calculated relative to the Vienna Pee Dee Belemnite standard as:

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000 \text{ (‰)}$$

where R_{sample} and R_{standard} are the $^{13}\text{CO}_2/^{12}\text{CO}_2$ ratios of the sample and the standard, respectively (Farquhar et al. 1989). The accuracy of the $\delta^{13}\text{C}$ measurements was $\pm 0.14\text{‰}$ (standard error, SE). Carbon isotope discrimination ($\Delta^{13}\text{C}$) between source air and bulk organic material was then calculated according to Farquhar and Richards (1984) as:

$$\Delta^{13}\text{C} = (\delta_{\text{air}} - \delta_{\text{plant}}) / (1 + (\delta_{\text{plant}}/1000)) \text{ (‰)}$$

where δ_{air} is the isotopic composition of the air (assumed to equal -8‰) and δ_{plant} is the isotopic composition of the leaf or wood organic matter. An increase in $\Delta^{13}\text{C}$ values is associated with a decrease in intrinsic water-use efficiency as evidenced by Farquhar and Richards 1984.

2.5.7 Nitrogen removal rate during harvests

The nitrogen removal rate (N_{removal} , $\text{kg N ha}^{-1} \text{ year}^{-1}$) corresponds to the nitrogen amount, coming from the soil or fixed from the atmosphere, exported from the plantation in the harvested biomass. It was calculated for the first rotation of the SRC as:

$$N_{\text{removal}} = (N_{\text{stem}} \times \text{Biomass} \\ \times \text{number of stools per hectare} \\ \times \text{tree survival}) / \text{number of growth years}$$

where N_{stem} is the stem nitrogen content (g kg^{-1}) and Biomass is the total shoot dry biomass per tree (kg). Here, the number of stools per hectare is 7272 and the number of growth years is 2.

2.6 Statistical analyses

Statistical analyses were performed with the R software (R Development Core Team, 2010). The data were found to meet the assumptions of homoscedasticity and residuals were normally distributed. All statistical tests were considered significant at $P \leq 0.05$. Means are expressed with their standard error.

The data were analyzed with a two-way ANOVA test according to the following model:

$$\text{var} = \text{Species} + \text{Planting density} + (S \times D) + \varepsilon$$

where “Planting density” refers to the planting density effect, considered fixed, and “ $S \times D$ ” refers to the species/planting density interaction. When a significant “Species \times Planting density” interaction effect was highlighted, a one-way ANOVA was run to account for the “Species” and “Planting density” effects independently.

To monitor growth and phenology, comparisons in time were done with the general linear model (GLM) procedure for repeated measurements (split plot in times).

For leaf traits measured during years 2010 and 2012 (LA, SLA, $\Delta^{13}\text{C}$, N_{leaf} , C/N), the data were also analyzed with a three-way ANOVA model as follows:

$$\text{var} = \text{Species} + \text{Planting density} + \text{Year} + (S \times D) \\ + (S \times Y) + (D \times Y) + (S \times D \times Y) + \varepsilon$$

where “Year” refers to the measurement year, a fixed variable; “ $S \times Y$ ” refers to the species/year interaction; “ $D \times Y$ ” refers to the planting density/year interaction; and “ $S \times D \times Y$ ” refers to the species/planting density/year interaction.

The correlation analysis among variables for black locust is presented only for 2010 (year with the most complete dataset; Fig. 2) for both SRC and SRF. We used linear correlations (Pearson correlation coefficients, r) to calculate the relationships among variables and principal component analysis (PCA) to illustrate them. The variables were standardized and orthogonal factors (i.e., the F1 and F2 axes) were successively built as linear combinations of the variables to maximize the fraction of variability they explained. The variables were first represented on the plane defined by the two main factors of the PCA; their coordinates were their linear correlation coefficients (r) with these factors. Only measured variables, not calculated variables, were used.

3 Results

3.1 Effect of planting density

The two black locust provenances (‘Nagybudmerii’ and ‘Nyirseg’) were not significantly different for most variables for a given planting density (Appendix Table 5); averaged values of the two provenances are presented in Tables 2 and 3. Based on the two-way ANOVA, planting density had a

Table 2 General means \pm standard error (SE) for stem height (cm), circumference (mm), and biomass production at tree (g_{DW}) and plantation levels (Yield; $\text{t ha}^{-1} \text{ year}^{-1}$) for poplar and black locust at the two planting densities (SRC/SRF) ($n = 400$ and 800 individuals for poplar and black locust, respectively, in the SRC; $n = 150$ and 300 individuals for poplar and black locust, respectively, in the SRF). Differences between species, planting density, and their interaction are presented in Table 4. When data are available for SRC only, the differences between species are indicated: ** $P \leq 0.01$, *** $P \leq 0.001$

	SRC		SRF	
	Black locust	Poplar	Black locust	Poplar
<i>Height (cm)</i>				
2009	115.2 \pm 8.1	137.5 \pm 19.3	138.3 \pm 11.4	140 \pm 11.5
2010	192.9 \pm 12.5	182.5 \pm 27.8	224.3 \pm 23.6	206.7 \pm 18.6
2011	218.7 \pm 11.5	277.5 \pm 21.4	355.8 \pm 31.1	350.0 \pm 25.2
2012	346.2 \pm 18.3	407.5 \pm 23.2	513.8 \pm 30.1	506.7 \pm 29.6
<i>Circ. (mm)</i>				
2010	94.8 \pm 5.6	81.0 \pm 4.2	113.8 \pm 6.7	82.5 \pm 5.6
2012	121.3 \pm 11.4	109.4 \pm 7.3	259.5 \pm 17.2	185.4 \pm 12.6
<i>Biomass (g_{DW})</i>				
2010	487.0 \pm 38.1 ***	222.8 \pm 29.8	-	-
2012	1490.6 \pm 69.0 ***	806.5 \pm 30.1	-	-
<i>Yield ($\text{t ha}^{-1} \text{ year}^{-1}$)</i>				
2010	1.46 \pm 0.11 ***	0.75 \pm 0.10	-	-
2012	2.21 \pm 0.10 **	2.66 \pm 0.10	-	-

