Crown morphology of Populus deltoides x P. nigra and Alnus glutinosa growing in agroforestry and forest mixture plantations

Anaïs Thomas, Pierrick Priault, Séverine Piutti, Erwin Dallé, Nicolas Marron

To cite this version:

Anaïs Thomas, Pierrick Priault, Séverine Piutti, Erwin Dallé, Nicolas Marron. Crown morphology of Populus deltoides x P. nigra and Alnus glutinosa growing in agroforestry and forest mixture plantations. Agroforestry Systems, 2023, 97 (4), pp.673-686. 10.1007/s10457-023-00818-2 . hal-04246795

HAL Id: hal-04246795
https://hal.inrae.fr/hal-04246795v1

Submitted on 17 Oct 2023

Crown morphology of *Populus deltoides* × *P. nigra* and *Alnus glutinosa* growing in agroforestry and forest mixture plantations

Anaïs Thomas[a], Pierrick Priault[a], Séverine Piutti[b], Erwin Dallé[a] and Nicolas Marron[a]*

[a]Université de Lorraine, AgroParisTech, INRAE, UMR 1434 Silva, 54000 Nancy, France;

[b]Université de Lorraine, INRAE, UMR 1121 Laboratoire Agronomie et Environnement (LAE), 54518 Vandœuvre-lès-Nancy, France;

*Corresponding author (nicolas.marron@inrae.fr)

Keywords: mixed tree plantation, agroforestry, crown architecture, aerial stratification, nitrogen fixation, species interaction

ABSTRACT

Many studies have highlighted the value of mixed plantations and their advantages over monocultures. The success of mixed plantations is usually assessed by measuring the increase in biomass and/or plant production compared to the corresponding monocultures. Among the structural determinants of growth, the vertical distribution of branches and crown shape are important to take into account because they directly impact access to light, which conditions tree growth. We evaluated the effect of two types of species mixtures in northeastern France (agroforestry and a forest mixture) on the crown architecture of poplars (*Populus deltoides* × *P. nigra*) and alder *(Alnus glutinosa*) after seven growing seasons and compared the mixtures to their respective monocultures. Four tree architecture variables (height, crown depth, crown projection area, crown volume) were evaluated. Our study shows that the poplars in the agroforestry plot altered their crown morphology through a true mixture effect due to the presence of clover, a N_2-fixing species, as well as to reduced competition for light due to larger spacing compared to the monoculture. In the forest mixture, despite a stratification of the canopy suggesting an optimized sharing of the aerial niche, thus possibly creating an additive effect, poplar crown morphology was not different compared to the monoculture. Finally, the different types of mixtures did not affect alder crown morphology. From an agronomic perspective, the more important crown development that occurred when the poplar was associated with an N_2-fixing crop makes this type of mixture a very promising way to increase the contribution of biomass to the renewable energy mix in Europe.

Introduction

Forest plantations cover about 3% of the land area worldwide, and 3.9% at the European scale (FAO 2020; Forest Europe 2020). Over the past three decades, numerous studies have highlighted the value of mixed plantations and their advantages over monospecific systems (Pretzsch et al. 2017). Indeed, mixed plantations are considered a sustainable way to produce more through more efficient use of the resources necessary for tree growth (i.e. water, light, nutrients), while also being more environmentally-friendly than monocultures (Loreau and Hector, 2001). The success of these plantations is usually assessed by measuring the increase in biomass and/or plant production compared to the corresponding monocultures. Tree biomass production is dependent on individual tree growth, which in turn is governed by (1) phenological (e.g. length of growing season, Elferjani et al. 2016), (2) biochemical (e.g. allocation of carbon, Benomar et al. 2012), (3) functional (e.g. water-use efficiency, Forrester 2015) and (4) structural (e.g. tree architecture, Broeckx et al. 2012) determinants. Among the structural determinants, the vertical distribution of branches and crown shape are important factors since they directly affect the tree's access to light, which conditions tree growth (Prescott 2002; Pretszch 2014).

Interactions between tree species can alter light interception; this phenomenon corresponds to aboveground competition for light (Kelty 1992). To reduce competition for light in mixed plantations, an association of species with complementary structural and functional traits should be chosen. The association of a light-demanding species with a shade-tolerant one can, for instance, be an interesting way to improve light interception at the plantation level (Forrester et al. 2004; Ishii et al. 2004). Indeed, complementarity (i.e. reduced competition) and / or facilitation effects are likely to occur between species in mixed plantations, resulting in higher productivity compared to a monoculture (Kelty 1992; Loreau and Hector 2001). Productivity has shown high responsiveness to light availability when trees are grown in mixtures (Forrester et al. 2013; Pretzsch et al. 2015; Williams et al. 2017). Higher productivity in mixtures than in monocultures is generally observed when species have developed stratified canopies or different crown architectures (Guariguata et al. 1995; Forrester et al. 2006). Moreover, mixed plantations seem to show improved light interception compared to monocultures through changes in crown shape and canopy structure (Forrester et al. 2013; Jucker et al. 2015; Duarte et al. 2021; Hildebrand et al. 2021). Williams et al. (2017), for instance, found that productivity was higher in two- and four-species mixtures due to the aboveground spatial complementarity of the different species' crowns, leading to higher global light interception than in monocultures. Forrester et al. (2013) suggested that species interactions resulted in a reduction in competition for light in mixed-stands of *Abies alba* Mill. and *Picea abies* L. due to contrasting crown morphology and stratification.

The structural differences observed between species in mixtures and in monocultures may be due to effects resulting directly from interactions between the species, i.e. where the new structural aspects result from the interspecific environment ("true mixing effects", Forrester et al. 2013). For example, true mixing effects can lead to intraspecific changes in crown size and shape; this is referred to as crown plasticity - or the morphological adjustment of individual trees to mixing-induced environmental variability (variability in canopy space; Longuetaud et al. 2013; Van de Peer et al. 2017; Kunz et al. 2019). However, structural differences may also be due to effects resulting from interspecific differences unaffected by species interactions, i.e. when the species in the mixture keep their different morphological or physiological traits ("additive effect", Forrester 2014). This was shown by Pretzsch et al. (2016) for Scots pines (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.); in monocultures, the species showed different, complementary structural traits which were preserved when the two species were mixed. Moreover, Williams et al. (2017) concluded that the positive effects of tree species associations on crown complementarity are mostly due to species-specific differences rather than to crown plasticity.

Changes in crown morphology and the occupation of different spatial niches in the canopy space may also depend on nutrient availability (Dieler and Pretzsch 2013). The presence of a nitrogen (N_2)-fixing species in the mixture may benefit the growth and crown development of the non-fixing species, and allow it to have better access to light than in a monoculture (Piotto 2008). Indeed, the association of an N_2-fixing species, either herbaceous or woody, with a non-fixing species is often encountered in agroforestry plantations, where trees and herbaceous crops are associated on the same plot (Dupraz and Liagre 2008; Munroe and Isaac 2014).

Our aim was to compare tree crown development in poplar and alder in three mixed scenarios (in a poplar / alder mix, in a poplar / clover mix, and in an alder / graminoid mix) with poplar and alder monocultures in a seven-year-old tree plantation in northeastern France. Studies on agroforestry systems have largely focused on the effect of light availability on the crop (Manceur et al. 2008; Bouttier et al. 2014) but the effect on the tree is poorly documented (e.g. Righi et al. 2016; Ribeiro and Righi 2020). Our study aimed to determine if there is a vertical stratification and / or modification in crown morphology in mixtures, in comparison to the respective tree monocultures, and whether these are true mixing effects or the result of additive effects. We hypothesized that trees in mixtures would occupy the canopy space in a more optimized way than in their respective monocultures, and that light interception by the trees would be improved due to reduced competition for light and / or a facilitation effect due to the presence of an N_2-fixing species in the mixture. Specifically, we assumed that we would observe (i) crown stratification in both species in the forest mixture, and (ii) higher vertical and broader horizontal crown development in the agroforestry system than in the monocultures.

