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MIXTURE EFFECT ON RADIAL STEM AND SHOOT GROWTH DIFFERS AND VARIES WITH TEMPERATURE

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ABSTRACT

The effect of species diversity on forest productivity and its temporal stability is known to be species-, climate- and site- dependent and is mostly apprehended through stem diameter. Therefore, it remains largely unknown whether the mixture effect on the growth of tree crowns is similar to its effect on the growth of tree diameter. However, it is commonly accepted that changes in crown architecture are an important component of tree response to tree species diversity. Moreover, the mixture effect on species is often asymmetric, i.e. the effect of a species A on a species B is not equal to the effect of species B on A. It then appears that considering the effects of both species mixture and climate on shoot growth could contrast the results coming mainly from stem growth.

We studied the effects of tree species mixture and temperature on the annual growth of shoots and basal area of stems in *Fagus sylvatica-Quercus pubescens* and *Fagus sylvatica-Abies alba* stands along a Mediterranean-Alpine gradient, for four years in five sites. The sample design was organized in 10 triplets: four triplets of mono- and bi-specific plots of *Quercus pubescens* and *Fagus sylvatica* and six triplets of mono- and bi-specific plots of *Abies alba* and *Fagus sylvatica* along an altitudinal gradient ranging from 725m to 1431m.

We found that the mixture effect on annual shoot volume increment (SVI) and on basal area increment (BAI) was asymmetrical in seven out of 10 cases and not significant in the three remaining cases. Mixture effect on SVI ranked from -56% to 157% and on BAI it ranked from -40% to 252%. Eventually we found that mixture effect was dependent on the type of limiting factor for growth, with at the driest sites a predominance of competition effects and at the coldest site a positive mixture effect on the two species studied.

Branch growth appears as a variable that can be at least as informative as radial growth regarding the tree response to species interactions. This implies that considering only stem diameter in the diversity-productivity relationship can lead to biased conclusions on the global mixture effect on tree growth, which calls for a comprehensive approach of the tree response to tree species diversity. Our results are discussed in the light of the species stress tolerances and strategies to cope with competition.

KEYWORDS

Diversity, productivity, temperature, temperate forest, stress gradient, species interactions

1.INTRODUCTION

1.1 DIVERSITY-PRODUCTIVITY RELATIONSHIPS IN FORESTS

Forest productivity is a key component of ecosystem functioning. Accumulated empirical evidence showed that tree species diversity may increase forest productivity, forest stability and dampen the effects of climate and of insect attack (Jactel and Brockerhoff, 2007; Jucker et al., 2014b; Liang et al., 2016). The positive effects of species diversity on forest productivity are explained through niche partitioning effects and facilitative effects (improvement of harsh abiotic conditions, improvement of resource acquisition, protection against herbivores, (Caspersen et al., 2018; Kunz and Fichtner, 2019)). If niche partitioning occurs, then a higher number of species in the community can improve resource uptake at the ecosystem level (Jucker et al., 2015; Schnabel et al., 2019). As light is a key resource in forests, niche partitioning focusing on light capture (Forrester et al., 2019; Ishii and Asano, 2010; Williams et al., 2017) has mostly been explained by the ‘canopy packing’ process, which corresponds to a morphological complementarity between interacting trees (Pretzsch, 2014). Trees with complementary architectures will have a higher interception of light and a densified structure. However, the mixture effect on tree productivity is generally apprehended from tree diameter increment. Results of such studies have often shown an asymmetrical effect at the species level (i.e. species-specific mixture effects in a given mixed stand may be of opposite signs, Forrester et al., 2018; Toigo et al., 2015) and appears highly dependent on soil and climatic conditions as well as on tree species identity and characteristics (Ammer, 2019; Mina et al., 2018). Exploring mixture effects on other compartments of trees is rarely done, while it seems that the joint consideration of radial and branch growth along environmental gradients would allow a more detailed understanding of tree responses to tree species mixture, especially those more directly linked to complementary processes such as canopy packing.