Abbreviations: SRC, short rotation coppice; SRF, short rotation forestry; Circ., stem circumference

Table 3 (A) Growth, phenology, branchiness, leaf, and wood traits for poplar and black locust measured in 2010 at the end of the first SRC rotation or at the end of the second year in the SRF ($n = 20$ individuals per planting density and per species). When data are available for SRC only, i.e., for wood traits, differences between species are indicated: ** $P \leq 0.01$, *** $P \leq$

0.001. (B) Leaf traits for poplar and black locust measured in 2012 at the end of the second SRC rotation or the end of the fourth year in the SRF ($n = 20$ individuals per planting density and per species). The differences between species, planting density, and their interaction are presented in Table 4

	SRC		SRF	
	Black locust	Poplar	Black locust	Poplar
A				
<i>Growth</i>				
dHt/dt (cm day ⁻¹)	0.61 ± 0.08	0.64 ± 0.06	0.73 ± 0.08	0.76 ± 0.07
dnl/dt (day ⁻¹)	0.13 ± 0.01	0.17 ± 0.01	0.16 ± 0.01	0.20 ± 0.01
<i>Phenology</i>				
Bud burst (day of year)	94.8 ± 1.8	96 ± 0.0	94.1 ± 1.6	96.0 ± 0.0
Bud set (day of year)	263.3 ± 2.8	271 ± 0.0	265.7 ± 3.6	273.8 ± 1.9
GSL (days)	168.8 ± 3.4	175 ± 0.0	171.8 ± 5.1	177.8 ± 1.9
<i>Leaf traits</i>				
LA (cm ²)	128.0 ± 9.7	52.9 ± 3.8	122.6 ± 8.0	69.2 ± 7.4
SLA (cm ² g ⁻¹)	136.7 ± 8.0	84.7 ± 2.8	147.2 ± 4.2	75.6 ± 2.0
N_{leaf} (mg g ⁻¹)	41.2 ± 1.1	11.3 ± 0.8	39.9 ± 1.7	15.9 ± 1.3
C/N	11.9 ± 0.3	41.0 ± 2.1	12.3 ± 0.5	31.5 ± 2.8
$\Delta^{13}C$ leaf (‰)	16.7 ± 0.3	20.4 ± 0.1	17.2 ± 0.3	20.4 ± 0.2
<i>Wood traits</i>				
N_{stem} (mg g ⁻¹)	9.6 ± 0.4 ***	5.0 ± 0.5	-	-
C/N	49.4 ± 2.2 ***	99.1 ± 8.6	-	-
$N_{removal}$ (kg N ha ⁻¹ year ⁻¹)	15.9 ± 2.6 ***	4.7 ± 0.7	-	-
$\Delta^{13}C$ wood (‰)	17.2 ± 0.2 **	19.3 ± 0.1	-	-
<i>Branchiness</i>				
Sylleptic number	8.7 ± 1.3	6.1 ± 1.7	10.9 ± 1.1	2.0 ± 0.9
B				
<i>Leaf traits</i>				
LA (cm ²)	180.7 ± 24.6	146.1 ± 9.4	177.0 ± 16.0	131.6 ± 16.7
SLA (cm ² g ⁻¹)	130.4 ± 7.2	132.4 ± 3.1	127.7 ± 6.4	109.8 ± 1.9
N_{leaf} (mg g ⁻¹)	37.9 ± 0.2	32.9 ± 0.2	43.2 ± 0.4	24.9 ± 0.2
C/N	12.2 ± 0.8	13.7 ± 0.8	11.1 ± 1.0	18.3 ± 1.1
$\Delta^{13}C$ leaf (‰)	17.4 ± 0.6	18.6 ± 0.8	18.2 ± 0.6	19.8 ± 0.2

Abbreviations: SRC, short rotation coppice; SRF, short rotation forestry; dHt/dt , stem height increase rate; dnl/dt , leaf increment rate; *GSL*, growing season length; *LA*, individual leaf area; *SLA*, specific leaf area; N_{leaf} , leaf nitrogen content; *C/N*, carbon/nitrogen ratio; $\Delta^{13}C$, carbon isotope discrimination; N_{stem} , stem nitrogen content; $N_{removal}$, nitrogen removal rate

significant effect on leaf C/N in 2010, SLA in 2012, and dnl/dt (Tables 3 and 4). The species/planting density interaction was significant for leaf C/N both in 2010 and in 2012, the number of sylleptic branches and stem heights after harvest. On the basis of the one-way ANOVA, poplar exhibited significantly higher values of N_{leaf} in 2010 and leaf C/N in 2012 under SRF than under SRC. Bud set also occurred later and SLA values and number of sylleptic branches were lower (both years) under SRF. For black locust, *Circ.* was significantly larger under SRF than under SRC.

