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Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir

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ABSTRACT

Context: Growth partitioning among trees in forest stands is pivotal to silviculture, making it crucial to understand its control by factors such as stand development, stand density, or thinning. Since growth partitioning primarily depends on the partitioning of environmental resources among individuals, climatic change further calls for extending this framework to explicit climatic factors. Recent debate on adapting management to such changes also requires larger density gradients to be encompassed. *Methods:* We primarily aimed to investigate the effects of stand density and climatic factors on growth partitioning, in even-aged stands of sessile oak and Douglas-fir, two species currently managed under contrasted silvicultural regimes. We used two original permanent plot networks designed to explore effects of large density gradients, from open-grown to self-thinning situations. Growth partitioning was assessed on basal area growth, using both the growth dominance index, and the within-stand size-growth relationship. Their dependence on stand density, age, thinning, and climatic predictors was modeled statistically. A one-at-a-time sensitivity analysis of these models was performed to evaluate the magnitude of the effect of each predictor on growth partitioning. Simulations of the effect of extreme climatic conditions on stand growth, and on dominant, intermediate and close-to-suppressed trees growth were also performed. *Results:* For both species, stand density was found to strongly increase growth partitioning toward the biggest trees. Stand growth in sessile oak was reduced by high summer soil water deficit, with a particularly severe growth reduction for suppressed trees, suggesting asymmetric belowground competition for water in this species. In Douglas-fir, a stand growth reduction was found for high summer temperatures, with an increase in growth dominance that suggested a higher temperature-driven stress for suppressed trees. In addition, age slightly increased/decreased growth dominance in sessile oak/Douglas-fir, respectively. *Conclusions:* Growth dominance and size-growth relationships offered complementary insight into growth partitioning. Stand density appears to be the major driver of growth partitioning. Climatic factors were also shown to significantly affect growth partitioning, with species differences, in addition to stand density and ageing. These results suggest to maintain stands at medium density levels to reduce rotation length and minimize risk of exposure to extreme climatic events.

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1. Introduction

Growth partitioning among trees in forest stands is a central concern to silviculture, and conditions forest stand development and forest structure. Growth partitioning may be actively controlled through stand density, thinning intensity and rotation age as dimensions of silviculture (Long et al., 2004). As stand develops and canopy closes, competition among trees becomes more intense, especially for small trees, which results in larger trees accounting for a disproportionately larger fraction of stand growth (Binkley, 2004; Binkley et al., 2006; Bradford et al., 2010). Later in stand development, the resource use efficiency of larger trees decreases, thus reducing the proportion of stand growth they represent (Binkley et al., 2004). Stand management effects on growth partitioning have stimulated much research (Dhôte, 1994; Deleuze et al., 2004), which are now integrated into simulators of forest dynamics (Pretzsch and Biber, 2010; Le Moguédec and Dhôte, 2012). These research are however mainly restricted to traditional (medium to high) density ranges.

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While many studies have focused on the effect of competition control (for example by thinning) on growth partitioning, fewer studies explicitly address the effect of a change in resource availability if trees were released from competition on growth partitioning. These studies are nevertheless crucial as growth partitioning results from resource partitioning among individual trees, including light, water or nutrient resources (Schwinning and Weiner, 1998). As the upper stratum of the forest intercepts most radiations (Pacala et al., 1996), light partitioning is inherently in favor of the tallest trees in the stand. Belowground competition for nutrient results in a more evenly distributed resource repartition (Casper and Jackson, 1997; Schwinning and Weiner, 1998), but little is known on the water partitioning process (Schwinning and Weiner, 1998; Craine and Dybzinski, 2013).

Adapting forest management to climatic change is of growing concern (Allen et al., 2010). It requires assessing the concomitant impact of climatic factors and stand structure on stand dynamics and growth partitioning. Some studies have attempted to explicit the role of site fertility in growth partitioning (Hein and Dhôte, 2006; Metsaranta and Lieffers, 2010; Pretzsch and Biber, 2010; Coomes et al., 2011). Site fertility however remains implicit as regards to environmental factors (Skovsgaard and Vanclay, 2008) and more analytic approaches are now largely implemented (Bontemps and Bouriaud, 2014). Other investigations have highlighted the specific role of water availability in growth partitioning but show contradictory results (Dhôte, 1994; Wichmann, 2001; Pretzsch and Dieler, 2011; Castagneri et al., 2012; Zang et al., 2012). Therefore, a substantial effort remains to be done for integrative approaches including factors reflecting forest structure (age, density), management (thinning intensity) and the abiotic environment (with a special focus on water availability).

The context of adapting management to climate change has further fostered debate about reducing tree density and stand leaf area in order to reduce stand water consumption (Martin-Benito et al., 2010; Sohn et al., 2013; Gebhardt et al., 2014), with however possible long-term drawbacks due to hydraulic architecture acclimation and higher individual leaf area in low density treatments, likely to increase drought vulnerability (McDowell et al., 2006; D'Amato et al., 2013). In this context, there is renewed need to properly assess the effect of stand density on growth partitioning, on much wider ranges than traditionally considered on permanent plot trials in North-America and Europe (Dhôte and Herve, 2000; Pretzsch, 2005; Zhang and Oliver, 2006). Ideally, the widest view on the issue would require considering open-grown to self-thinning tree communities.

We based our analysis on a network of silvicultural experiments (Bédénaux et al., 2001), that includes different species, sampled over their production area, and encompasses large density gradients from open-grown to self-thinning stands. We restricted the analysis to *Quercus petraea Liebl.* (sessile oak), the second largest broadleaved growing stock in France with 281 Mm^3 (IFN, 2013) and a high commercial interest, and *Pseudotsuga menziezii* (Douglas-fir), constituting the first Douglas-fir resource in Europe (Schmid et al., 2014) and outside its region of origin with 107 Mm^3 of growing stock in France (IFN, 2013). Sessile oak growth is known to have a low response to climatic conditions; yet, its main climatic driver is summer water stress (Lebourgeois et al., 2004; Friedrichs et al., 2009; Merian et al., 2011). Sessile oak growth has further been identified as sensitive to climatic change (Dolezal et al., 2010). Douglas-fir is thought to be more resistant to drought than other vulnerable coniferous species (Lévesque et al., 2013), yet it requires higher levels of precipitation than sessile oak (Angelier, 2007; Waring et al., 2008; Carnwath et al., 2012) and it is also considered as sensitive to climate change (Sergent et al., 2012).