1.2 MIXTURE EFFECT ON TREE GROWTH CAN BE MODIFIED BY SPECIES, SITE CHARACTERISTICS AND CLIMATIC CONDITIONS

It has long been recognised that the nature and intensity of species interactions depend on the growing conditions of species (Bertness and Callaway, 1994). Originally, the stress gradient hypothesis states that the effect of facilitation is stronger in the most stressful environments, whereas competition between species is stronger in less stressful environments. The positive effect of a protective nurse plant on the survival of a beneficiary plant is a typical example (Castro et al., 2004). This theory has since been refined: firstly, it would apply only when the stress gradient is not a resource gradient. Thus, when the gradient considered is a resource gradient, the effect of facilitation would follow a bell-shape curve with competition predominating at both ends (Holmgren and Scheffer, 2010; Maestre et al., 2009). Secondly, positive effects would depend on the index used to quantify competition and facilitation: if the persistence of a species through facilitation is possible in extreme environments, the performance of a species would be improved only under intermediate conditions of stress. Thirdly, the effect of facilitation would depend on the stress tolerance of the species considered. Examples of facilitation under intermediate conditions exist in forest ecosystems, mostly on seedlings: positive effect of shading in seedlings in temperate forests (Devaney et al., 2020; Simard et al., 2012) and nurse shrubs and tree seedlings at intermediate drought stress (Callaway, 1992; Guignabert et al., 2020). More recently, a theoretical framework has been proposed linking complementary resource use and stress gradient (Forrester, 2014) suggesting that the positive effect of complementary use of light resources is only possible when the water or nutrient resource is sufficient. This hypothesis has been verified in boreal forests (Searle and Chen, 2020), in mountain (Caspersen et al., 2018; Jourdan et al., 2020a) and along a water availability gradient (Steckel et al., 2019, but see Mina et al., 2018). In addition, not only the environmental stress gradient but also species ecological strategies are critical in positive mixture effect: species tolerance to shade, drought and cold determines whether or not species benefit from the mixture of species (Jucker et al., 2014b; Searle and Chen, 2020; Toïgo et al., 2017; Zhang et al., 2012).

1.3 THE IMPORTANCE OF CONSIDERING MIXTURE EFFECT ON BRANCH GROWTH

Tree productivity is usually apprehended either through the calculation of basal area increment (Toigo et al., 2015), tree volume increment (Pretzsch et al., 2015) or total above-ground biomass increment (Jucker et al., 2014a) and thus do not explicitly consider shoot growth. Classically, allometric relationships are used to assess volume and total aerial biomass of a tree from dimensions more easily measurable (especially tree circumference or diameter, Vallet et al., 2006), while height growth is actually estimated from stand age. These allometric relations were mostly established in pure stands, while species mixture can modify height growth of trees (Vallet and Perot, 2016) or the allometry between diameter and height (Forrester et al., 2018; Trouvé et al., 2017). Thus, crown plasticity is an aerial characteristic of trees that is important in the response of trees to species mixture. Crown competition is a primordial component of tree competition for space (Hajek et al., 2015; Seidel et al., 2011). Adjusting crown growth allows a reduction in inter-specific competition (Longuetaud et al., 2013). For instance, crown plasticity and inherent interspecific differences contributed nearly equally in explaining patterns of overyielding, in a young plantation (Williams et al., 2017). In European forests, canopy packing appears to be driven more by crown plasticity than by vertical stratification (Jucker et al., 2015). The much denser and more plastic canopy space filling in mixed stands may increase light interception, stand density, productivity, and growth resilience to disturbances (Pretzsch, 2014). It appears then that beyond the simple consideration of tree diameter, tree growth strategies reflect on all of the tree aerial compartments (Fichtner et al., 2013; Van de Peer et al., 2017). If mixture effect on tree productivity is conditioned by site and climatic conditions and that crown plasticity is a part of the species strategy to face competition, then branch growth should also be dependent both on the neighbourhood and site conditions. However, the vast majority of studies on the effect of diversity on stand productivity have relied on diameter measurements, and the effect of species mixture on branch growth is thus largely under-studied. Therefore, focusing on different aerial compartments of the tree may possibly shed a new light on the effects of species mixture to obtain a more comprehensive picture of the forest functioning.

The diversity- and stability- productivity relationships in forests have been studied through different complementary approaches going from experimental methods to modelling methods (Kambach et al., 2019; Morin et al., 2011). At one end, experimental designs manipulating directly tree diversity offer the advantage of controlling the different factors that may bias the comparison between pure and mixed stands, but trees are still relatively young (Tobner et al., 2016; Van de Peer et al., 2018; Williams et al., 2017). At the other end, due to the long lifespan of trees, experiments investigating long term behaviour of forests are scarce, and modelling approaches allow to simulate the diversity-productivity relationship on the long term (Morin et al., 2018). Between these two extremes, observational data coming from national inventories allow to investigate the diversity-productivity relationship in mature stands and along large environmental gradients (*e.g.* Bourdier et al., 2016; Caspersen et al., 2018; Ruiz-Benito et al., 2014). Besides, in recent years the approach by triplet of plots has been receiving a growing attention (*e.g.* del Río et al., 2017; Heym et al., 2017; Pretzsch et al., 2020; Steckel et al., 2019; Jourdan et al., 2020a). A triplet of plots consists of a plot in a two-species mixed stand and two plots in pure stands of corresponding species. The plots within a triplet are established under similar site conditions allowing comparison between pure and mixed stands. This approach has the advantage of being implemented in a mature forest and along controlled environmental gradients.