3.2 Comparison between species

Black locust exhibited higher values of stem circumference and biomass production at tree level than poplar, but no significant differences in stem height or stem increase rate were observed during the first rotation; this was likely due to the development of more (sylleptic) branches in black locust than in poplar (Tables 2, 3, and 4). Yield at plantation level of the

first SRC rotation was almost twice as high for black locust as that for poplar, while it was significantly higher for poplar during the second rotation due to black locust mortality (Table 2 and Fig. 3). Lower values of leaf increment (dnl/dt) were found for black locust compared to those for poplar at both planting densities, but the individual size of the leaves was superior for black locust. During the driest period of the year 2010 (around days 190–200), black locust trees continued to grow in height while poplar growth was nearly stopped (Fig. 1B). Black locust wood and leaves were richer in nitrogen than poplar. $N_{removal}$ was more than three times as high for black locust as that for poplar. For SRC, black locust presented significantly lower values of leaf $\Delta^{13}C$ than did poplar. The difference between poplar and black locust for wood $\Delta^{13}C$ was not significant. Stem height measured after harvest (2011) was not significantly different between species at either planting density, but poplar trees were taller than black locust in SRC while black locust trees were slightly taller than poplar in the SRF (Table 2).

Table 4 Results of the two-way (species, planting density, and their interaction) and one-way (planting density) ANOVAs for traits measured during the 2009–2010 (A) and 2011–2012 (B) periods: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; ns, non-significant

	Two-way ANOVA			One-way ANOVA	
	Species	Planting density	S × D	Black locust	Poplar
A					
<i>Growth</i>					
Height 2009	ns	ns	ns	ns	ns
Height 2010	ns	ns	ns	ns	ns
Circ. 2010	**	ns	ns	*	ns
dHt/dt	ns	ns	ns	ns	ns
dn/dt	**	*	ns	ns	**
<i>Phenology</i>					
Bud burst	ns	ns	ns	ns	ns
Bud set	*	ns	ns	ns	*
GSL	ns	ns	ns	ns	ns
<i>Leaf traits</i>					
LA	***	ns	ns	ns	ns
SLA	***	ns	ns	ns	*
N_{leaf}	***	ns	ns	ns	**
C/N	***	**	***	ns	*
$\Delta^{13}\text{C}$ leaf	***	ns	ns	ns	ns
<i>Branchiness</i>					
Sylleptic number	***	ns	*	ns	*
B					
<i>Growth</i>					
Height 2011	ns	***	*	**	*
Height 2012	ns	***	*	*	*
Circ. 2012	ns	***	*	***	***
<i>Leaf traits</i>					
LA	***	ns	ns	ns	ns
SLA	***	*	ns	ns	***
N_{leaf}	**	ns	ns	ns	*
C/N	**	ns	*	ns	*
$\Delta^{13}\text{C}$ leaf	*	ns	ns	ns	ns

Abbreviations: Circ., stem circumference; dHt/dt, stem height increase rate; dn/dt, leaf increment rate; GSL, growing season length; LA, individual leaf area; SLA, specific leaf area; N_{leaf} , leaf nitrogen content; C/N, carbon/nitrogen ratio; $\Delta^{13}\text{C}$, carbon isotope discrimination; S×D, species/planting density interaction

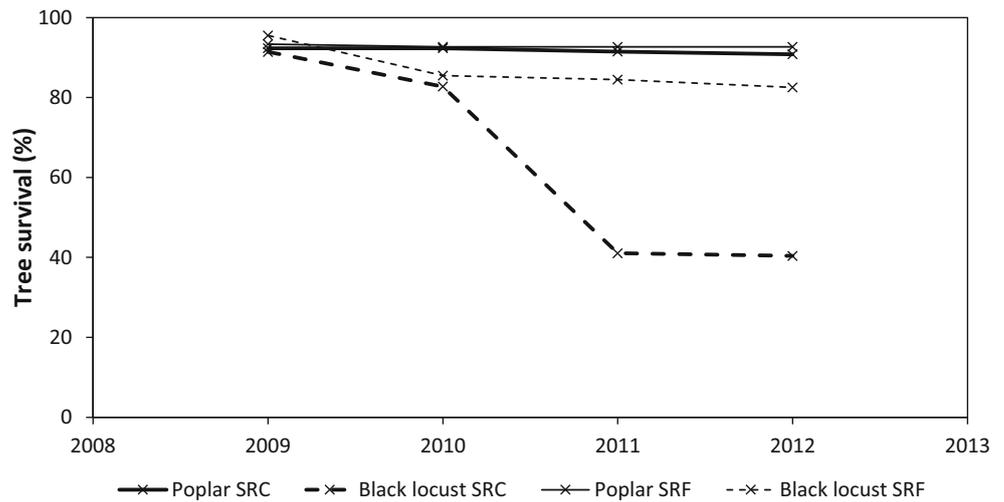
3.3 Comparison between rotations

Two rotations of the SRC plantations were included during the experiment. Except for stem height, which was measured every year, tree dimensions and leaf traits were measured during the second year of each rotation (i.e., 2010 and 2012) (Fig. 2). In the SRC, stem height and circumference as well as tree biomass and plantation yield were much higher for both species during the second rotation than those during the first (Table 2). For black locust only, the SRC harvest in 2010 had a huge effect on tree survival: only 40% of the trees resprouted the following spring, while survival remained above 80% for poplar (and for black locust in the SRF) (Fig. 3). For all leaf traits, the year and species/year interaction were significant ($P \leq 0.01$; data not shown). In both silvicultural systems and for both species, leaves were larger in 2012 than in 2010. Poplar showed higher SLA and N_{leaf} during the second rotation; the reverse was true for black locust. Leaf $\Delta^{13}\text{C}$ was also higher for black locust during the second rotation, while it was the other way around for poplar (Table 3).