Materials and methods

Study site

The experiments took place at the experimental plantation of La Bouzule in northeastern France (48°44′19” N, 6°18′50″ E, 219 m asl), described in detail in Thomas et al. (2021). Briefly, the plantation was installed during the spring of 2014 and is 448 m long and 73 m wide, for a total area of 3.27 ha. Thirty-cm-long poplar cuttings of the Euramerican poplar clone Dorskamp (*Populus deltoides* Bartr. ex Marsh.× *P. nigra* L.) and one-year-old rooted alder *(Alnus glutinosa* L. Gaertn.) seedlings measuring from 50 to 80 cm in height were planted in lines of trees oriented in a north-south direction. The forest plots (monocultures and forest mixture) were planted at a density of 2000 trees per hectare while the agroforestry plots have a density of 1000 trees per hectare, every other row of trees being replaced by the herbaceous crop (clover and graminoids for agroforestry poplars and alders, respectively) as compared to the forest plots. Between 2014 and 2020, average annual precipitation was 607 mm and the mean temperature was 11.6°C. A detailed soil description is available in Clivot et al. (2019). All the measurements reported in this paper were performed during the winter of 2020-2021, i.e. after the trees’ seventh growing season, except for the crown illumination index, which was measured during summer 2021. The measurements were carried out on 180 poplars and 180 alders: 60 trees per species × 3 treatments (monoculture, agroforestry, forest mixture), corresponding to a representative sample of tree height classes defined in 2015.

Tree crown description

Crown radii (r, m) in eight directions (cardinal and subcardinal) and the mean crown radius (CR, m) of each tree were determined according to Dieler and Pretzsch (2013) (Fig.1). Then, the crown projection area (CPA, m²), i.e. the projected surface occupied by a tree canopy on the ground, was estimated according to the following equation:

$$\mathrm{CPA} = \pi\,\mathrm{CR}^2$$

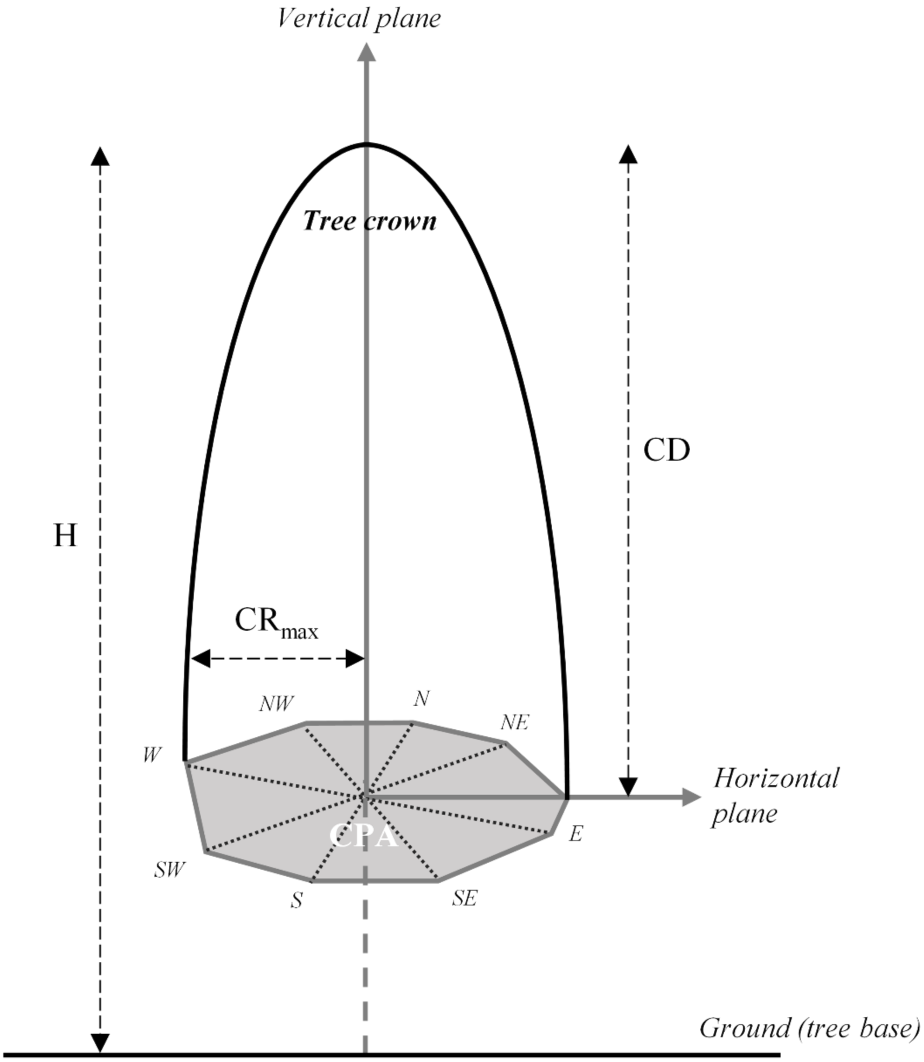

Fig.1 Schematic representation of the crown profile of a tree, where H is total tree height, CD is crown depth, $\mathrm{CR}_{\max}$ is crown maximum radius, CPA is crown projection area (grey area), and *N, NE, E, SE, S, SW, W, NW* are the eight cardinal and subcardinal directions.

For each tree, tree height (H, m) was measured from the base of the tree to the last bud of the tallest stem with a graduated pole; diameter at breast height (DBH, cm) was measured with a digital caliper; maximum crown radius ($\mathrm{CR}_{\max}$, m) was defined as the longest crown radius; and crown depth (CD, m) was defined as the difference between H and the height of the first living branch (Fig.1). The live crown ratio (LCR, %), which is an effective indicator of growth vigor, was determined as the ratio of live crown length (CD) to total tree height (H). These variables were then used to estimate the crown volume (CV, m^3) of each tree according to Jucker et al. 2015:

$$\mathrm{CV} = \frac{\pi\, \mathrm{CR^2}_{\mathrm{max}}\, \mathrm{CD}}{2\beta + 1}$$

Crown shape coefficients (β) for poplar and alder were obtained from Purves et al. (2007).

Crown illumination index

Crown volume can be used as a proxy for leaf area density and light interception (Binkley et al. 2013; Pretzsch 2014; Pretzsch et al. 2017). In our study, the light interception index (LI) was estimated with the following equation according to the approach developed by King et al. (2005):

$$\mathrm{LI} = \mathrm{CPA}\ \times \mathrm{CI}^2$$

where:

CPA = crown projection area (m^2) of each tree

CI = crown illumination index

CI was determined for each tree according to Clark and Clark (1992). This index score accounts for the vertical and lateral illumination of the crown, and the relative amount of crown lighting (Verryckt et al. 2022). Although the CI is an indirect way to characterize the light environment, as shown through a multi-parameter calibration, it is a reliable method to rapidly describe forest light environments (Keeling and Phillips 2007).

Data analyses

We used the free R software, version 2022.02.1 (R Core Team 2022) to carry out statistical tests on our results. We tested species (poplar and alder) and treatment effects (three treatments:

monoculture, agroforestry, forest mixture) and their interaction (species × treatment) on crown description variables with a linear model (‘lm’ procedure). Means were expressed with their standard errors. The statistical tests were considered significant at $*P \leq 0.05$, $**P \leq 0.01$ or $***P \leq 0.001$. When a significant effect was recorded ($P \leq 0.05$), Tukey contrasts (‘glht’ procedure, ‘multcomp’ package) were used for multiple comparisons among different factor levels.