In the present study, we aimed to explore the effects of stand structure and management (age, relative density and thinning intensity) and climate (precipitation, soil water content, vapor pressure deficit and air temperature) factors on growth partitioning, and to integrate these factors in models in order to weight their respective contributions. Growth partitioning was analyzed through both the stand-scale growth dominance index (Binkley et al., 2006), and the tree-scale size-growth relationship between diameter and basal area growth over a tree population (Dhôte, 1994). Growth consequences of drought for trees belonging to differing social statuses were also investigated.

The hypotheses tested were: (i) stand growth is more concentrated in the biggest trees in high-density stands than in low-density stands. (ii) Summer drought is expected to reduce tree growth and the magnitude of the growth reduction depends on tree social status, modifying growth dominance within the stand under drought conditions. In addition, we paid a specific attention at behavioral differences between the two species under study as regards drought effects.

2. Material

2.1. Study area and sampling design

We focused on sessile oak and Douglas-fir in their production area in France. Our data originate from two long-term experimental networks belonging to the "coopérative de données des peuplements forestiers" (Bédénaux et al., 2001), specifically designed to explore the effect of large density gradients, from open grown tree to self thinning stands situations, on forest dynamics of even-aged stands. The network area covers the plains of Northern France for sessile oak and mid elevation mountainous areas for Douglas-fir (Fig. 1). As is common practice for even-aged forestry in France, stands have been naturally regenerated in the oak network (Huffel, 1927; Jarret, 2004) and planted in the Douglas-fir network (Oswald and Pardé, 1984). Each network includes trials,

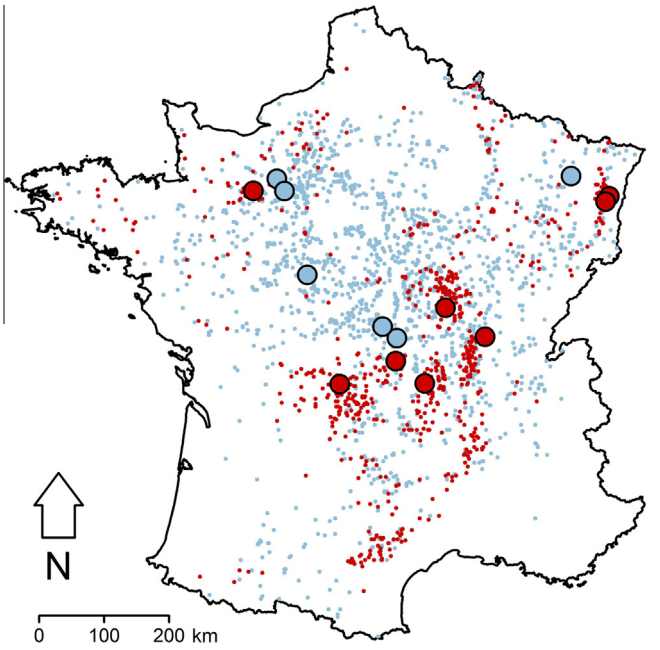

Fig. 1. Geographical location of the experimental sites in Northern France. Large circles indicate sessile oak (light blue) and Douglas-fir (dark red) sites, while small points represent the distribution of pure stands of sessile oak and Douglas-fir according to NFI data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

each of these corresponding to a single site which includes several experimental plots (0.36 ha for sessile oak and 0.11–0.20 ha for Douglas-fir) of the same age (from 11 to 42 years for sessile oak and from 18 to 49 years for Douglas-fir), experiencing contrasted thinning regimes defined through a density index scenario. In terms of experimental factors, RDI is therefore nested within 'site'. Stand thinning is triggered at the beginning of a period (after each measurement) whenever the relative stand density of the plot is above the target relative density of the associated thinning regime. Selected trees for thinning are evenly spread between size classes.

In the Douglas-fir network, each tree circumference was periodically measured (around every 3 years) at a height of 1.3 m. In the sessile oak network, two cases occurred in the measurement protocol: where trees were less than 1000 per plot, all of them were numbered and periodically measured (exactly every 4 years); otherwise (usually in young self-thinning stands) a statistical inventory was conducted. This statistical inventory consists of 30 rectangular samples of fixed length (in-between two silvicultural racks, from 5 to 10 m), each of them wide enough (from 1 to 4 m) to contain around 15 trees and for which circumferences at breast height are measured (Appendix A). Two subsequent measures on the same tree allowed us to calculate circumference and basal area increment for the given period. Table 1 portrays general information on the trials.

2.2. Dendrometric variables

Age, relative stand density and thinning intensity were used to give a synthetic representation of stand management. The age was that of the stand at the beginning of the growth period. A density index based on Reineke idea (RDI, expressing the current density in number of stems ha^{-1} relative to the potential self-thinning density at a same quadratic mean diameter dg) (Reineke, 1933) was used to measure stand density on a relative scale. Oak RDI was calculated using $rdi_{oak} = N/(125242 \cdot dg^{-1.566})$ from Le Goff et al. (2011) and Douglas-fir RDI using $rdi_{Douglas} = N/(185907 \cdot dg^{-1.646})$ from Charru et al. (2012), with N the number of tree per ha and dg the quadratic mean diameter. Thinning intensity (TI) was calculated for each period as a ratio between the RDI removed during thinning and the RDI before thinning.

Dominant circumference (Co) was defined as the circumference of the 100 largest trees per ha. Close-to-suppressed trees were defined as below $0.4 * Co$ for sessile oak and $0.55 * Co$ for Douglas-fir. These values were chosen empirically to reflect the circumference of trees occupying the lower part of the canopy in stands with RDI above 0.5 (Appendix B). Intermediate trees were defined as $0.7 * Co$ for sessile oak and $0.775 * Co$ for Douglas-fir.