3.4 Relationships among variables for black locust in 2010

The main planes of the PCA (F1 × F2) explained 66.4% of the variation for the SRF, with 48.2% for F1 alone; and 52.6% for the SRC, with 33.1% for F1 alone (Fig. 4). The F3 axis did not significantly differentiate the trees in either planting density (data not shown). For both planting densities, the growth variables (Ht, dn/dt, dHt/dt, Biomass) were closely correlated (Fig. 4). Under SRC, leaf $\Delta^{13}\text{C}$ was positively correlated to wood $\Delta^{13}\text{C}$ ($r = 0.67$, $P \leq 0.01$), and negatively correlated to Circ. (-0.53 , $P \leq 0.05$). N_{leaf} was positively correlated to most growth variables: Circ. (0.53 , $P \leq 0.05$), Ht (0.67 , $P \leq 0.01$), and dHt/dt (0.68 , $P \leq 0.01$), and negatively correlated to N_{wood} (-0.49 , $P \leq 0.05$). Logically, N_{wood} was negatively correlated to the growth variables, for example, Ht (-0.52 , $P \leq 0.05$) and Biomass (-0.48 , $P \leq 0.05$). Under SRF, $\Delta^{13}\text{C}_{\text{leaf}}$ was negatively correlated to dn/dt (-0.57 , $P \leq 0.05$), dHt/dt (-0.62 , $P \leq 0.05$), and LA (-0.54 , $P \leq 0.05$). N_{leaf} was positively correlated to most growth variables, notably to Ht (0.59 , $P \leq 0.05$) and

Fig. 3 Timeline of poplar and black locust tree survival in the SRF and SRC plantations at Guémené-Penfao between 2009 and 2012.



dHt/dt ($0.67, P \leq 0.01$). Bud burst was negatively correlated to bud set ($-0.60, P \leq 0.05$) for the SRF only.

4 Discussion

4.1 Black locust and poplar biomass production

The yield values we observed in this study for the first rotation in the black locust SRC were low ($1.46 \text{ t ha}^{-1} \text{ year}^{-1}$). This is in the lower range of observed values in the literature (for planting densities of around 10,000 trees per ha), most probably because of the youth of our trees: $1.3 \text{ t ha}^{-1} \text{ year}^{-1}$ for a 6-year-old unfertilized plantation (Kanzler et al. 2015) to $7.6 \text{ t ha}^{-1} \text{ year}^{-1}$ for 3-year-old fertilized trees after three rotations (Grünewald et al. 2009). Much higher yields ($14 \text{ t ha}^{-1} \text{ year}^{-1}$) were observed by Geyer (1989) after four growing seasons on highly

productive arable lands, but the growth conditions (irrigation, fertilization) were not specified in the study. This author also showed that annual increases in biomass were higher year after year. Much higher yields have indeed been observed for older black locust trees ($5.8 \text{ t ha}^{-1} \text{ year}^{-1}$ for the second rotation period of a 3-year rotation in Grünewald et al. 2007; $9.5 \text{ t ha}^{-1} \text{ year}^{-1}$ for 14-year-old trees in Grünewald et al. 2009). Boring and Swank (1984) observed stem height values of around 8 m for 4-year-old black locust trees (compared to 5 m in our case) while Rédei et al. (2011) measured stem height increase rates ranging between 2 and 6 cm per day for black locust in its juvenile stage (0.6 to 0.7 cm day^{-1} in our case). In addition to the fact that the plantation was young, the low values we found are also likely due to pedoclimatic conditions at our study site. The summer was particularly dry during the second growing season (148 mm of rainfall between May and August) and the soil water content dropped to 10% during the driest

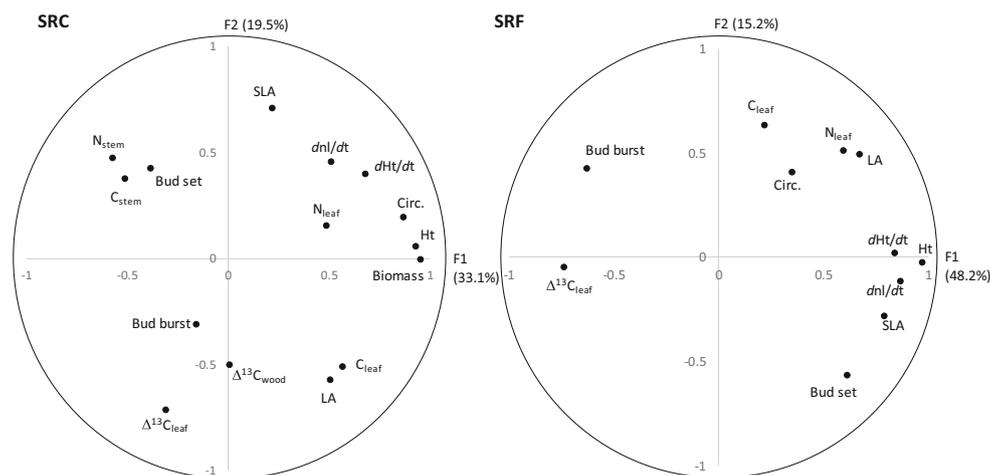


Fig. 4 Distribution of the variables in the main factorial plane $F1 \times F2$ of the principal component analysis (PCA) for the black locust trees under SRC (left) and SRF (right) conditions during the 2010 growing season. The numbers (in %) next to each axis represent the variance explained by the respective principal components. Abbreviations: SRC, short rotation