Results

Tree and crown dimensions

Stem height (H), diameter at breast height (DBH), crown depth (CD), mean crown radius (CR) and live crown ratio (LCR) were higher for the poplars than for the alders ($P \leq 0.001$; Table 1). Poplar H in the agroforestry and monoculture plots did not differ significantly (6.4 ± 0.3 m and 6.1 ± 0.3 m, respectively), while poplar H in the forest mixture was significantly lower than in the other two treatments (4.9 ± 0.2 m) (Table 1). The DBH of the agroforestry poplars was significantly higher than in the monoculture and mixed forest plots (69.8 ± 4.3 mm in agroforestry, 52.3 ± 3.1 mm in the monoculture and 44.0 ± 3.6 mm in the forest mixture). The DBH, CR and LCR of the poplars in the monoculture and the forest mixture did not differ significantly while the CD was significantly higher in the monoculture than in the forest mixture. The CD, CR and LCR of the poplars were all significantly higher in the agroforestry treatment than in the forest mixture and monoculture plots (Fig.2a). For the alders, there was no significant treatment effect regardless of the variable. When poplars and alders were compared, poplar CD and H were significantly higher than alder CD and H in the forest mixture (Fig.2b).

Table 1. Mean and maximum stem height (H, m), stem diameter at breast height (DBH, cm), crown depth (CD, m), crown radius (CR, m) and live crown ratio (LCR, %) of the poplars and alders in the agroforestry, forest mixture and monoculture treatments. Within each column, significant differences between species and treatment are indicated with different letters. The effects of treatment (*T*), species (*S*) and their interaction (*T*×*S*) are indicated for $P \leq 0.05$*, $P \leq 0.01$** and $P \leq 0.001$***. Means ± standard errors are shown.

Species	Treatment	Mean H	Max H	Mean DBH	Max DBH	Mean CD	Max CD	Mean CR	Max CR	Mean LCR	Max LCR
Poplar	Agroforestry	6.4 ± 0.3 ^{c}	9.8	69.8 ± 4.3 ^{d}	125.0	5.3 ± 0.3 ^{d}	8.7	1.5 ± 0.1 ^{c}	2.5	77.1 ± 1.9 ^{d}	88.6
	Forest mixture	4.9 ± 0.2 ^{b}	10.1	44.0 ± 2.6 ^{bc}	113.5	3.6 ± 0.2 ^{b}	8.4	1.0 ± 0.0 ^{ab}	1.8	69.6 ± 1.2 ^{bc}	85.2
	Monoculture	6.1 ± 0.3 ^{c}	10.5	52.3 ± 3.1 ^{c}	112.0	4.5 ± 0.3 ^{c}	8.3	1.1 ± 0.0 ^{b}	1.8	72.6 ± 1.2 ^{c}	85.0
Alder	Agroforestry	3.5 ± 0.1 ^{a}	5.7	34.6 ± 1.7 ^{ab}	75.6	2.4 ± 0.1 ^{a}	4.5	1.0 ± 0.0 ^{ab}	2.0	65.0 ± 1.0 ^{ab}	79.0
	Forest mixture	3.6 ± 0.1 ^{a}	5.2	30.7 ± 1.2 ^{a}	45.0	2.4 ± 0.1 ^{a}	3.8	0.9 ± 0.0 ^{a}	1.4	65.5 ± 1.2 ^{ab}	76.6
	Monoculture	3.5 ± 0.1 ^{a}	5.2	31.1 ± 1.4 ^{a}	57.2	2.3 ± 0.1 ^{a}	4.1	0.9 ± 0.0 ^{a}	1.7	63.9 ± 1.3 ^{a}	78.0
		S ***		*S* ***		*S* ***		*S* ***		*S* ***	
		T **		*T* ***		*T* ***		*T* ***		*T* *	
		S×*T* ***		*S*×*T* ***		*S*×*T* ***		*S*×*T* ***		*S*×*T* *	

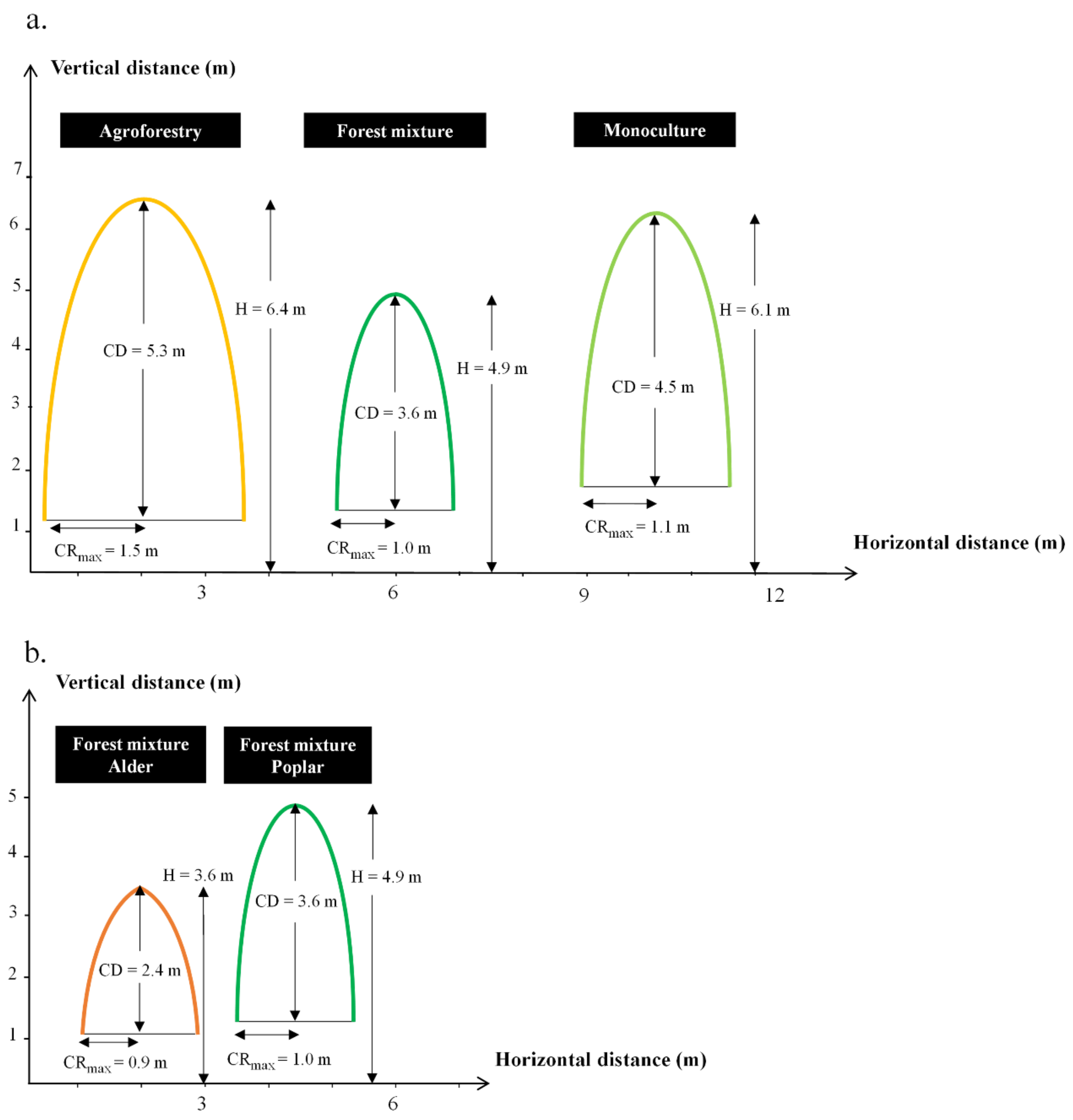

Fig.2 Schematic representation of the crown profiles of (a) the poplars in the agroforestry, forest mixture and monoculture treatments and (b) the poplars and alders in the forest mixture, where H is total tree height, CD is crown depth, and CR_{max} is crown maximum radius.