2.3. Climatic data

Data for monthly precipitation (P) and mean monthly temperature (T) were extracted for each site, year and month from the Safran spatial climate model (Quintana-Seguí et al., 2008; Vidal et al., 2010). The resolution of the Safran grid is 8 km, and we noticed a significant elevation difference between Douglas-fir sites and simulated location in Safran. Since elevation affects temperature and precipitation, we locally corrected Safran variables for each site by using regional regressions of monthly mean temperature and monthly mean precipitation on elevation using meteorological stations of the French National Climatic Network Meteo-France in a 100 km radius of each site (mean of −0.48 °C and +8 mm per 100 m of elevation). Because oak plots were located in plains, no correction was needed. We further calculated vapor pressure deficit (VPD) as an index of atmospheric evaporative demand (Appendix C), and soil water content (SWC) and soil water deficit (SWD) as indices of belowground water availability (Appendix D). These aboveground and belowground indices of water resources are often jointly used in process-modeling (Dufrêne et al., 2005; Waring and Landsberg, 2011; Meinzer et al., 2013) and are expected to be better indicators of the influence of climate on tree growth than raw climatic data (Lebourgeois et al., 2013; Piedallu et al., 2013). Monthly climatic data were then aggregated by season for a given year, and averaged by growth period in-between two measurements.

2.4. Growth dominance index

Growth dominance was used as a stand level index of growth partitioning between trees. It relates the distribution of tree growth to the distribution of tree size within a stand (Binkley et al., 2006) and provides a global estimation of unevenness of growth distribution over trees. Higher growth dominance is found where larger trees contribute more than proportionally to their size to stand growth, and conversely for the smaller trees. A growth dominance index (GDI) for basal area increment was adapted from Binkley et al. (2006). In practice, a dominance curve was computed for each plot and period by ranking trees by size: trees were ordered from smallest to largest, and the proportion of cumulative basal area increment was plotted against the proportion of cumulative basal area (Fig. 2). The GDI, bounded between −0.5 and 0.5, is calculated as the area under the 1:1 line minus the area under the dominance curve. When all trees contribute proportionally to their size to stand growth, all points lie in the 1:1 line and the GDI is equal to zero. Positive GDI values (large trees contribute more than proportionally to their size to stand growth) portray curves below the 1:1 line, while negative GDI values (small trees contribute more than proportionally to their size to stand growth) portray curves above the 1:1 line. We did not calculated GDI for sessile oak stands under statistical inventory regime, as not all trees were measured.

Multiple ordinary least square (OLS) regression was used to model the effect of stand variables (age, RDI, TI) and seasonal climatic variables (P, T, VPD, SWC, SWD) on the GDI (Eq. (1)). In order to take account of possible nonlinearities and interactions in the predictor effects, second-order polynomials and first-order interactions were tested.

$$\mathrm{GDI} = XB_{\mathrm{GDI}} + \varepsilon \quad (1)$$

where X is the matrix of explicative predictors, B the parameter vector to be estimated and ε is an additive error term assumed to follow a Gaussian distribution with constant variance and independent errors. Variable selection was ensured through a forward stepwise procedure minimizing a penalized-likelihood criterion. Bayesian Information Criterion (BIC) (Schwarz, 1978) was preferred to e.g. AIC because it allows more parsimonious models to be selected (Koehler and Murphree, 1988; Bolker, 2008). New variables were added to the model when they reduced the BIC by at least 2 points and were significant (p value <0.05). To measure the respective contribution of the different predictors in the model, a semi-partial R^2 was computed for each of them, calculated for each variable i by subtracting the R^2 from the full model minus the variable i to the R^2 of the full model.

2.5. Growth partitioning among trees: size-growth relationship

The partition of growth in a stand at a given period was described by a segmented regression of individual basal area increment against circumference (Eq. (2) and Fig. 3). This functional form was introduced in forestry by Ford (1975), and it has then been successfully used for different species in even-aged stands (Dhôte, 1994; Saint-André et al., 2002; Deleuze et al., 2004; Hein and Dhôte, 2006; Pérot et al., 2007).

Table 1
Experimental sites used in the two networks, dendrometrical and environmental parameters measured in each site.

Species	Trial	Site description					Dendrometrical variables						Environmental variables[d]					
		Starting date[a]	Mean plot size (ha)	*n* plot per trial	*n* growth periods	*n* individual increment	Age		Cg[b] Range[c]		RDI Range[c]		SWHC[e]	*T*	*P*	SWC	SWD	VPD
							Start	End	Start	End	Start	End						
Sessile oak	Grosbois	1996	0.36	3	4	3234	14	26	5–9	24–49	0.04–0.58	0.10–0.88	130	11.2 (0.26)	762 (28)	50 (8)	28 (6)	6.8 (0.5)
	Montrichard	1995	0.36	5	4	4118	11	23	6–8	16–44	0.04–0.96	0.09–1.20	104	11.5 (0.33)	703 (59)	16 (5)	53 (11)	5.8 (0.9)
	Moulins-Bonmoulins	2005	0.36	4	1	1302	11	11	7–14	7–14	0.05–1.03	0.05–1.03	127	10.4 (0)	801 (0)	56 (0)	27 (0)	4.9 (0)
	Parroy	1996	0.36	4	4	3882	17	29	19–26	37–74	0.15–0.83	0.17–1.06	102	10.3 (0.41)	845 (18)	32 (5)	31 (6)	5.8 (0.5)
	Reno-valdieu	1997	0.36	5	3	7525	31	39	29–36	42–55	0.43–0.89	0.31–0.95	66	10.7 (0.06)	858 (56)	15 (6)	40 (3)	5.2 (0.4)
	Tronçais	2001	0.36	4	2	2815	38	42	33–44	40–58	0.34–0.81	0.12–0.8	95	11.5 (0.1)	810 (1)	28 (3)	33 (1)	7.0 (0.4)
Douglas-fir	Bernstein	2000	0.11	1	3	865	18	25	41	51	1.16	1.38	43	10.6 (0.05)	833 (84)	5 (3)	37 (15)	7.0 (1.2)
	Chissey-Grison	1992/1999	0.20	4	4	1741	28	37	51–141	73–157	0.35–1.14	0.53–1.25	77	10.4 (0.18)	1194 (62)	41 (10)	17 (8)	7.3 (0.9)
	Colettes	2004	0.18	7	2	1002	18	21	61–89	67–104	0.15–0.85	0.20–0.96	108	9.3 (0.04)	1044 (3)	74 (12)	12 (7)	5.6 (0.8)
	Ecouves	1965/1992	0.12	9	5	2686	44	49	83–151	105–202	0.65–1.46	0.72–1.62	64	9.2 (0.18)	1059 (101)	20 (8)	27 (6)	4.9 (0.4)
	Larochemillay	1997	0.15	5	4	1586	23	32	67–77	71–119	0.27–0.97	0.45–0.79	96	10 (0.19)	1320 (142)	45 (18)	21 (12)	5.7 (1.1)
	Saint-Pardoux	1997	0.19	4	5	1295	28	39	78–95	101–136	0.32–0.68	0.46–0.80	96	9.0 (0.09)	1321 (73)	59 (4)	12 (3)	4.3 (0.5)
	Thiers	1994	0.15	3	6	1709	19	31	60–69	91–117	0.89–0.99	0.54–0.65	116	10.4 (0.45)	909 (83)	55 (18)	23 (13)	5.3 (0.9)
	Vancelle	2000	0.11	1	3	710	19	26	41	52	0.99	1.18	85	11.2 (0.05)	627 (84)	15 (4)	39 (14)	7.0 (1.2)