coppice; SRF, short rotation forestry; Circ., stem circumference; Ht, stem height; dHt/dt , stem height increase rate; dnl/dt , leaf increment rate; LA, individual leaf area; SLA, specific leaf area; N_{leaf} , leaf nitrogen content; C_{leaf} , leaf carbon content; $\Delta^{13}\text{C}$, carbon isotope discrimination; N_{stem} , stem nitrogen content; C_{stem} , stem carbon content.

period in 2010. The soil organic matter and nitrogen contents at Guémené-Penfao (39.4 and 1.7 g kg⁻¹, respectively) could also have limited tree growth before the black locust–rhizobium association could be efficient enough to symbiotically fix atmospheric nitrogen (see Toillon et al. 2013a for a comparison with other sites). A recent review of literature has highlighted synergistic effects of mycorrhizal association with the symbiotic N₂ fixation by rhizobium, greatly enhancing the ecological and physiological performances of black locust by improving its rate of growth, nutrition status, and resistance to stress conditions such as drought (Liu et al. 2020). The relatively low soil nitrogen content at our site also resulted in lower nitrogen removal at harvest (15.9 kg ha⁻¹ year⁻¹) as compared to black locust trees of a similar age cultivated at a similar planting density (31.8 kg ha⁻¹ year⁻¹ in Quinkenstein et al. 2012). The difference is likely due to the cumulative effects of the slightly lower wood nitrogen content, the slightly lower aboveground biomass production, and the higher tree mortality in our study.

In spite of the relatively low biomass production under the conditions in our study, black locust trees were still much more productive than the poplar trees growing at the same site (0.75 t ha⁻¹ year⁻¹ for the first poplar SRC rotations). Poplar yields ranging between 5 and 15 t ha⁻¹ year⁻¹ are commonly observed for a first rotation for planting densities between 2000 and 10,000 trees per ha (e.g., Armstrong et al. 1999; Berthelot et al. 2000; Dillen et al. 2013), with yields peaking at 28 or 35 t ha⁻¹ year⁻¹ when the trees are irrigated and/or fertilized (Heilman and Stettler 1986; Scarascia-Mugnozza et al. 1997). Grünwald et al. (2007) showed that, on poor, reclaimed mine soils, poplar trees could equal black locust yield (around 6 t ha⁻¹ year⁻¹) only if site conditions were improved with mineral fertilizers or compost. However, due to very high black locust mortality after the first SRC harvest, plantation yield in our study was higher for poplar than that for black locust at the end of the second SRC rotation. At high planting densities, black locust has been shown not to cope well with successive harvests: survival rates become lower and lower. For instance, only 22% of the trees had survived after the fourth harvest in Geyer (1989). In any case, the biomass production was far below the average yields needed to make short rotation tree plantations economically viable (10–12 t ha⁻¹ year⁻¹ according to Heath et al. 1994 or 5–6.5 t ha⁻¹ year⁻¹ according to Panoutsou and Alexopoulou 2020). Such high yields are unlikely under poor or dry site conditions, even with a promising species like the black locust. However, yields are not the only factor affecting plantation profitability. Market selling prices and silvicultural costs (costs related to planting, cleaning, etc.) are also important factors influencing system profitability (Panoutsou and Alexopoulou 2020). Moreover, short rotation plantation using N₂-fixing species has the advantage to reduce fertilization and management costs as compared to arable crops or non-fixing trees. Perennial energy crops have demonstrated the potential to

provide habitat for biodiversity, improve soil health, enhance water quality, mitigate dryland salinity, and sequester carbon (Baumber 2017). These economic, environmental, and management benefits must also weight in the balance.

It should be noted that slightly larger ranges have been observed for most black locust variables than those for poplar due to the fact that black locust trees are grown from seed while poplar trees are grown from genetically similar cuttings. Black locust has a very different ecology from poplar. In our study, under both SRC and SRF, growth in height was similar for the two species, while the increase in leaf number was lower for the black locust trees. Due to an earlier bud set than poplar, the length of the growing season was shorter for black locust. However, black locust leaves were much larger, the stems were much thicker, and the sylleptic branches were much more numerous than for poplar. As a result, black locust biomass production in the SRC was twice as high as for poplar at the first rotation. Black locust trees seem to promote growth in volume rather than growth in height; the limit of this strategy is that growth in volume can be rapidly restricted by neighboring trees at high planting densities.

Only a few effects of the initial planting density (SRF, 1428 trees per ha vs. SRC, 7272 trees per ha) on plant growth and physiology were visible 2 years after planting. However, black locust trees were significantly smaller and had thinner stems in the SRC than in the SRF. This effect was less marked for the poplar trees, probably due to slower growth for poplar than for black locust during the first rotation. Such differences are likely to be due to a more intense competition for soil resources at higher planting densities, especially when water is a limiting factor. The theory states that primary growth is promoted at the expense of secondary growth at higher planting densities (Benomar et al. 2012). Due to the poor soil resource content in our study, both primary growth and secondary growth were reduced in response to increased planting density. Similar effects of planting density were observed for poplar in Toillon et al. (2013b) at two different sites.