Tree crown shape

The poplars generally developed longer and more horizontal branches than did the alders; this difference was more pronounced between the agroforestry poplars and the alders regardless of treatment ($P \leq 0.001$; Table 2). The poplars in the agroforestry treatment developed longer branches than in the corresponding monoculture and the forest mixture, regardless of branch orientation, with the highest values found for the three western directions (*P* $\leq$ 0.001; Table 2). For the agroforestry poplars only, significantly lower branch-length values were recorded for the North and South, than for the East and West (Fig.3). In the forest mixture, the poplars and the alders developed similar branch lengths, regardless of branch orientation (*P* = 0.31).

Table 2. Sizes of the longest branches in the eight cardinal and subcardinal directions (north N, northeast NE, east E, southeast SE, south S, southwest SW, west W, northwest NW) of the poplars and alders in the agroforestry, forest mixture and monoculture treatments. Within each column, significant differences between species and treatment are indicated with different letters. The effects of treatment (*T*), species (*S*) and their interaction (*T*×*S*) are indicated for $P \leq 0.05$*, $P \leq 0.01$** and $P \leq 0.001$***, *ns* for non-significant. Mean ± standard errors are shown.

Species	**Treatment**	**Mean N**	**Mean NE**	**Mean E**	**Mean SE**	**Mean S**	**Mean SW**	**Mean W**	**Mean NW**
Poplar	Agroforestry	116.6 ± 6.3 ^{c}	124.4 ± 6.4 ^{b}	123.7 ± 6.3 ^{c}	129.5 ± 7.0 ^{c}	116.1 ± 6.5 ^{c}	130.9 ± 7.0 ^{c}	131.6 ± 7.0 ^{b}	131.1 ± 7.1 ^{b}
	Forest mixture	84.7 ± 3.4 ^{ab}	84.4 ± 4.0 ^{a}	79.7 ± 3.7 ^{ab}	80.1 ± 4.0 ^{ab}	80.6 ± 3.7 ^{ab}	82.1 ± 3.9 ^{ab}	77.1 ± 4.1 ^{a}	83.7 ± 4.2 ^{a}
	Monoculture	88.1 ± 3.6 ^{ab}	84.8 ± 4.1 ^{a}	83.9 ± 4.6 ^{b}	83.5 ± 4.9 ^{b}	88.2 ± 4.2 ^{b}	86.8 ± 4.4 ^{b}	79.9 ± 4.3 ^{a}	83.8 ± 4.1 ^{a}
Alder	Agroforestry	89.0 ± 3.6 ^{b}	84.9 ± 2.5 ^{a}	82.0 ± 4.5 ^{ab}	83.5 ± 4.6 ^{ab}	80.5 ± 3.5 ^{ab}	80.8 ± 3.8 ^{ab}	77.4 ± 3.9 ^{a}	83.7 ± 3.3 ^{a}
	Forest mixture	73.8 ± 2.9 ^{ab}	73.6 ± 3.4 ^{a}	76.4 ± 3.4 ^{ab}	74.5 ± 3.5 ^{ab}	70.4 ± 3.1 ^{a}	71.3 ± 3.7 ^{ab}	66.0 ± 2.8 ^{a}	73.3 ± 3.2 ^{a}
	Monoculture	75.1 ± 3.0 ^{ab}	76.6 ± 3.4 ^{a}	66.0 ± 3.6 ^{a}	68.2 ± 3.0 ^{a}	67.2 ± 3.4 ^{a}	66.5 ± 3.1 ^{a}	69.1 ± 3.4 ^{a}	73.2 ± 3.6 ^{a}
		S *** *T* * *S*×*T* *ns* (*P* = 0.07)	*S* *** *T* *** *S*×*T* ***	*S* *** *T* *** *S*×*T* ***	*S* *** *T* *** *S*×*T* ***	*S* *** *T* *** *S*×*T* **	*S* *** *T* *** *S*×*T* ***	*S* *** *T* *** *S*×*T* ***	*S* *** *T* *** *S*×*T* ***

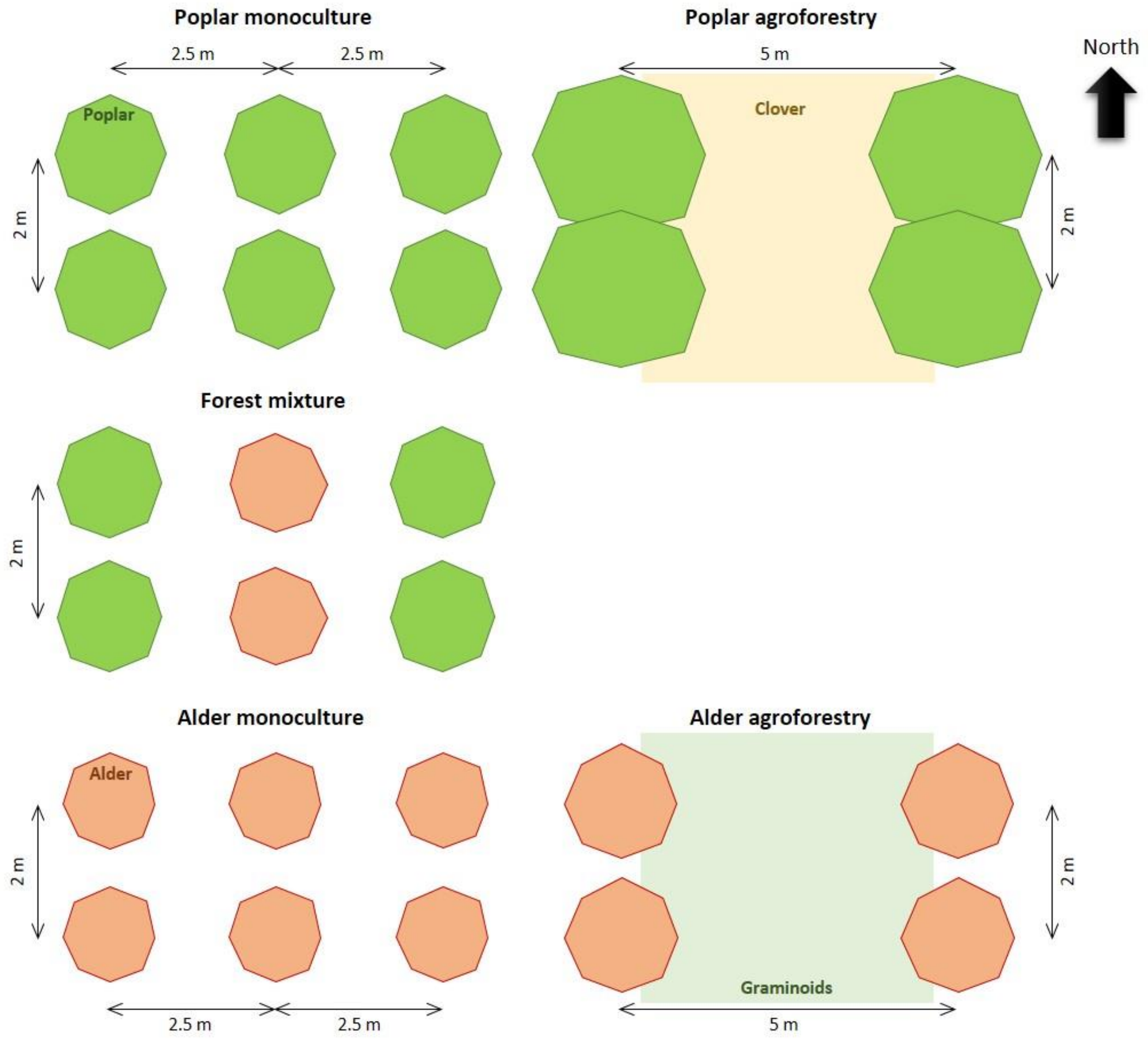

Fig.3 Crown projection area (CPA) based on mean crown size of the poplars (in green) and alders (in orange) in the different treatments (agroforestry, forest mixture and monoculture). Mean size of the crowns in the eight cardinal and subcardinal directions are respected. The spacing between two trees in the same row and between two different rows of trees is indicated.