[a] Installation of trials and first measurement date used are separated by a slash symbol when they are different.
[b] Quadratic mean circumference (cm).
[c] Min and max range of the studied variable.
[d] Averages and standard deviation (inside brackets) per trial. *T* and *P* are yearly mean and sum values, respectively. SWC, SWD and VPD are mean summer values.
[e] Soil water holding capacity (SWHC). They are GIS interpolation of NFI data extracted from Piedallu et al. (2011).

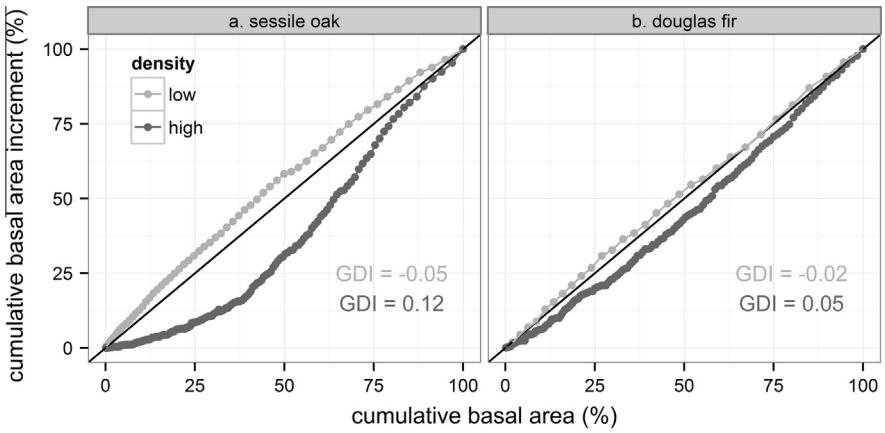

Fig. 2. Dominance curves and growth dominance index for various stands of sessile oak and Douglas-fir with contrasted thinning regimes. (a) Sessile oak stand in Montrichard during the 2003–2007 period (age = 19 years, RDI = 0.06 and 1.14 for low and high density treatments). (b) Douglas-fir stand in Larochemillay during the 2003–2006 period (age = 29 years, RDI = 0.38 and 1.1 for low and high density treatments).

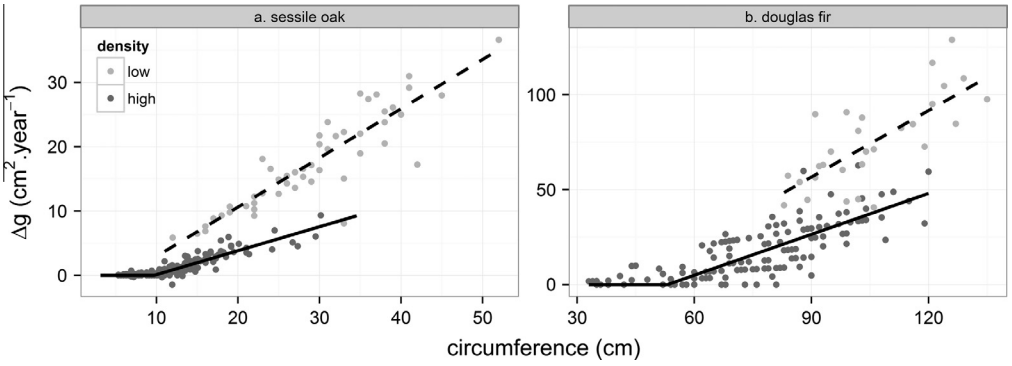

Fig. 3. Relationship between individual tree basal area increment and circumference for various stands of sessile oak and Douglas-fir with contrasted thinning regimes. (a) Sessile oak stand in Montrichard during the 2003–2007 period (age = 19 years, RDI = 0.06 and 1.14 for low and high density treatments). (b) Douglas-fir stand in Larochemillay during the 2003–2006 period (age = 29 years, RDI = 0.38 and 1.1 for low and high density treatments). Lines were fitted using Eq. (2). Note that the *X* and *Y* scales differ for the two species.

$$\begin{cases} \text{if } c > \beta_{threshold}; & \Delta g = \beta_{slope} \cdot (c - \beta_{threshold}) + \varepsilon \\ \text{if } c \leqslant \beta_{threshold}; & \Delta g = 0 + \varepsilon \end{cases} \quad (2)$$

where c is the circumference of the tree, Δg is the individual basal area increment of the tree, ε are Gaussian errors assumed independent and with constant variance, while $\beta_{threshold}$ and β_{slope} are parameters to be estimated.

A four-step modeling approach was used to relate tree-level growth partitioning to stand and climatic variables. As a first step, Eq. (2) was independently fitted to each plot and period using non-linear OLS regression (segmented models later referred to as "elementary models"), providing one $\beta_{threshold}$ and one β_{slope} value for each plot and period.