4.2 Resource acquisition and use of black locust compared to poplar

As expected, nitrogen content, both in leaves and wood, was much higher for the nitrogen-fixing species, black locust, than for poplar. Even though, in our case, it was not possible to differentiate the origin of the nitrogen present in the plants (i.e., from the soil or from symbiotic fixation), the large differences between species (almost twice as much nitrogen in the stem and almost three times as much in the leaf for black locust during the second year) could indicate that a large part of the nitrogen in the black locust tissues originated from symbiotic fixation, as shown by Mantovani et al. (2015) in 2-year-old black locust trees. This is a very interesting property of the nitrogen-fixing species, which can grow on soils with low

nitrogen levels and even reclaim poor soils (Zeleznik and Skousen 1996; Grünewald et al. 2009). Drought may trigger large increases in nodule biomass (up to 80%) for black locust, improving its nitrogen fixation and growth relative to other species, and making it very well adapted to dry nitrogen-deficient environments (Wurzburger and Miniat 2014; Mantovani et al. 2015). However, other nutrients such as P, K, or Ca could have been limiting and were not measured in our experiment. For instance, it has been shown that an increase in N availability may be associated with a decrease in P availability, as N₂ fixing species generally need more P for sustaining symbiotic root nodules and N₂ fixation processes; availability of P and N is one of the main soil fertility constraints to crop production in many soils (Koutika et al. 2014).

The ability to fix atmospheric nitrogen is used in plantations mixing fixing and non-N₂-fixing tree species since a long time. An increase in the nitrogen content of non-fixing species indeed occurs when they are grown in mixtures with nitrogen fixers, both in tropical and temperate climates (Coté and Camire 1984; Epron et al. 2013; Marron and Epron 2019). However, the benefits provided by natural nitrogen inputs can be counterbalanced by high competition between the two species in the mixture (e.g., Marron et al. 2018; Rebola-Lichtenberg et al. 2020).

The differences between the two species in our study were less marked during the fourth year; most notably, black locust showed leaf N values similar to the second year. On the other hand, poplar leaf N increased quite dramatically between the second and the fourth years. It should be noted that the 2 years during which leaves were collected (2010 and 2012, the second year of each SRC rotation) were quite contrasted in terms of water supply. Precipitation was much lower in 2010 than that in 2012, and consequently, soil water was likely to be more limiting in 2010. Poplar growth is known to closely depend on an adequate water supply; in our study, the physiology and biomass production of the two species was probably affected by the drought during summer 2010. A recent meta-analysis by Xu et al. (2020) showed that, overall, leaf N is not significantly affected by drought, despite the important variability that can occur between and within tree species (Joseph et al. 2021; Monclus et al. 2006). In poplars, an important genotypic variability in the drought response of leaf N has been observed, usually leading to a decrease in leaf N in the case of drought (Monclus et al. 2006), although a positive effect of drought on nitrogen assimilation, leaf N content, and biomass production was observed in four poplar genotypes (Durand et al. 2020). On the other hand, black locust is well known for its ability to grow on poor and dry soils (Grünewald et al. 2009; Böhm et al. 2011); and therefore, its growth was undoubtedly less affected by the dry conditions in 2010 than that of the poplars. Inversely, year 2012, less binding in terms of water supply, was more favorable to poplar. This different species response to climate can also be associated with an

effect of the cutting, affecting more the growth and physiology of black locust resprouts.

Carbon isotope discrimination ($\Delta^{13}\text{C}$) has been extensively used as a surrogate for water-use efficiency for many species including black locust (Zheng and Shangguan 2007a; Tanaka-Oda et al. 2010). In our study, black locust exhibited much lower $\Delta^{13}\text{C}$ values than poplar, especially during the second year (2010). At the leaf level, a difference of 4‰ with poplar was found, suggesting that the black locust's water use was much more efficient than the poplar's, under the conditions in our study. Indeed, studies dealing with a wide range of woody species have shown that nitrogen-fixing species generally have more efficient water use than non-fixing species (Schulze et al. 1998; Zheng and Shangguan 2007a, 2007b; King et al. 2013; Adams et al. 2016). This is probably because leguminous plants have higher leaf nitrogen contents due to nitrogen fixation, leading to greater photosynthetic capacity and higher WUE. This combination of higher leaf N and greater WUE probably enhanced black locust performance under the dry conditions in 2010. This is in accordance with Adams et al. (2016), who linked the two factors with an enhanced adaptation of N₂-fixing species to arid and semi-arid conditions.

During the fourth year (2012), the gap between the two species in terms of $\Delta^{13}\text{C}$ was less marked due to the fact that poplar $\Delta^{13}\text{C}$ decreased (increase in WUE), while black locust $\Delta^{13}\text{C}$ slightly increased (decrease in WUE). As already observed for poplar genotypes (Toillon et al. 2013b), constraining conditions (here mostly in terms of water supply) exacerbate differences among species in terms of $\Delta^{13}\text{C}$. Indeed, poplar leaves exhibited higher SLA and lower $\Delta^{13}\text{C}$ in 2012 than in 2010, while the same foliar traits in black locust only slightly changed between 2010 and 2012. Differences between species in both leaf and wood $\Delta^{13}\text{C}$ were observed, suggesting that differences in black locust and poplar WUE existed irrespective of time scale: leaf life span vs. tree life span. No significant correlation was observed between $\Delta^{13}\text{C}$ and leaf nitrogen; therefore, variations in WUE are likely to be mainly related to variations in the stomatal conductance of water vapor (Farquhar et al. 1989). Moreover, the weak or insignificant correlations between tree biomass and $\Delta^{13}\text{C}$ found in our study consolidate this hypothesis. Finally, the consistency of results in leaf and wood material suggests that potential post-photosynthetic fractionations (e.g., during phloem transport or wood formation) do not blur $\Delta^{13}\text{C}$ occurring during CO₂ diffusion to chloroplasts and assimilation during photosynthesis.