1.4 OBJECTIVES AND HYPOTHESIS

Through an observational design based on triplets of plots (Jourdan et al., 2020a, 2020b), this work aimed at assessing and comparing the influence of tree species mixture on the growth of two aerial compartments of trees: stems and branches. Two types of species mixtures (*Fagus sylvatica-Abies alba* or *Fagus sylvatica-Quercus pubescens*) were studied at five study sites, distributed along a Mediterranean-Alpine gradient of forests. These three species are major species in Europe: *Fagus sylvatica* is found up to 2000 m of elevation in central and western Europe (Durrant et al., 2016). *Quercus pubescens* has an optimum growth between 200 and 800 m of elevation but can be found up to 1300 m (Pasta et al., 2016). *Abies alba*, on the other hand, is restricted to mountainous regions with a distribution from 500 to 2000 m of elevation (Mauri et al., 2016). The study of beech-oak and beech-fir associations along a Mediterranean-Alpine gradient is of interest on several point: (i) *Fagus sylvatica* is a very competitive species on sites that are favourable. The environmental gradient considered makes it possible to cover the limits of its growing conditions in terms of temperature and precipitation with different environmental constraints (drought in the south and cold in the north); (ii) In the southern sites, *Fagus sylvatica* is accompanied by *Quercus pubescens*, that is a broadleaf species less tolerant to shade but more tolerant to drought (Niinemets and Valladares, 2006). In sites where water is a limiting factor, species growth should suffer from interspecific competition, particularly in the hottest years and for the least drought-tolerant species. On the other hand, in milder years, positive mixture effect should emerge from two different processes: a competitive advantage for *Fagus sylvatica* and a change in resource allocation for *Quercus pubescens* from stem to shoot. (iii) In the northern sites, *Fagus sylvatica* is accompanied by a coniferous species, *Abies alba* that is shade- and cold-tolerant (Niinemets and Valladares 2006). We expected that mixture effect would be positive on shoot and branch growth at the coldest site, particularly on shade and cold tolerant species.

We sought to determine the effects of tree species mixture and climate on stem and branch growth by (i) considering a possible interaction effect between stand composition (pure *vs.* mixed stand) and temperature on tree growth (ii) comparing tree reaction to stand composition and temperature between stem and shoot growth in pure and mixed stands.

2. MATERIAL AND METHODS

2.1 STUDY SITES AND SAMPLE DESIGN

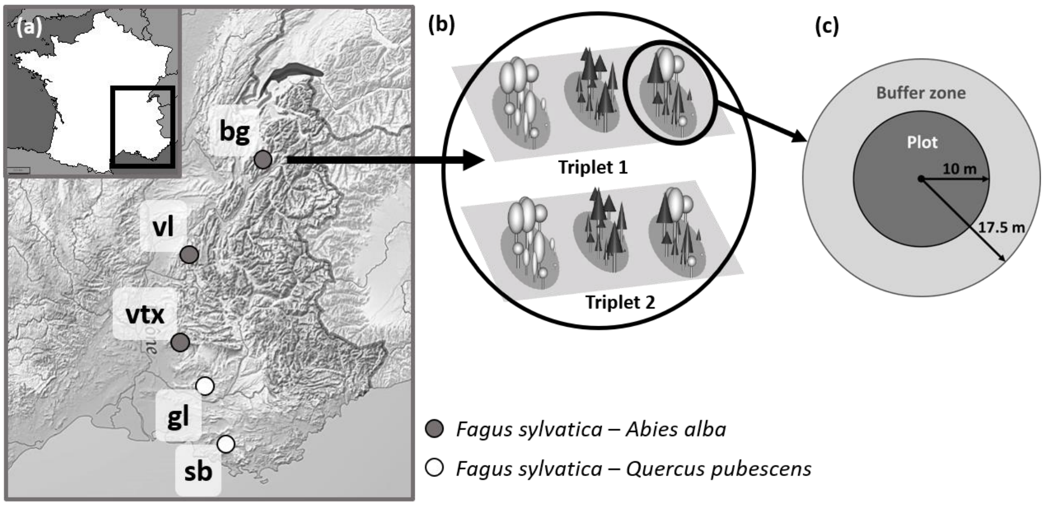

Figure 1 Overview of the experimental design: (a) the five study sites are located in south-eastern France along a latitudinal gradient going from Mediterranean area to the Alps (*sb*: Sainte-Baume; *gl*: Grand-Luberon; *vtx*: Ventoux; *vl*: Vercors-Lente; *bg*: Bauges). The association of tree species in stands changes according to the sites: *Fagus sylvatica* and *Quercus pubescens* in the southern sites (*sb* and *gl*), *Fagus sylvatica* and *Abies alba* in the northern sites (*vtx, vl* and *bg*); (b) In each of the five sites, the two triplets of plots are at different elevations. A triplet of plots consists in one plot in a mixed stand and two plots in pure stands of the corresponding tree species; (c) Individual plots are

delimited as circular plots with a radius of 17.5 m made of a central area (10 m radius) where trees are sampled and a buffer zone (7.5 m radius).