In step 2, we used multiple OLS regression to model the effect of stand variables (age, RDI, TI) and seasonal climatic variables (P, T, VPD, SWC, SWD) on the two parameters series obtained from the elementary models (Eqs. (3) and (4)). The method used is the same than for the multiple OLS regression on GDI: X represents the matrix of explicative predictors (including second-order polynomials and first-order interactions), B the parameter vector to be estimated and ε is an additive error term. Variable selection was ensured through a forward stepwise procedure minimizing the BIC, and semi-partial R^2 were calculated to measure the contribution of different predictors to the overall fit.

$$\beta_{threshold} = XB_{threshold} + \varepsilon_{threshold} \quad (3)$$

$$\beta_{slope} = XB_{slope} + \varepsilon_{slope} \quad (4)$$

In step 3, we built a tree-level model of the size-growth relationship (latter referred as "integrated model", Eq. (5)) building on the segmented regression, by nesting the multiple regression models of β_{slope} and $\beta_{threshold}$ parameters within the size-growth relationship model (Eqs. (3) and (4)) in Eq. (2):

$$\begin{cases} \text{if } c > XB_{threshold}; & \Delta g = XB_{slope} \cdot (c - XB_{threshold}) + \varepsilon \\ \text{if } c \leqslant XB_{threshold}; & \Delta g = 0 + \varepsilon \end{cases} \quad (5)$$

Simultaneous estimation of all parameters on all plots and periods was done using nonlinear OLS regression. Due to the strong correlation between the threshold and slope parameters, it would have been unreasonable to assemble all previously selected variables and we used the BIC criterion to perform some further selection on the integrated model (for example, if a climatic variable was included in the regression of the slope parameter, we also tested its inclusion in the regression of the threshold parameter). Goodness-of-fits of the two integrated models were assessed with the coefficient of determination (R^2), the root mean squared error (RMSE) and the relative root mean squared error (rRMSE). We implemented a K-fold like cross-validation procedure to assess the robustness of the integrated models: For each species, the integrated model was calibrated on all sites minus one, and validated on the remaining site. The procedure was repeated by excluding

each site in turn, so that we had 6 validations samples for the sessile oak model and 8 validations samples for the Douglas-fir model, on each of which validation R^2, RMSE and rRMSE were calculated (Appendix E). A validation of the integrated model was done at stand level by comparing predicted with observed stand growth for each stand and period. Predicted stand growth was calculated by summing up predicted tree growth for all trees in a stand per ha. The correlation coefficient between predicted and observed stand growth was computed. All statistical analyses were performed using the R software (R Development Core Team, 2012).

In step 4, a one-at-a-time sensitivity analysis of the integrated model was conducted to weight the contribution of the different predictors in the integrated model. Several simulations were performed, where the value of the studied predictor were evenly distributed along their range in the dataset. Extreme values were set at their 5% and 95% quantiles, while the central value was set at the interquantile (setting it at its median value would have triggered visual confusion when the distribution of the variable is non-symmetrical). Non-studied variables were fixed at their interquantile value in the dataset so that central values always represent the same position over the different predictors. To avoid extrapolation, the range of tree circumference was restricted to the range of circumference of the stand that closest matches the simulation in terms of RDI and age.

2.6. Simulation study

We used the integrated tree-level models to simulate the effect of extreme climate events on stand growth and dominant, intermediate and close-to-suppressed tree growth (defined as explained in 2.2). Age, RDI, thinning intensity and circumference distributions for each plot and each period were taken from the dataset, while climatic variables values were replaced with their 5% and 95% quantile in the dataset to represent extreme values, and by the interquantile value for normal climatic conditions. A relative growth difference between extreme climatic period and the norm was computed as: $(\Delta y_{extreme} - \Delta y_{norm})/\Delta\tilde{y}_{norm}$. Depending on the studied response variable, Δy represents stand growth, dominant, intermediate or close-to-suppressed tree growth. $\Delta y_{extreme}$ represents Δy simulated under extreme climatic situations (5% or 95% quantiles), while Δy_{norm} represents Δy simulated growth under normal climatic situation. $\Delta\tilde{y}_{norm}$ represents the median of Δy simulated under normal climatic situation. Close-to-suppressed tree growth was not simulated when it was below the range of circumference distribution of the stand (usually for stands of low RDI).

3. Results

Table 2 displays results from the multiple regressions of stand and climatic variables on the GDI. Models were highly explicative, with R^2 values of 0.94 for sessile oak and 0.84 for Douglas-fir, and consistently showed a strong and positive effect of RDI. For sessile oak, a slight positive effect of age and a slight negative effect of summer SWC were also found on the GDI. In Douglas-fir, a slight negative effect of age and a slight positive effect of spring VPD were found.

Models of the threshold parameter (Table 2) were also highly explicative, with R^2 values over 0.7. They showed consistent positive effects of age and RDI on the threshold parameter. Models of the slope parameter (Table 2) showed lower goodness-of-fits, with R^2 of 0.54 for sessile oak and 0.32 for Douglas-fir. They revealed a strong negative effect of RDI on the slope. For sessile oak there was also a slight negative effect of thinning intensity and summer SWD, while there was a slight negative effect of summer T for Douglas-fir. In these models, the contribution of climatic variables was low, compared to that of dendrometric variables.

Table 3 presents the best integrated models for sessile oak and Douglas-fir. Due to the high number of observations, p-values were all zero. R^2 coefficients of 0.85 for sessile oak and 0.78 for Douglas-fir showed that a high proportion of the initial variance in tree growth was explained by the integrated models. The mean validation R^2 was equal to 0.78 for sessile oak and 0.53 for Douglas-fir, showing a fair to good predictive accuracy of the models (Appendix E). Validation sites lying outside the range of calibration (for age and density factors in particular) were less well predicted than the others (Appendix E). When assembling multiple regression models for the threshold and the slope (Table 2) into an integrated model (Table 3), the goodness-of-fit was improved when adding the same climatic variable in the threshold and the slope. For sessile oak, adding the effect of summer SWD on the threshold lowered the BIC of the integrated model by 94 points. For Douglas-fir, adding the effect of summer T on the threshold lowered the BIC by 36 points. Correlation coefficient between observed and predicted stand growth for each plot and each period was 0.76 and 0.66 for sessile oak and Douglas-fir, respectively.

Outputs from the one-at-a-time sensitivity analyses for the best models are plotted in Fig. 4. For both species, the threshold of the size-growth relationship, that is, the minimum size needed for a tree to grow, was positively influenced by the age of the stand and to a lesser extent by RDI. We also noticed slight positive effects of summer SWD (for sessile oak, Fig. 4a) and summer T (for Douglas-fir, Fig. 4b) on the threshold. For both species, the slope of the

Table 2
Multiple regression on the growth dominance index, the threshold and the slope parameters of the elementary segmented regressions. $N = 74$ ($N = 49$ for growth dominance) for sessile oak and $N = 139$ for Douglas-fir.