5 Conclusions

In practical terms, black locust would appear to be a very interesting option for biomass production at sites prone to water shortage. Indeed, the species combined a water-use efficiency and a biomass production largely superior to the poplars grown

under the same conditions. Moreover, black locust's ability to fix atmospheric nitrogen symbiotically in association with rhizobium is an interesting asset, allowing the tree to grow in nitrogen-poor environments without adding mineral fertilizers or residues (wastewater, sewage sludge, etc.). Nitrogen removal at harvest was much higher for black locust than that for poplar, but the removed nitrogen had probably been fixed from the atmosphere and therefore would not cause soil fertility loss. However, black locust under the SRC regime was very sensitive to harvesting and this caused very high tree mortality (nearly 60%), leading to

a much smaller yield during the second SRC rotation. Longer rotations (SRF regime) could be more adapted to this species and vigilance during the transition periods between rotations would be required.

Appendix

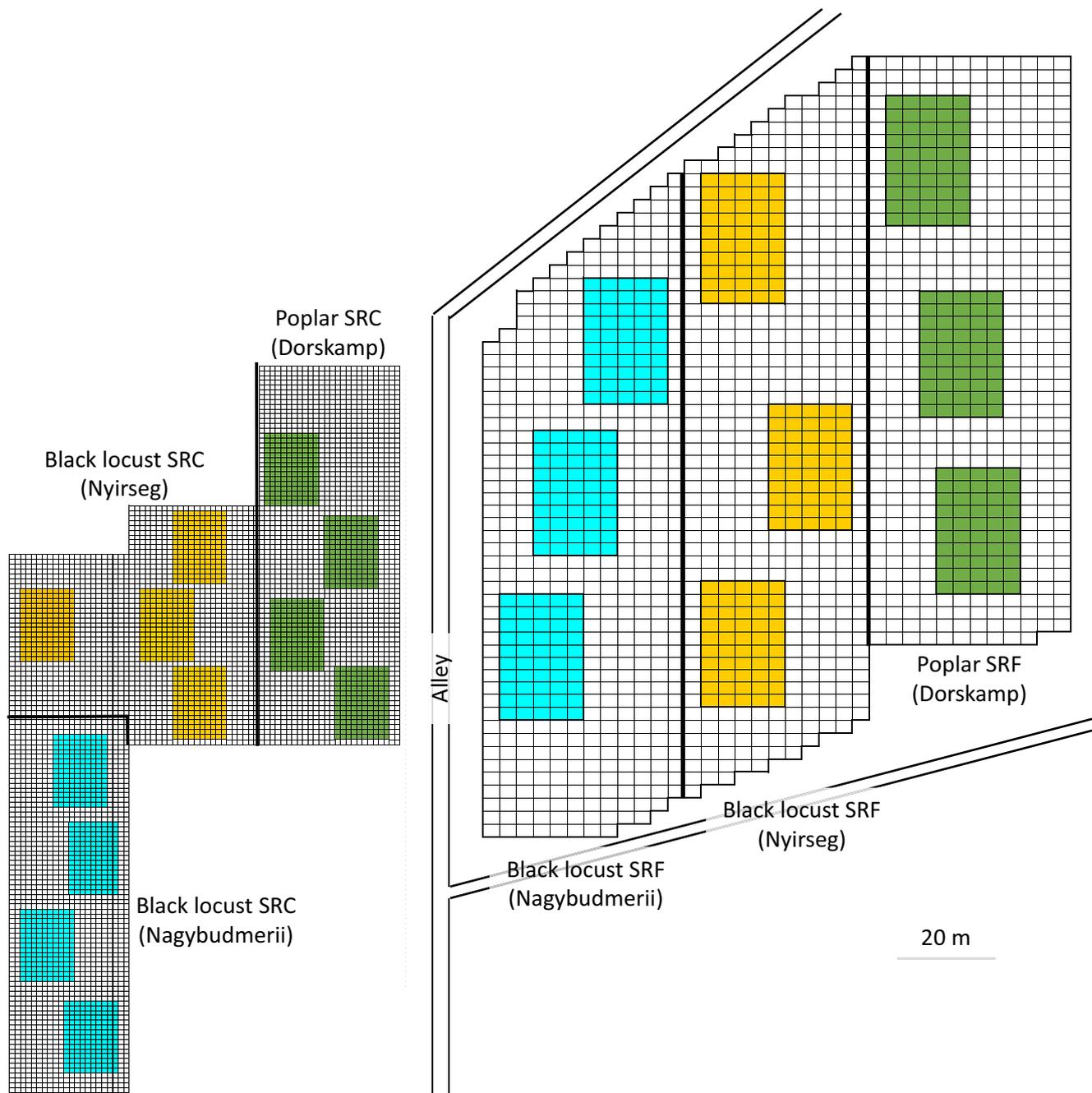


Fig. 5 Layout of the experimental plantation at Guémené-Penfao. Each square represents one tree. The zones in color highlight the trees monitored once a year for stem height and used for biomass assessment