Study sites were located in the French Alps along a latitudinal gradient (More detailed information on the experimental design is provided by Jourdan et al., 2019) and belong to the experimental network GMAP (https://oreme.org/observation/foret/gmap/). The association of tree species in stands varied across the five sites considered (Fig 1a): *Fagus sylvatica* and *Abies alba* in northern sites (Bauges, Vercors-Lente, Ventoux), *Fagus sylvatica* and *Quercus pubescens* in southern sites (Grand-Luberon, Sainte-Baume). Each of these sites was made of two triplets (Fig 1b) associating a plot in a two-species mixed stand and the two pure plots of the corresponding species. The latitudinal gradient allows testing a wide range of climatic conditions, which is necessary to study the environmental determinants of the mixture effect. Each triplet of plots allowed the comparison of tree growth in pure and mixed stands in homogenous environmental conditions within a site. Individual plots were delimited as circular plots with a radius of 17.5 m made of a central area (10 m radius) where the measurements were conducted, and a buffer zone (7.5 m radius) to ensure the plot was surrounded by homogeneous conditions (Fig 1c). Forest management was restricted in the plots so that human perturbation inside each stand was avoided.

In each triplet, air temperature was recorded every two hours with a sensor Tinytag Plus 2 - TGP-450 along the study period (2015-2018), and was averaged to obtain mean monthly and annual temperatures at the triplet level. Monthly precipitation records were obtained from Meteo France at the site level. We calculated annual soil water deficit from monthly time series of precipitation and temperature and soil water holding capacity according to the Thornthwaite and Mather’s methods (Thornthwaite and Mather, 1957). Temperatures and annual soil water deficit in *Fagus sylvatica*-*Quercus pubescens* sites were higher and precipitation lower than in *Abies alba-Fagus sylvatica* sites (Table 1): the driest site being Grand Luberon and the wettest and coldest site being Vercors-Lente.

Table 1 Tree and site characteristics: stem diameter at breast height, annual stem basal area increment (BAI) and annual shoot volume increment (SVI) from 2015 to 2018 for *Fagus sylvatica*, *Quercus pubescens* and *Abies alba* in the five sites studied (*bg* Bauges; *gl* Grand Luberon; *sb* Sainte Baume; *vl* Vercors-Lente; *vtx* Ventoux), carbon to nitrogen ratio (C:N), soil water holding capacity (SWHC), precipitation (P), soil water deficit (SWD) and temperature (T). We ranked the studied sites per couple of species and from the most productive site to the least productive site (*F. sylvatica-Q. pubescens*: $\mathrm{BAI}_{sb}>\mathrm{BAI}_{gl}$; *F. sylvatica-A. Alba*: $\mathrm{BAI}_{bg}>\mathrm{BAI}_{vl}>\mathrm{BAI}_{vtx}$).

	Variable	Species			Site		
			sb	*gl*	*bg*	*vl*	*vtx*
Tree characteristics (mean; q25-q75)	Stem diameter at breast height (cm)	*Fagus sylvatica*	34.1	21.7	56.8	37.7	28.6
			25-39.2	19.5-24.1	46.3-59.3	25.9-48.2	23.6-34.2
		Quercus pubescens	34.2	18.2			
			27.3-41.1	15.5-23.1			
		Abies alba			71.3	41.5	40.5
					52.5-82.9	35.2-51.2	30.4-46.9
	BAI (cm^2)	*Fagus sylvatica*	6.4	3.4	20.9	10.1	5.1
			3.5-8.3	1.8-4.6	8.4-23.5	5.4-15	1.9-6.9
		Quercus pubescens	8.9	2.5			
			6.5-9.4	1.4-3.3			
		Abies alba			90.7	30.7	15.2
					55-108	17-40.1	7.7-18.4
	SVI (cm^3)	*Fagus sylvatica*	267.4	387.5	1004.3	761.6	470
			67.6-315	109.9-528.8	295-1330.3	197.8-1065.8	110.3-473.1
		Quercus pubescens	780.7	760.1			
			233.3-1148.4	316.2-883.7			
		Abies alba			2443.9	3058.8	769.1
					788.4-3371.6	620.8-4106.4	230.1-980
Site characteristics (mean; min-max)	Latitude		43.3°N-5.7°E	43.8°N-5.5°E	45.7°N-6.2°E	44.9°N-5.3°E	44.2°N-5.2°E
	Altitude (m) (triplet n°1-n°2)		736-746	872-1005	1025-1203	1137-1390	1328-1354
	C:N		18.2	14.6	14.5	14.3	19.9
			16.5-19.9	13.7-15.8	12.9-15.7	12-16.7	18.6-21.1
	SWHC (mm)		168	121	173	163	144
			158-174	106-130	153-180	139-177	135-149
	P (mm)		837.6	731.9	1182.4	1485.1	1159
			655-1101	500-1031	1048-1330	1377-1598	790-1471
	SWD (mm)		220	238	22	17	101
			97-346	161-338	13 -35	8-32	40-177
	T (°C)		12.1	11.1	8.2	6.7	8.4
			11.8-12.3	10.8-11.4	7.7- 8.6	5.7-7.7	8.0-8.9