Species		Growth dominance index				$\beta_{threshold}$				β_{slope}			
		Estimate	p-value	spR^2	R^2	Estimate	p-value	spR^2	R^2	Estimate	p-value	spR^2	R^2
Oak	Intercept	−0.057	<0.001		0.94	−9.15	<0.001		0.72	0.99	<0.001		0.54
	Age	0.00073	0.013	0.01		0.67	<0.001	0.508					
	RDI	0.0279	0.451	0.553		10.57	<0.001	0.185		−0.41	<0.001	0.366	
	RDI^2	0.1409	<0.001										
	Thinning									−0.002	0.006	0.053	
	Summer SWD									0.003	0.013	0.043	
	Summer SWC	−0.00033	0.038	0.007									
Douglas-fir	Intercept	−0.06926	<0.001		0.84	−3.86	0.199		0.76	1.954	<0.001		0.32
	Age	−0.00058	0.001	0.022		0.084	<0.001	0.76					
	RDI	0.11327	<0.001	0.673		3.25	<0.001			−0.383	<0.001	0.296	
	Spring VPD	0.0078	0.002	0.013									
	Summer T									−0.044	0.001	0.056	

Table 3
Models equations, parameters estimates and goodness of fit for the best integrated models for sessile oak and Douglas-fir. Eqs. (6) and (7) must be substituted to the β parameters in Eq. (2). N = 22,876 for sessile oak, N = 11,594 for Douglas-fir.

Species	$\beta_{threshold}$					β_{slope}					
Models equations											
Sessile oak	α_0 +	α_1·age +	α_2·RDI +	α_3·summer SWD		α_5 +	α_6·RDI +	α_7·thinning +	α_8·summer SWD		(6)
Douglas fir	α_0 +	α_1·age +	α_2·RDI	+	α_4·summer T	α_5 +	α_6·RDI			+ α_9·summer T	(7)
Parameters estimates											
	α_0	α_1	α_2	α_3	α_4	α_5	α_6	α_7	α_8	α_9	
Sessile oak	−9.19	0.7	8.03	0.069		1.068	−0.618	−0.0021	−0.022		
Douglas fir	−32.74	1.23	23.85		1.012	1.51	−0.454			−0.023	
Models fits											
	R^2	RMSE	rRMSE								
Sessile oak	0.85	3.02	0.45								
Douglas fir	0.78	13.2	0.42								

size-growth relationship decreased with RDI, that is, the growth of trees above the threshold decreased proportionally to their size with increasing RDI. Slight negative effects of thinning intensity and summer SWD on the slope of the size-growth relationship was observed for sessile oak (Fig. 4a), while a slight negative effect of summer temperatures on the slope was observed for Douglas-fir (Fig. 4b).

Relative growth differences between simulated extreme climatic situations and the norm are depicted in Fig. 5. Simulated stand growth under low or high SWD for sessile oak were 24% above and 22% below the norm, respectively (Fig. 5a). The relative difference between low and high SWD and the norm was less pronounced on dominant tree growth (14% above and 13% below the norm) and intermediate trees (18% above and 16% below) than on stand growth. Close-to-suppressed trees appeared to be particularly affected by climatic extremes, with a mean relative difference 78% above the norm under simulated low summer SWD and 61% below the norm under simulated high summer SWD. In Douglas-fir, relative growth differences around 10% above or 10% below the norm were found for stand growth, dominant, and intermediate tree growth, at low or high temperature, respectively (Fig. 5b). Again, suppressed trees appeared to be more affected by climatic conditions than others, with a mean relative difference of 43% above the norm during simulated low summer T, and 37% below the norm during simulated high summer T.

4. Discussion

This research allowed quantify the combined effects of stand density and climate conditions on tree growth partitioning for even-aged stands of sessile oak and Douglas-fir. The threshold and the slope of the within-stand size-growth relationship were both affected by stand density and climatic conditions, and we found growth dominance to be higher at higher density and in drier conditions. The main driving climatic factor identified differed between the two species: summer SWD was the main factor for sessile oak while summer T was the main factor for Douglas-fir. In their respective production areas, sessile oak suffered more acutely from drought conditions than Douglas-fir.

4.1. Effect of RDI and thinning intensity on growth partitioning

Overall, for both species, RDI has a strong positive effect on growth dominance, larger trees accounting for a disproportionately larger fraction of stand growth in high density stands, compared to low density stands. In agreement with Deleuze et al. (2004), we observed that stand density has a negative effect on the slope and a positive effect on the threshold of the size-growth relationship. The threshold of the size-growth relationship represents the minimum size that separates lowerstorey from upperstorey (Dhôte, 1991) and under which available resources are too scarce for a tree to grow. Higher stand density implies higher competition for nutrient, water and light resources (Bréda et al., 1995; Aussenac, 2000). Light is known to be pre-empted by the tallest trees in the stand (Pacala et al., 1996; Aussenac, 2000) and strong growth dominance is most often associated with strong competition for light (Binkley et al., 2006), especially for light-demanding species. Thus, the higher threshold value found in dense stands may be mainly (but not only) due to an increase in light competition (although see the effect of summer SWD on sessile oak for an effect of water resource on the threshold). The slope of the segmented regression represents the size-growth relationship of trees in the upper storey. Accordingly, increased competition at higher stand density decreases the slope of the size growth relationship, and thus decreases tree growth in the upperstorey. However, the present approach gives no hint at what the limiting or co-limiting resources in the upperstorey may be.

For sessile oak, a slight reduction of the slope of the size-growth relationship with thinning intensity was found, leading to a reduced tree growth in the upperstorey. This effect may reflect the canopy disturbance that follows thinning (Long et al., 2004), the beneficial effect of thinning on tree growth being already taken into account in the model as thinning reduces RDI. No effect was detected in Douglas-fir stands. This may stem from that thinning in Douglas-fir plantations were less intense than in sessile oak natural regeneration (especially during the installation of the experimental plots): the 95% quantile of TI amounts to 85% for sessile oak and 45% for Douglas-fir. No effect of TI on growth dominance was detected in either species. These results are consistent with that change in tree growth with thinning is proportional to tree size, and that GDI is invariant to such changes. Affecting growth dominance would require e.g. a change in the threshold of the size-growth relationship, which was not observed here. Note that these results might depend on the thinning method used (Bradford et al., 2010).