The poplars in the agroforestry and the monoculture treatments had a higher crown projection area (CPA) and crown volume (CV) than did the alders, but there was no significant difference between the two species in the forest mixture (Fig.3; Fig.4). CPA was higher for the poplars in the agroforestry treatment than in either of the forest plots, with a value of 5.6 ± 0.4

m^2 versus 2.4 ± 0.2 m^2 in the forest mixture and 2.6 ± 0.2 m^2 in the monoculture (Fig.3; Fig.4a). It is noteworthy that, on the tree line, crown overlap occurred only for the poplars in agroforestry (Fig.3). CV was much higher for the poplars in agroforestry than for the poplars in the forest plots, with a value of 19.5 ± 2.1 m^3 versus 5.5 ± 0.5 m^3 in the forest mixture and 9.2 ± 1.0 m^3 in the monoculture (Fig.4b). For the alders, CPA and CV were not significantly different among treatments; CPA values were around 2.0 ± 0.15 m^2 and CV values ranged from 3.2 ± 0.2 m^3 (forest mixture) to 4.7 ± 0.6 m^3 (agroforestry) (Fig.3; Fig.4). A trend towards higher CPA values was nevertheless visible for the agroforestry alders (Fig.3).

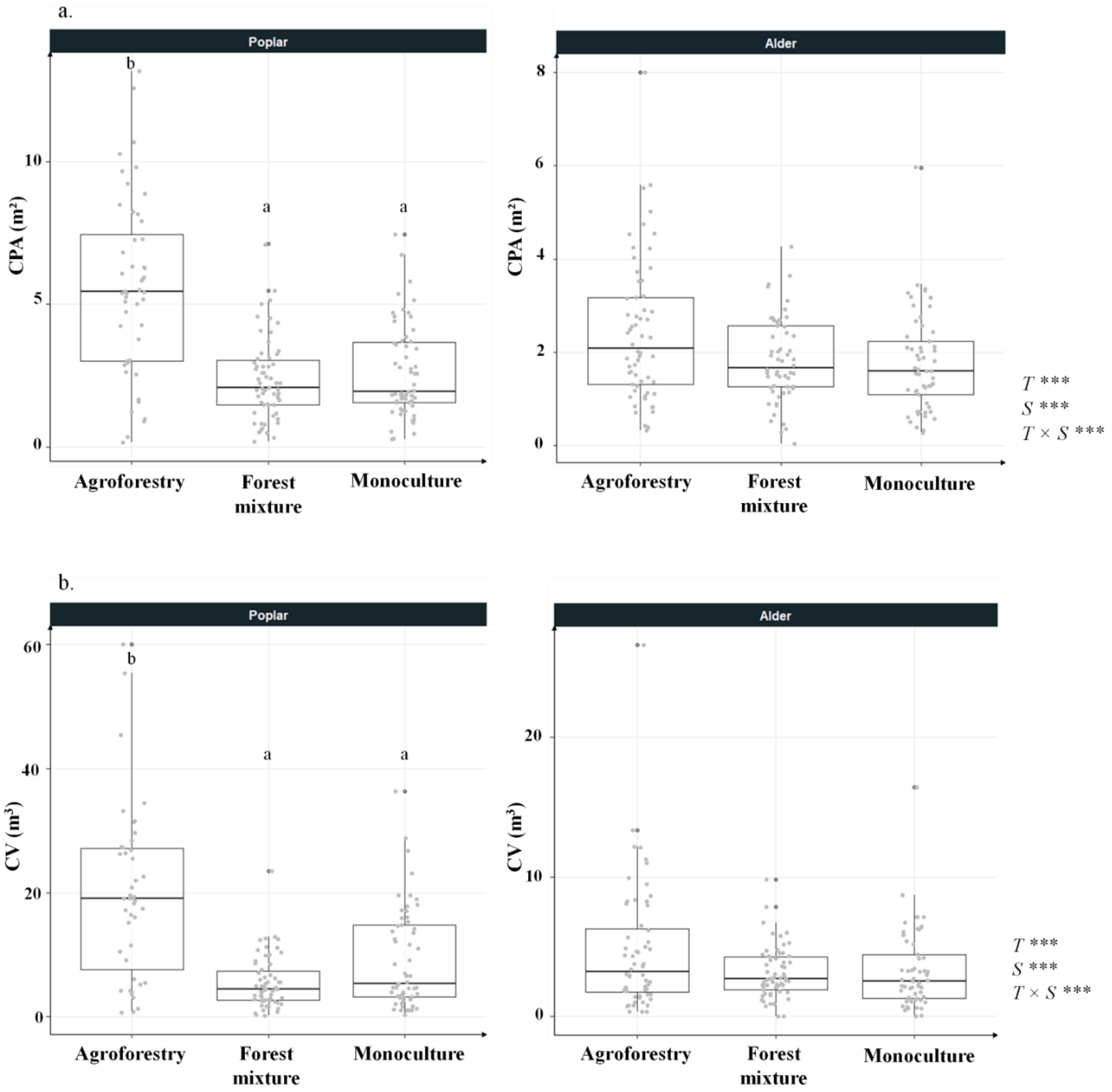

Fig.4 (a) Crown projection area (CPA, m²) and (b) crown volume (CV, m^3) of the poplars and alders in the agroforestry, forest mixture and monoculture treatments. For each species, different letters indicate significant differences between treatments. The effects of treatment (*T*), species (*S*) and their interaction (*T*×*S*) are indicated for $P \leq 0.001$***. Each box represents the quartile below (Q1) and above (Q3) the median value. Vertical bars represent minimum and maximum values.

Light interception index

The light interception index (LI) was higher for both poplars and alders in the agroforestry plots (93 and 61, respectively) than in the forest mixture (45 and 29, respectively) and in their respective monocultures (45 and 39, respectively; Fig.5). Poplar LI was not significantly different from alder LI in the forest mixture; however, LI was significantly higher for poplar than for alder in the agroforestry treatment.