2.2 SHOOT GROWTH AND BASAL AREA INCREMENT

Trees were sampled during a field campaign in 2018 in 10 triplets (2 triplets at each of the five sites), corresponding to 30 plots. Only dominant trees, belonging to the upper canopy layer, were selected: 5 co-dominant trees of the target species in pure stands, and 5 co-dominant trees of each of the two species in mixed stands for a total of 20 trees per triplet or 40 trees per sites (see Table S1). Tree height and diameter at breast height (1.30 m) were measured in 2018. Three to four terminal branches per tree were collected in the upper part of the crown exposed to the sun. Annual shoot growth in diameter and length from bud scar to bud scar for the years 2015 to 2018 were measured with a calliper. Then, we combined measurements of shoot length and diameter to calculate an annual shoot volume increment (SVI in cm^3). SVI was estimated as a cylinder. Finally, SVI from the same year of the three to four individual branches of a tree were averaged to obtain an SVI per tree for each studied year. One increment core per tree was collected from the bark to the pith at breast height using a Pressler borer. The ring profiles of the selected trees were assessed by X-ray microdensitometry and ring widths from 2015 to 2018 were used to calculate the annual basal area increment (BAI in cm^2) of trees. BAI represents the surface of wood at breast height (1.30 m) formed during the year. Tree and site characteristics are summarized in Table 1.

2.3 STATISTICAL ANALYSIS

To determine the effects of species mixture and climate per site and species (*Fagus sylvatica*, *Abies alba* and *Quercus pubescens*) on SVI and BAI we used a linear mixed-effects model by species and tree compartment (shoot and stem) at tree level. According to our hypotheses we integrated an interaction term between site, temperature and stand composition (pure or mixed). We simplified models by removing any non-significant interactions starting from the highest order level to get an accurate estimate of simple effects. Moreover, we added tree diameter as covariate to account for the effect of tree size on BAI and SVI. We also included a random effect at the triplet level to account for the sampled design. BAI and SVI were log-transformed to ensure normality of residuals.

The analyses were performed with R 4.0.2 (R Core Team, 2020) and packages car, emmeans and nlme for statistical analyses.