Table 5 General mean \pm standard error (SE) of (A) growth, phenology, branchiness, and leaf and wood traits measured in 2010 (at the end of the first SRC rotation or the end of the second year in SRF) and (B) growth and leaf traits measured in 2012 (at the end of the second SRC rotation or the end of the fourth year in SRF) for the two black locust provenances,

‘Nagybudmerii’ and ‘Nyirseg,’ and the two planting densities (SRC/SRF). $n = 10$ individuals per provenance and per planting density, except for Height, Circ., Biomass, and Yield: $n = 150$ individuals per provenance for the SRF or $n = 400$ for the SRC

	SRC		SRF	
	Nagybudmerii	Nyirseg	Nagybudmerii	Nyirseg
A				
<i>Growth</i>				
dH/dt (cm day ⁻¹)	0.65 \pm 0.11	0.57 \pm 0.11	0.70 \pm 0.10	0.76 \pm 0.14
dnl/dt (leaves day ⁻¹)	0.13 \pm 0.01	0.14 \pm 0.02	0.16 \pm 0.02	0.15 \pm 0.02
Height (cm)	199.5 \pm 9.9	187.6 \pm 22.0	132.0 \pm 2.0	144.5 \pm 26.5
Circ. (mm)	92.6 \pm 7.8	97.0 \pm 8.2	114.6 \pm 7.5	113.1 \pm 11.6
Biomass (g _{DW})	504.7 \pm 54.3	470.3 \pm 54.0	-	-
Yield (t ha ⁻¹ year ⁻¹)	1.51 \pm 0.16	1.41 \pm 0.16	-	-
<i>Phenology</i>				
Bud burst (day of year)	92.2 \pm 2.1	97.3 \pm 2.6	95.1 \pm 2.9	93.4 \pm 1.9
Bud set (day of year)	268.2 \pm 3.5	258.4 \pm 3.9	268.9 \pm 4.4	262.4 \pm 5.7
GSL (days)	175.7 \pm 4.4	162.0 \pm 4.3	176.1 \pm 7.3	168.4 \pm 7.3
<i>Leaf traits</i>				
LA (cm ²)	122.0 \pm 15.9	133.4 \pm 12.0	107.3 \pm 8.2	137.9 \pm 12.2
SLA (cm ² g ⁻¹)	143.5 \pm 4.6	130.7 \pm 14.8	149.6 \pm 5.4	144.9 \pm 6.7
N_{leaf} (mg g ⁻¹)	41.5 \pm 1.9	41.0 \pm 1.4	39.7 \pm 2.5	40.1 \pm 2.5
C/N	11.7 \pm 0.5	12.0 \pm 0.4	12.4 \pm 0.8	12.2 \pm 0.7
$\Delta^{13}\text{C}$ leaf (‰)	16.4 \pm 0.4	16.9 \pm 0.5	17.7 \pm 0.5	16.7 \pm 0.3
<i>Wood traits</i>				
N_{stem} (mg g ⁻¹)	9.6 \pm 0.6	9.7 \pm 0.5	-	-
C/N	50.5 \pm 3.9	48.4 \pm 2.4	-	-
N_{removal} (kg N ha ⁻¹ an ⁻¹)	15.5 \pm 3.2	20.6 \pm 3.8	-	-
$\Delta^{13}\text{C}$ wood (‰)	16.9 \pm 0.2	17.6 \pm 0.4	-	-
<i>Branchiness</i>				
Sylleptic number	8.9 \pm 1.7	8.5 \pm 2.1	10.7 \pm 1.6	11.2 \pm 1.6
B				
<i>Growth</i>				
Height (cm)	381.0 \pm 12.6	318.4 \pm 26.1	377.0 \pm 15.0	334.5 \pm 68.5
Circ. (mm)	83.5 \pm 1.8	69.2 \pm 1.9	159.6 \pm 5.6	144.4 \pm 6.4
Biomass (g _{DW})	1634.4 \pm 95.3	1328.0 \pm 90.5	-	-
Yield (t ha ⁻¹ year ⁻¹)	2.43 \pm 0.14	1.97 \pm 0.13	-	-
<i>Leaf traits</i>				
LA (cm ²)	167.2 \pm 32.9	192.0 \pm 38.1	186.5 \pm 27.9	168.6 \pm 18.2
SLA (cm ² g ⁻¹)	126.4 \pm 10.7	133.8 \pm 10.4	138.0 \pm 6.1	118.4 \pm 10.3
N_{leaf} (mg g ⁻¹)	41.6 \pm 1.9	34.2 \pm 2.6	42.6 \pm 8.3	43.8 \pm 4.2
C/N	11.1 \pm 0.8	13.3 \pm 1.3	11.4 \pm 2.0	10.8 \pm 1.1
$\Delta^{13}\text{C}$ leaf (‰)	16.9 \pm 0.6	17.9 \pm 1.0	18.5 \pm 0.9	17.9 \pm 0.9

Abbreviations: SRC, short rotation coppice; SRF, short rotation forestry; Circ., stem circumference; dH/dt , stem height increase rate; dnl/dt , leaf increment rate; GSL, growing season length; LA, individual leaf area; SLA, specific leaf area; N_{leaf} , leaf nitrogen content; C/N, carbon/nitrogen ratio; $\Delta^{13}\text{C}$, carbon isotope discrimination; N_{stem} , stem nitrogen content; N_{removal} , nitrogen removal rate

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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