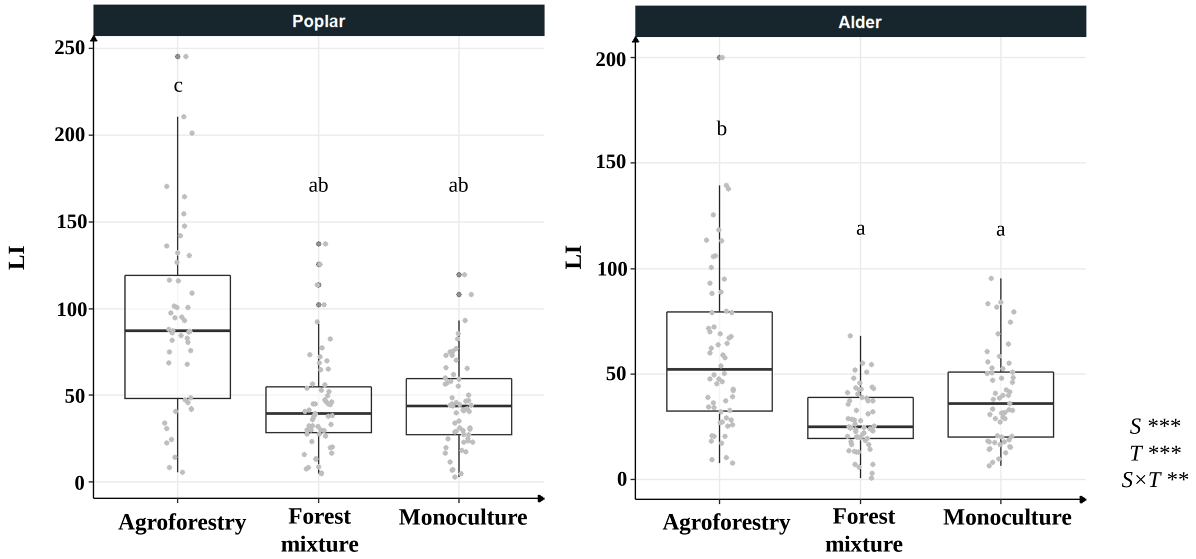

Fig.5 Light interception index (LI) of the poplars and alders in the agroforestry, forest mixture and monoculture treatments. For each species, different letters indicate significant differences between treatments. The effects of treatment (*T*), species (*S*) and their interaction (*T*×*S*) are

indicated for $P \leq 0.01$** and $P \leq 0.001$***. Each box represents the quartile below (Q1) and above (Q3) the median value. Vertical bars represent minimum and maximum values.

Discussion

This study investigated how tree crown development was affected after seven growing seasons in three different contexts: poplars and alders associated in a forest mixture, poplars and alders in association with clover or graminoids (agroforestry), and poplar and alder monocultures. We hypothesized that the trees would occupy the canopy space in a more optimized way in the two types of mixtures than in their respective monocultures, thus improving light interception by the trees, thanks to reduced competition for light and / or a facilitation effect due to the presence of an N_2-fixing species in the mixtures.

In our study, the poplars and the alders in the forest mixture did not benefit from any true mixing effects; indeed, they did not have longer and wider crowns, therefore crown volume remained the same as in the monocultures. Our results contrast with those of Jucker et al. (2015), who reported that trees growing in mixtures were shorter than in monocultures, but had wider and deeper crowns and longer horizontal branches than in their monocultures. Guillemot et al. (2020) also showed greater space exploration along the vertical crown gradient for tropical trees growing in a mixture due to a greater investment in branches than in the monocultures. However, the poplars in our forest mixture may have benefited from additive effects. Indeed, as the poplars in our plantation were taller than the alders, they may have had more access to light in the mixture than in their monoculture due to aerial canopy stratification (Forrester et al. 2004). According to William et al. (2017), canopy stratification can lead to a reduced competition for light, compared to monocultures. The light interception index of the poplars in our forest mixture was no higher than that of the alders, meaning that the vertical stratification of the two species did not improve poplar light interception. Thus, our hypotheses 1 (additive effects on the changes in crown morphology of the poplars in the forest mixture) and 2 (a facilitation effect due to the presence of alders resulting in true mixing effects) were refuted. Indeed, the poplars in the forest mixture did not exhibit any new structural aspects resulting from the interspecific environment, indicating that the presence of alders, even though they are an N_2-fixing species, did not benefit the poplars. In the same plantations, Thomas et al. (2021) found that the soil mineral N was more than five times higher in the poplar agroforestry than in the forest mixture, associated with better poplar growth performances in the agroforestry, while there was no significant effect of the presence of alder on either soil N content or poplar growth in the forest mixture. This suggests that the beneficial effects of N enrichment are likely to be seen more quickly with an herbaceous N_2-fixing species due to the shorter rotations and may be delayed when a woody N_2-fixing species is involved (Binkley et al. 1992, Forrester 2014). Moreover, poplar/alder mixtures are sometimes unsuccessful, as shown by Teissier du Cros et al. (1984). In their study, the poplar/alder association with a 1.5 × 2 m spacing was no more productive than the poplar monoculture because the N_2 fixed by the alder (*A. glutinosa*) was not yet beneficial to the poplar (*P. trichocarpa* Torr. & Gray × *P. deltoides*, Belgian clone 'Unal') after only three years of growth.

The poplars in our agroforestry treatment modified both their crown size and architecture. Indeed, they had longer and wider crowns than in the forest plots (both mixed and monoculture), which resulted in a crown volume twice as large. Our results are in line with Ribeiro and Righi (2020), who showed that crown projection area and crown volume for eucalyptus hybrids (*Eucalyptus grandis* Hill ex Maiden × *E. camaldulensis* Dehnh, hybrid COP-1277) were higher in an agroforestry system compared to the monoculture. In addition, Kunz et al. (2019) found that diversifying neighboring species allowed trees to optimize their crown morphology. The changes in crown shape for the poplars in our agroforestry treatment resulted from true mixing effects. These true mixing effects could be attributed to a facilitation effect due to the presence of a leguminous crop in the mixture. Indeed, as an N_2-fixing species, the clover planted in the inter-rows may have benefited the growth of the poplars by increasing the availability of nitrogen in the soil compared to the monoculture, as shown in Thomas et al (2021). Taghiyari and Efhami (2011) showed a positive effect on the diameter increment of *P. nigra* L. var. betulifolia in mixtures with alfalfa, which is also an N_2-fixing species. This is consistent with what we found for our agroforestry poplars. Since every other tree line in the forest plots was replaced with clover, it is also likely that tree-planting density influenced the crown morphology of our agroforestry poplars. Indeed, Benomar et al. (2012) showed that larger planting spacing can lead to increased poplar crown volume through increased branch length and diameter at breast height. Moreover, *Populus sp.* crown architecture exhibits high morphological plasticity in response to spacing (Ceulemans et al. 1990). In our study, the agroforestry poplars had a larger diameter at breast height and a higher live crown ratio (i.e. tree vigor) than in their monoculture, even though they were no taller. The trees may have allocated more carbon to diameter and branchiness than to height due to the reduced competition for light in the agroforestry treatment (i.e. where tree-planting density was lower) (Benomar et al. 2013). Moreover, many studies have shown that crown and stem diameter growth are more sensitive to competition than height growth, which can remain stable over a wide range of planting densities (Piotto 2008; Pretzsch et al. 2015). Han et al. (2020) showed that the diameter at breast height of 11-year-old *Populus* × *tomentosa* Carrière clones was higher in treatments with a planting density of 417 and 833 stems ha^{-1} than in treatments with a planting density of 1667 stem ha^{-1}. Zhang et al. (2020) showed higher leaf and branch biomass production for poplar clones in wide-spaced than in narrow-spaced plantations.

The larger planting spacing in the agroforestry plot probably lead to a reduced competition for light compared to the monoculture. This was shown by Benomar et al. (2011) for two hybrid poplar clones (*P. balsamifera* L. × *P. trichocarpa* and *P. maximowiczii* Henry × *P.*

balsamifera) growing in wider spacings (3 m × 3 m and 5 m × 5 m) compared to those growing in a closer spacing (1 m × 1 m). Indeed, the poplars in our agroforestry treatment had a higher light interception index than the poplars in the monoculture. Thus, intraspecific competition among poplars in the monoculture was stronger than interspecific competition in the agroforestry treatment. These results are consistent with the competition indices calculated previously by Thomas et al. (2021) for the two treatments after six years of growth at the same experimental site. Moreover, the higher live crown ratio for the agroforestry poplars reflects the fact that the trees had branches and foliage lower down on the stem than in the forest treatments. In Forrester et al. (2004), eucalyptus (*E. globulus* ssp. *pseudoglobulus* Naudin ex Maiden Kirkpatr.) in a monoculture did not produce branches and foliage along the first few meters of the stem due to higher intraspecific competition for light compared to the eucalyptus in a mixture with acacia *(Acacia mearnsii* De Wild.). A natural pruning process is common in trees to mitigate intraspecific competition for light, as shown by Van de Peer et al. (2017) for birch (*Betula pendula* Roth.) – the trees decreased the number of first order branches. This is consistent with height measurements of the first live branch in our study, which show greater natural pruning for the poplars in the monoculture.