3. RESULTS

3.1 MIXTURE EFFECT ON BASAL AREA INCREMENT (BAI) AND SHOOT VOLUME INCREMENT (SVI)

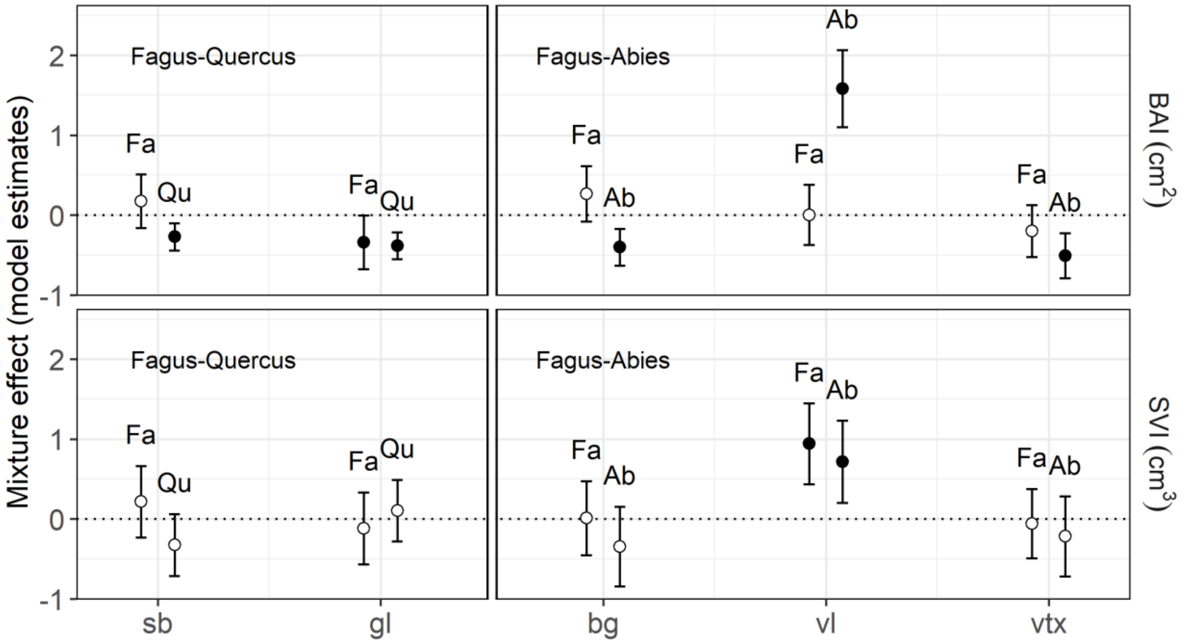

Figure 2 Mixture effect on basal area increment (BAI) and shoot volume increment (SVI) of *Quercus pubescens* (Qu), *Fagus sylvatica* (Fa) and *Abies alba* (Ab) in the five studied sites (*sb*: Sainte Baume; *gl*: Grand Luberon; *bg*: Bauges; *vl*: Vercors-Lente; *vtx*: Ventoux). Dots indicate model coefficients (on the log scale). Error bars indicate confidence intervals at 95 % of model coefficients. Significant mixture effects (p-values < 0.1) are represented by black dots, non-significant effects (p.values >= 0.1) are represented by white dots.

Fagus sylvatica-Quercus pubescens stands

At the most productive site (*sb*), neither the BAI nor the SVI of *Fagus sylvatica* were significantly impacted by species mixture (Fig 2). Tree species mixture had a significant effect on BAI but not on SVI of *Quercus pubescens*: BAI of *Quercus pubescens* decreased by - 24 % when mixed with *Fagus sylvatica* compared to pure stands.

At the least productive and driest site (*gl*), BAI of *Fagus sylvatica* and *Quercus pubescens* decreased significantly by - 29 % and by - 32 %, respectively, in mixture compared to pure stand. The mixture effect on SVI was not significant neither on *Fagus sylvatica* nor on *Quercus pubescens* (Fig 2).

Fagus sylvatica-Abies alba stands

At *Fagus sylvatica-Abies alba* sites, BAI of *Fagus sylvatica* was never significantly impacted by the presence of *Abies alba* (Fig 2). In other cases, mixture effect depended on site condition: At the most and at the least productive site (*bg* and *vtx*, respectively), BAI of *Abies alba* decreased in mixture with *Fagus sylvativa* compared to pure stand by - 33 % and by - 0.36 %, respectively (Fig 2). Conversely SVI of *Quercus pubescens* were not significantly impacted by species mixture (Fig 2). At the coldest site (*vl*), BAI of *Abies alba* increase by + 67 % when mixed with *Fagus sylvatica* compared to pure stand. This increase was accompanied by an increased SVI in both species in mixture of + 105 % for *Abies alba* and of + 157 % for *Fagus sylvatica*.