4.2. Effect of climate conditions on growth partitioning

Beside stand structure, we found evidence that summer climatic conditions affect individual tree growth and tree growth partitioning. For both species, the relative growth of close-to-suppressed trees was found to be more reduced than the relative growth of dominant trees in stressful climatic conditions. Conversely, this implies that close-to-suppressed trees benefit more from favorable climatic conditions than other social statuses, which in turn will result in lower growth dominance under favorable climatic conditions. This effect, however, is an order of magnitude lower than that of stand density (Table 2 and Fig. 4).

It appears that tree growth and growth partitioning of the two species are sensitive to different climatic variables, as detected in

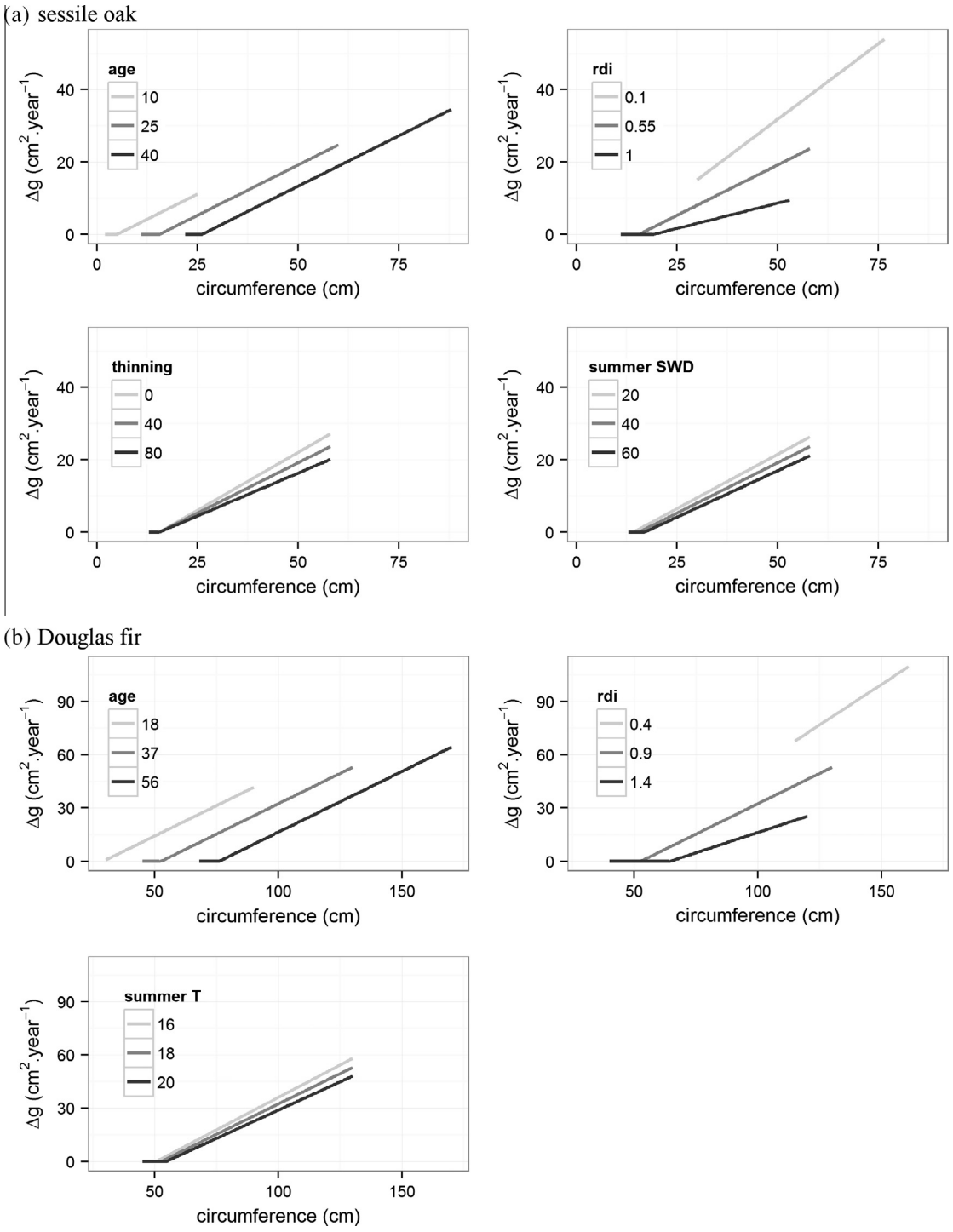

Fig. 4. One-at-a-time sensitivity analysis of the integrated tree level models. For each predictor, 5% and 95% extremes and central value were simulated (see text). Non-studied variables were fixed at their interquantile value in the dataset so that central values (medium grey) always represent the same simulation. To avoid extrapolation, the range of tree circumference was restricted to the range of circumference of the stand that closest matches the simulation in terms of RDI and age. (a) Sessile oak. (b) Douglas-fir.

sessile oak and in Douglas-fir models. Sessile oak growth in its production area is mostly limited by belowground water availability during summer, while Douglas-fir is mostly limited by atmospheric water content or a temperature stress during summer. The reduction in stand growth during a climatic stress was also less severe in Douglas-fir than in sessile oak (Fig. 5). Such difference may be related to the environmental conditions covered in the different sampling designs: in the Douglas-fir network, contexts without strong water constraints were considered (5–95% precipitation range of 840–1450 mm/year in the experimental network), and reflect the recommendations for Douglas-fir plantation (Angelier, 2007). The sessile oak network (5–95% precipitation range of 610–920 mm/year) includes the western part of its production area, where it has been found to be constrained by