The different crown architecture we found for the agroforestry poplars, with a higher crown volume and better light interception than in the monoculture, may partially explain the increased growth performance found previously in Thomas et al. (2021) as well as the higher water use efficiency demonstrated in Thomas et al. (2022). However, vertical stratification of the two species in the forest mixture did not lead to higher growth performance than in the monoculture. For the alders, there were no additive or true mixing effects on crown size and shape in any of the treatments, although they tended to have a higher crown projection area in the agroforestry plot. This could be explained by a higher LI in the agroforestry treatment than in the forest treatments, probably due to the lower planting density and the subsequent reduced competition for light.

Conclusion

After seven growing seasons, positive interactions seem to be at play in the poplar / clover association, in agreement with our main hypothesis. Our results show that intercropping poplar with an N_2-fixing crop can significantly improve tree crown volume through changes in crown morphology (lateral and vertical extension) as compared to trees growing in the monoculture. Thus, the agroforestry poplars were able to benefit from true mixing effects, probably due to the presence of clover, an N_2-fixing species, as well as to reduced competition for light due to the larger planting spacing than in the monoculture. On the other hand, in the poplar / alder association, poplar crown volume was unaffected compared to their monoculture, despite a stratification of the canopy suggesting a shared aerial niche and a subsequent additive effect. This lack of effect could be because nitrogen fixed by the alders was not yet sufficient to benefit the poplars. Finally, alder crown morphology did not appear to be affected by the different types of mixtures, although a trend toward an increased crown volume seemed to emerge for the agroforestry alders.

From an agronomic point of view, the increase in crown volume, and therefore in biomass production, that occurs when poplar is grown in association with an N_2-fixing crop make these mixtures a promising way to increase biomass production for renewable energy in Europe. However, broader lateral development and branches growing lower on the stem in agroforestry could potentially pose a problem for the passage of agricultural machinery on the crop close to the trees. Moreover, while the development of more numerous branches on trees growing in agroforestry can be an asset for the production of biomass in a system where the whole tree is valorized, branchiness could also be an inconvenience when the objective is to produce timber/lumber in a system where trees are commonly pruned to avoid knots in the wood due to the presence of branches.

Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Acknowledgments

The UMR Silva and the experimental site are supported by the French National Research Agency through the Cluster of Excellence ARBRE (ANR-11-LABX-0002-01). The experiment was part of the SOERE F-ORE-T network supported by GIP ECOFOR, AllEnvi and AnaEE France. We thank the Ferme Expérimentale de la Bouzule (Université de Lorraine) for the management of the agricultural component.

Authors' Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Anaïs Thomas, Pierrick Priault, Erwin Dallé and Nicolas Marron. The first draft of the manuscript was written by Anaïs Thomas and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References

Benomar L, DesRochers A, Larocque GR (2011) Changes in specific leaf area and photosynthetic nitrogen-use efficiency associated with physiological acclimation of two hybrid poplar clones to intraclonal competition. Can. J. For. Res. 41: 1465–1476.

https://doi.org/10.1139/x11-073

Benomar L, DesRochers A, Larocque GR (2012) The effects of spacing on growth, morphology and biomass production and allocation in two hybrid poplar clones growing in the boreal region of Canada. Trees 26: 939–949.

https://doi.org/10.1007/s00468-011-0671-6

Benomar L, DesRochers A, Larocque GR (2013) Comparing growth and fine root distribution in monocultures and mixed plantations of hybrid poplar and spruce. J. For. R. 24(2): 247–254

Binkley D, Campoe OC, Gspaltl M, Forrester DI (2013) Light absorption and use efficiency in forests: Why patterns differ for trees and stands. For. Ecol. Manag. 288: 5–13.

https://doi.org/10.1016/j.foreco.2011.11.002

Binkley D, Dunkin K, DeBell D, Ryan M (1992) Production and Nutrient Cycling in Mixed Plantations of Eucalyptus and Albizia in Hawaii. For. Sci. 38: 393–408.

Bouttier L, Paquette A, Messier C, Rivest D, Olivier A, Cogliastro A (2014) Vertical root separation and light interception in a temperate tree-based intercropping system of Eastern Canada. Agroforest. Syst. 88: 693–706.

https://doi.org/10.1007/s10457-014-9721-6

Broeckx LS, Verlinden MS, Vangronsveld J, Ceulemans R (2012) Importance of crown architecture for leaf area index of different Populus genotypes in a high-density plantation. Tree Physiol. 32: 1214–1226.

https://doi.org/10.1093/treephys/tps083

Ceulemans R, Stettler RF, Hinckley TM, Isebrands J.G, Heilman, P.E., 1990. Crown architecture of *Populus* clones as determined by branch orientation and branch characteristics. Tree Physiol. 7: 157–167.

https://doi.org/10.1093/treephys/7.1-2-3-4.157

Clark DA, Clark DB (1992) Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest. Ecol. Monogr. 62: 315–344.

https://doi.org/10.2307/2937114

Clivot H, Petitjean C, Marron N, Dallé E, Genestier J, Blaszczyk N, Santenoise P, Laflotte A, Piutti S (2019) Early effects of temperate agroforestry practices on soil organic matter and microbial enzyme activity. Plant Soil: 453, 189–207.

https://doi.org/10.1007/s11104-019-04320-6

Côté B, Camiré C (1987) Tree growth and nutrient cycling in dense plantings of hybrid poplar and black alder. Can. J. For. Res. 17: 516–523.

https://doi.org/10.1139/x87-086

Dawson JO, Hansen EA (1983) Effect of *Alnus glutinosa* on hybrid populus growth and soil nitrogen concentration in a mixed plantation. In Intensive Plantation Culture: 12 years research. Hansen JO and Edward A, editors. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 29–34

DeLong SC (1991) The light interception index: a potential tool for assisting in vegetation management decisions. Can. J. For. Res. 21: 1037-1042

Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. For. Ecol. Manag. 295: 97–108.

https://doi.org/10.1016/j.foreco.2012.12.049

Duarte MM, Moral R de A, Guillemot J, Zuim CIF, Potvin C, Bonat WH, Stape JL, Brancalion PHS (2021) High tree diversity enhances light interception in tropical forests. J. Ecol. 109: 2597–2611.

https://doi.org/10.1111/1365-2745.13669

Dupraz C, Liagre F (2008) Agroforesterie, des arbres et des cultures. Paris : Editions France Agricole.

Elferjani R, DesRochers A, Tremblay F (2016) Plasticity of bud phenology and photosynthetic capacity in hybrid poplar plantations along a latitudinal gradient in northeastern Canada. Environ. Exp. Bot. 125: 67–76.

https://doi.org/10.1016/j.envexpbot.2016.01.007

FAO (2020) The State of the World's Forests 2020. FAO and UNEP. Forests, biodiversity and people. Rome, Italy.

https://doi.org/10.4060/ca8642en

Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manag. 193: 81–95.

https://doi.org/10.1016/j.foreco.2004.01.024

Forrester DI, Bauhus J, Cowie AL, Vanclay JK (2006) Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: A review. For. Ecol. Manag. 233: 211–230.

https://doi.org/10.1016/j.foreco.2006.05.012

Forrester DI, Kohnle U, Albrecht AT, Bauhus J (2013) Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. For. Ecol. Manag. 304: 233–242.

https://doi.org/10.1016/j.foreco.2013.04.038

Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. For. Ecol. Manag. 312: 282–292.

https://doi.org/10.1016/j.foreco.2013.10.003

Forrester DI (2015) Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. Tree Physiol. 35: 289–304.

https://doi.org/10.1093/treephys/tpv011

Guariguata MR, Rheingans R, Montagini F (1995) Early woody invasion under the tree plantation in Costa Rica: implications for forest restoration. Restor. Ecol. 3 (4): 252-260.