3.2 CHANGES IN MIXTURE EFFECT ON BASAL AREA INCREMENT (BAI) AND SHOOT VOLUME INCREMENT (SVI) WITH TEMPERATURE

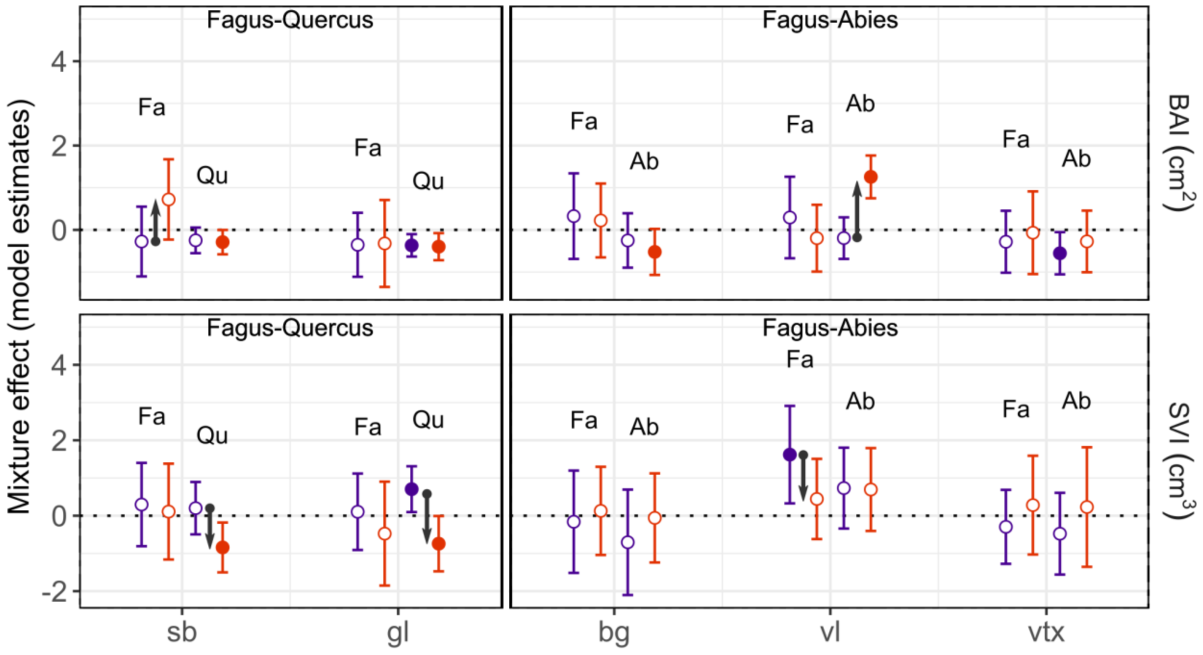

Figure 3 Model estimates of the changes in mixture effect on basal area increment (BAI) and shoot volume increment (SVI) with temperature in *Quercus pubescens* (*Qu*), *Fagus sylvatica* (*Fa*) and *Abies alba* (*Ab*) in the five studied sites (*sb* Sainte Baume; *gl* Grand Luberon; *bg* Bauges; *vl* Vercors-Lente; *vtx* Ventoux). Dots indicate model coefficients (on the log scale). Error bars indicate confidence interval of model coefficients. Mixture effects at a minimal and maximal temperature values are in violet and in orange, respectively. Arrows represent the changes in mixture effect from a low to a high value of temperature when it is significant. Significant mixture effects (p-values < 0.1) are represented by violet and orange dots, not significant effect (p-values >= 0.1) are represented by white dots.

Quercus pubescens-Fagus sylvatica stands

Mixture effect on BAI tended to be temperature-dependent only for *Fagus sylvatica* (estimates ± se: 1.00 ± 0.53; p-value = 0.06) at the most productive site (*sb*): the effect of temperature was positive and significant in mixed stands (2.46 ± 0.90; p-value = 0.007) but not in pure stands (0.31 ± 0.81; p-value = 0.70; Fig S1). Nevertheless, the difference in BAI in *Fagus sylvatica* between mixed stands and pure stands was significant neither at low temperature nor at high temperature (Fig 3).

Mixture effect on SVI depended on temperature in *Quercus pubescens* in the two studied sites (*sb*: - 1.4 ± 0.56; p-value = 0.07 and *gl*: - 1.44 ± 0.55; p-value = 0.01). At the most productive site (*sb*), the effect of temperature on SVI of *Quercus pubescens* was positive and significant in pure stands (2.42 ± 0.86; p-value = 0.006) but not significant in mixed stands (0.18 ± 0.95; p-value = 0.85; Fig S1): the difference between SVI in mixed and pure stands going from not significant (Fig 3) at a minimal annual value of temperature (11.8 °C) to a decrease in SVI of - 57 % in mixed stand compared to pure stand at a maximal annual value of temperature (12.3 °C). At the least productive and driest site (*gl*), the effect of temperature was not significant in pure stand (0.62 ± 0.70; p-value = 0.4), but was negative in mixed stand (- 1.46 ± 0.71; p-value = 0.04): the difference between SVI in mixed and pure stands going from an increase of + 102 % in SVI in mixed stand compared to pure stand (Fig 3) at a minimal value of temperature (10.7 °C) to a decrease of - 52 % in SVI in mixed stands compared to pure stands (Fig 3) at a maximal value of temperature (12.3 °C).

Abies alba-Fagus sylvatica stands

At the coldest site (*vl*), mixture effect on BAI of *Abies alba* depended on temperature (1.45 ± 0.29; p-value < 0.001). An elevation of annual temperature caused a decrease in BAI of *Abies alba* in pure stands (- 0.67 ± 0.10; p-value < 0.001) but not in mixed stands (0.05 ± 0.10; p-value = 0.6; Fig S1): the difference between BAI in mixed and pure stands going from non-significant (Fig 2) at a minimal value of annual temperature (5.7 °C) to an increase in BAI of 252 % in mixed stand compared to pure stand at a maximal value of annual temperature (7.7 °C). In *Fagus sylvatica* the change in mixture effect with BAI was not significant. Conversely mixture effect on SVI of *Fagus sylvatica* depended on temperature (- 1.18 ± 0.65; p-value = 0.07). The positive effect of temperature on SVI of *Fagus sylvatica* was lower in mixed stand (1.75 ± 0.66; p-value = 0.009) compared to pure stand (2.33 ± 0.63; p-value = 0.0003; Fig S1): the difference between SVI in mixed and pure stands going from an increase of 405 % (Fig 2) at a minimal value of annual temperature (5.7 °C) to a non-significant difference at a high value of temperature (7.7 °C).