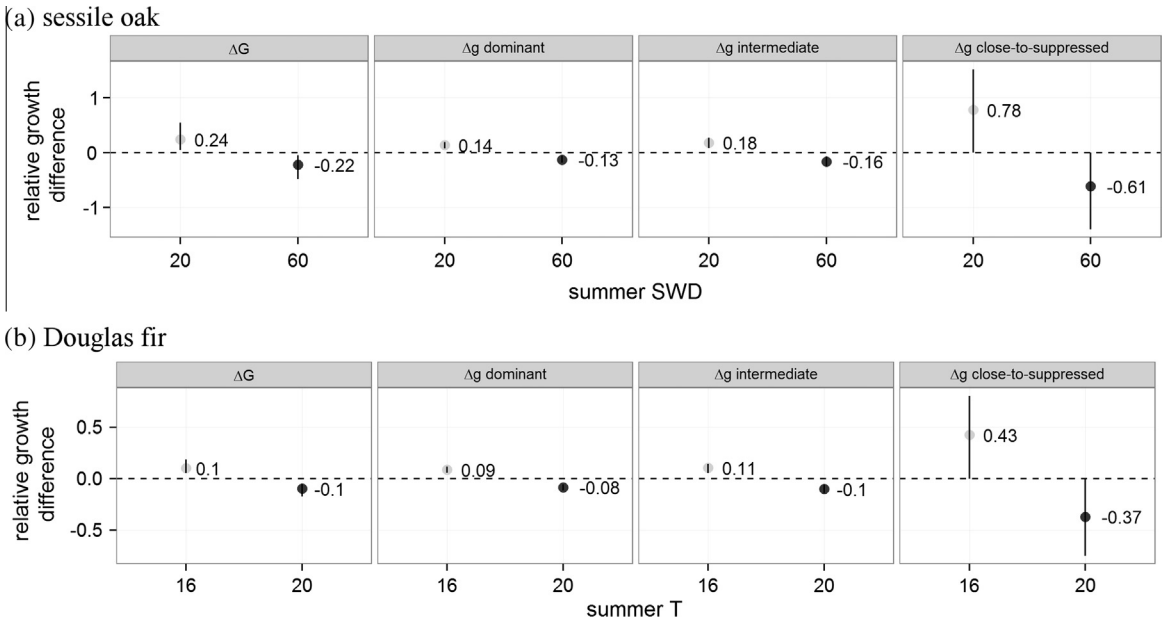

Fig. 5. Effect of simulated climate on stand growth, dominant, co-dominant and close-to-suppressed tree growth. The effect is presented as a relative growth difference between the growth predicted during extreme climatic conditions (summer SWD of 20 or 60 for sessile oak, summer *T* of 16 or 20 for Douglas-fir) and the norm (summer SWD = 40 for sessile oak, summer *T* = 18 for Douglas-fir). Points and their associated numbers represent the mean, while error bars represent the 5–95% quantile range of simulated relative differences. (a) Sessile oak. (b) Douglas-fir.

belowground water resources (Berges et al., 2005; Merian et al., 2011).

For sessile oak, high summer SWD both increased the threshold and decreased the slope of the size-growth relationship, resulting in an overall stand and individual tree growth reduction. The growth reduction is particularly severe for close-to-suppressed trees when their sizes approach the threshold, resulting in higher growth dominance. Dhôte (1994) have reported similar patterns in beech stands, when suppressed trees stopped growing for almost 10 years during a severe drought period. On the basis of these results alongside those of Dhôte (1994), it appears that larger trees may intercept a disproportionate fraction of water resource during the partitioning process. This phenomenon might be explained by the deeper and denser root prospection of dominant trees compared to those of suppressed trees (LeGoff and Ottorini, 2001; Bolte et al., 2004), giving them higher access to water while increasing their water use efficiency at the same time (Fernández and Gyenge, 2009; Gebhardt et al., 2014).

In Douglas-fir, a stand growth reduction was identified at higher summer temperature. The growth decrease was more severe in close-to-suppressed than in dominant trees. Since temperature is an environmental factor, this suggests a negative interaction between higher temperature and atmospheric or soil water availability (warmer soils), which drives leaf transpiration, stomatal conductance and photosynthesis rate (Macfarlane et al., 2004). It is also likely that the higher spatial heterogeneity of soil water holding capacity (SWHC) in mountainous areas made the GIS predictions of SWHC (and thus SWC and SWD) less accurate in Douglas-fir than in sessile oak. This phenomenon might explain the higher goodness-of-fit obtained with models including simpler climatic variables such as temperature and VPD in Douglas-fir. Accordingly, spring VPD was also found to increase growth dominance, also suggesting a higher stress for small trees. Given the high correlations between summer *T* and summer VPD (0.9) or spring VPD (0.8), and the fact that the climatic effect on growth partitioning is small, such causal uncertainties are not surprising. In this case, differences in the response to atmospheric water across social statuses are more likely to come from physiological differences between social statuses, e.g. a lower water use efficiency in suppressed trees (Binkley et al., 2002) or from microclimatic conditions within the stand (Aussenac, 2000) than from a resource partitioning process.

4.3. Silvicultural consequences

As relative stand density and stressful climatic conditions increase, the contribution of small trees to stand growth becomes even more negligible. In these conditions, it is the growth of intermediate and dominant trees that determine stand growth. In our view, maintaining stands at medium density levels promote high growth rate of intermediate and dominant trees and would therefore allow to reduce rotation length and minimize the risk of exposure to extreme climatic events. It also maintains a closed canopy, allowing to maximize stand growth and to lower the development of concurrent species. In sessile oak stands, RDIs of 0.45–0.50 appear as a good compromise between tree and stand growth. This range of value corresponds to the heavy thinning scenario (as opposed to the classical thinning scenario) defined in French silvicultural recommendations (Sardin, 2008). Similarly, RDI values around 0.6 may be recommended for Douglas-fir, which is slightly below the recommended density in Angelier (2007). Note that such dynamic silvicultural scenarios will produce trees with larger ring width, which may not be suitable for all wood products types (e.g. oak veneer) (Jarret, 2004).

5. Conclusions

Stand density appears to be a major driver of growth partitioning in even-aged forest stands of sessile oak and Douglas-fir. The models developed further allow derive new silvicultural prescriptions to reach a given state of growth partitioning and lower the consequences and uncertainties associated with climate change. Cross-validation of these models provides them with a fair to high degree of confidence for simulation or predictive purposes, but also

stresses the importance to remain in the validity domain (calibration) of these models.

Suppressed trees appear to be more sensitive to climatic stress than dominant trees. However climatic effects where an order of magnitude lower than stand density effects over the investigated permanent plot networks, making the benefit of including the effect of climatic conditions on growth partitioning minor. Since adapting management to climatic change is a crucial issue, there is a clear interest to widen investigations in more stressful contexts, e.g. by considering national forest inventory plots (Charru et al., 2010), and by extending current experimental networks to drier or warmer contexts.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.09.020.

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