Guillemot J, Kunz M, Schnabel F, Fichtner A, Madsen CP, Gebauer T, Härdtle W, von Oheimb G, Potvin C (2020) Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. New Phytol. 228: 1256–1268. https://doi.org/10.1111/nph.16722

Han Q, Zhang Y, Geng X, Du K, Yang J, Kang X (2020) Response of tree growth, crown, and branch development to planting density. Austrian J. For. Sci. 137: 179-198.

Hildebrand M, Perles-Garcia MD, Kunz M, Härdtle W, von Oheimb G, Fichtner A (2021) Tree-tree interactions and crown complementarity: The role of functional diversity and branch traits for canopy packing. Basic Appl. Ecol. 50: 217–227.

https://doi.org/10.1016/j.baae.2020.12.003

Ishii HT, Tanabe S, Hiura T (2004) Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. For. Sci 50(3): 342-355.

https://doi.org/10.1093/forestscience/50.3.342

Jucker T, Bouriaud O, Coomes DA (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. 29: 1078–1086.

https://doi.org/10.1111/1365-2435.12428

Keeling HC, Phillips OL (2007) A calibration method for the crown illumination index for assessing forest light environments. For. Ecol. Manag. 242: 431–437. https://doi.org/10.1016/j.foreco.2007.01.060

Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. In: Kelty MJ, Larson BC, Oliver CD (Eds.) The Ecology and Silviculture of Mixed-Species Forests. Springer, Netherlands, Dordrecht, pp. 125–141.

https://doi. org/10.1007/978-94-015-8052-6_8

King DA, Davies SJ, Nur Supardi MN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Func. Ecol. 19: 445–453

Kunz M, Fichtner A, Härdtle W, Raumonen P, Bruelheide H, von Oheimb G (2019) Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. Ecol. Lett. 22: 2130–2140.

https://doi.org/10.1111/ele.13400

Longuetaud F, Piboule A, Wernsdörfer H, Collet C (2013) Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. Eur. J. Forest. Res. 132: 621–634.

https://doi.org/10.1007/s10342-013-0699-9

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72–76.

https://doi.org/10.1038/35083573

Manceur AM, Boland GJ, Thevathasan NV, Gordon AM (2008) Dry matter partitions and specific leaf weight of soybean change with tree competition in an intercropping system. Agroforest. Syst. 76: 295.

https://doi.org/10.1007/s10457-008-9181-y

Munroe JW, Isaac ME (2014) N2-fixing trees and the transfer of fixed-N for sustainable agroforestry: a review. Agron. Sustain. Dev. 34: 417–427.

https://doi.org/10.1007/s13593-013-0190-5

Piotto D (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. For. Ecol. Manag. 255: 781–786.

https://doi.org/10.1016/j.foreco.2007.09.065

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. Tree Physiol. 22: 1193–1200.

https://doi.org/10.1093/treephys/22.15-16.1193

Pretzsch H (2014) Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manag. 327: 251–264.

https://doi.org/10.1016/j.foreco.2014.04.027

Pretzsch H, del Río M, Schütze G, Ammer Ch, Annighöfer P, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Drössler L, Fabrika M, Forrester DI, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Skrzyszewski J, Sramek V, Sterba H, Svoboda M, Verheyen K, Zlatanov T, Bravo-Oviedo A (2016) Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. For. Ecol. Manag. 373: 149–166.

https://doi.org/10.1016/j.foreco.2016.04.043

Pretzsch H, Biber P, Uhl E, Dahlhausen J, Rötzer T, Caldentey J, Koike T, van Con T, Chavanne A, Seifert T, Toit B du, Farnden C, Pauleit S (2015) Crown size and growing space requirement of common tree species in urban centres, parks, and forests. Urban For. Urban Green. 14: 466–479.

https://doi.org/10.1016/j.ufug.2015.04.006

Pretzsch H, Forrester DI, Bauhus J (Eds.) (2017) Mixed-Species Forests. Springer Berlin Heidelberg, Berlin, Heidelberg.

https://doi.org/10.1007/978-3-662-54553-9

Purves DW, Lichstein JW, Pacala SW (2007) Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PLOS ONE 2, e870.

https://doi.org/10.1371/journal.pone.0000870

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www. r-project.org/

Ribeiro G da S, Righi CA (2020) Canopy architecture of an agroforestry system: initial evaluation of a waveform system. Agroforest. Syst. 94, 487–498.

https://doi.org/10.1007/s10457-019-00415-2

Righi CA, Couderc V, Pereira CR, Couto HTZ, Silva LD (2016) Effect of shade on biomass accumulation and partitioning for *Eucalyptus camaldulensis* sprouts. J. Sust. For. 35: 75–87. https://doi.org/10.1080/10549811.2015.1102072

Taghiyari HR, Efhami D (2011) Diameter Increment Response of *Populus nigra* var. betulifolia Induced by Alfalfa. Austrian Jour. For. Sci. 128: 112–127.

Teissier du Cros E, Jung G, Bariteau M (1984) Alder-Frankia interaction and alder-poplar association for biomass production. Plant Soil 78: 235–243.

https://doi.org/10.1007/BF02277854

Thomas A, Priault P, Piutti S, Dallé E, Marron N (2021) Growth dynamics of fast-growing tree species in mixed forestry and agroforestry plantations. For. Ecol. Manag. 480:118672.

https://doi.org/10.1016/j.foreco.2020.118672

Thomas A, Marron N, Bonal D, Piutti S, Dallé E, Priault P (2022) Leaf and tree water-use efficiencies of *Populus deltoides* × *P. nigra* in mixed forest and agroforestry plantations. Tree Physiol. tpac094

https://doi.org/10.1093/treephys/tpac094

Van de Peer T, Verheyen K, Kint V, Van Cleemput E, Muys B (2017) Plasticity of tree architecture through interspecific and intraspecific competition in a young experimental plantation. F For. Ecol. Manag. 385: 1–9.

https://doi.org/10.1016/j.foreco.2016.11.015

Verryckt LT, Vicca S, Van Langenhove L, Stahl C, Asensio D, Urbina I, Ogaya R, Llusià J, Grau O, Peguero G, Gargallo-Garriga A, Courtois EA, Margalef O, Portillo-Estrada M, Ciais P, Obersteiner M, Fuchslueger L, Lugli LF, Fernandez-Garberí PR, Vallicrosa H, Verlinden M, Ranits C, Vermeir P, Coste S, Verbruggen E, Bréchet L, Sardans J, Chave J, Peñuelas J, Janssens IA (2022) Vertical profiles of leaf photosynthesis and leaf traits and soil nutrients in two tropical rainforests in French Guiana before and after a 3-year nitrogen and phosphorus addition experiment. Earth Syst. Sci. Data 14: 5–18.

https://doi.org/10.5194/essd-14-5-2022

Williams LJ, Paquette A, Cavender-Bares J, Messier C, Reich PB (2017) Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. 1: 0063.

https://doi.org/10.1038/s41559-016-0063

Zhang Y, Tian Y, Ding S, Lv Y, Samjhana W, Fang S (2020) Growth, Carbon Storage, and Optimal Rotation in Poplar Plantations: A Case Study on Clone and Planting Spacing Effects. Forests 11: 842.

https://doi.org/10.3390/f11080842