4. DISCUSSION

Despite the fact that most of the studies dealing with the diversity-productivity relationship in forests rely on tree diameter increment, we found that mixture effects on shoot volume increment do not mirror the mixture effect on stem growth. Mixture effect was more often neutral on branch growth than on stem growth along the studied stands, while positive mixture effect changed with temperatures and site conditions. We also found that on the driest site (*gl*) in *Fagus sylvatica-Quercus pubescens* stands, the negative effect of competition was predominant, as opposed to the coldest site (*vl*) where the effect of mixing on branch and stem growth was positive.

4.1 ASYMMETRIC MIXTURE EFFECT BETWEEN BRANCH AND STEM GROWTH

Mixture effect on branch growth did not necessarily mirror mixture effect on stem growth as illustrated by the case of beech in Vercors-Lente. This implies that considering only stem diameter in the diversity-productivity relationship can lead to an under- or an overestimation of the mixture effect. An asymmetric mixture effect may be caused by species strategies in response to competition. In plastic species such as oaks, an elongation of the stem with a development of the branches to access the light is typical of a competition avoidance strategy (MacFarlane and Kane, 2017; Pretzsch and Rais, 2016; Van de Peer et al., 2017) especially in mixture with species with low crown transparency such as *Fagus sylvatica*. *Fagus sylvatica,* on its side, tends to increase its branchiness, at least in the young stages (Van de Peer et al., 2017), its branch length increment being uncorrelated to light availability (Hajek et al., 2015). We did not observe any competition avoidance effects in *Abies alba* mixed with *Fagus sylvatica*, which highlights the fact that strategies to face competition are highly species-specific. This lack of branch response to mixture can be explained by a weak crown plasticity related to competition in shade-tolerant coniferous species (Vieilledent et al., 2010).

4.2 POSITIVE EFFECT OF MIXTURE ON STEM AND BRANCH GROWTH DEPENDS ON SITE AND TEMPERATURE

Radial stem of *Fagus sylvatica* was affected by intraspecific or interspecific competition at the site with the lowest soil field capacity with *Quercus pubescens*, at the edge of its distribution range. In young development stages, beech growing in harsh environmental conditions tend to outcompete oak (Van de Peer et al., 2018) likely because interspecific interactions at such young development stages rely more on species growth rates than at later development stages. Moreover, negative mixture effect on both stems and branches appear when temperature increases, replacing the competition avoidance strategy for *Quercus pubescens*. Such pattern has already been pointed out in forests at the global scale, with an increase of the positive mixture effect on productivity with increasing precipitation (Jactel et al., 2018). Complementarity between species could occur if resources such as water and nutrients are not limiting for growth (Forrester, 2014) and the southern-most sites that we studied are the driest of the latitudinal gradient. Yet, a transition from competition to facilitation with abiotic stress exist in forests (He et al., 2013). The only positive mixture effect on both branch and stem growth that we found occurred in the coldest site supporting the hypothesis of a complementary use of light resource. Thus, *Abies alba* can benefit from a better light absorption and a more efficient use of light in mixture, which is accompanied by a higher growth in height (Forrester and Albrecht, 2014). However, our results show that mixture effect on tree crown do not necessarily reflect on stem growth in diameter (see beech in *gl*). The fact that a positive effect on *Fagus sylvatica* shoot was observed in only one of the study sites is most probably due to the particularity of the Mediterranean-Alpine gradient. It is also known that beech is a species which benefits from a competitive reduction in mixture, reflected in an enlarged crown size (Dieler and Pretzsch, 2013). On one side our results confirm that shoot growth may increase in case of competition reduction (Pretzsch and Rais, 2016) and prove that this effect is also varying with temperature. On the other side, this result is consistent with the idea that the nature of abiotic stress determines the mixture effect. Contexts where species are more limited by temperatures than by drought favours positive mixture effects (Toigo et al., 2015) possibly through species complementarity or facilitative effect *via* the control of microclimatic conditions by forest cover that benefit to the dynamics of the associated vegetation (Zellweger et al., 2020).

5. CONCLUSION

Mixture effect on growth of stems and branches can be asymmetrical. Our results prove that tree crown is a key component of the productivity-diversity relationship. The nature of mixture effect on stems and branches was strongly dependent on the geographical context and on the type of abiotic factor limiting growth: tree species in a Mediterranean context can be particularly subject to interspecific competition, while we highlighted a positive effect of species complementarity on stem and branch growth in the coldest and wettest mountainous site. It then appears that the consideration of tree crown along with stem productivity in the diversity-productivity relationship in forest is needed to further understand and quantify the effect of mixing on tree productivity.

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