

Consequences of decreasing the number of cored trees per plot on chronology statistics and climate–growth relationships: a multispecies analysis in a temperate climate

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Abstract: Existing literature investigates the effect of the number of cored trees per plot (N) on chronology statistics. The present study sought to highlight (i) the effect of N on the reliability of both chronology and climate–growth relationships and (ii) its variability across five European tree species with differentiated ecophysiological patterns. Fifty-eight pure, even-aged forests were sampled across France. For each plot, dendroecological investigations were carried out using chronologies built from 28 to three trees. Chronology reliability was studied using the mean intertree correlation (r_{bt}) and the expressed population signal (EPS), whereas the climate–growth relationships were evaluated through the bootstrapped correlation coefficients (BCC). The accuracy of the dendroecological investigations decreased with decreasing N : EPS and BCC approached zero, implying that the signal common to all trees weakened. Thus, most of the significant correlations became nonsignificant when the sample size decreased from 28 to three trees per plot. Differences were found between species. For a given sample size, the shade-intolerant species *Quercus petraea* and *Pinus sylvestris* displayed lower intertree differences in growth-index series (higher r_{bt}) and higher EPS than the shade-tolerant species *Abies alba*, *Fagus sylvatica*, and *Picea abies*. These latter species also displayed a greater sensitivity to sample size decrease, with a stronger BCC weakening and a higher proportion of changes in correlation significance. The EPS threshold of 0.85 was reached for around six to 10 trees for shade-intolerant species versus 20–30 for the shade-tolerant ones and generally corresponded to a mean correlation precision of around 0.06. We finally propose a general method to estimate this precision.

Résumé : La littérature examine l'effet du nombre d'arbres carottés par placette (N) sur les statistiques de la chronologie. La présente étude a cherché à mettre en évidence (i) l'effet de N sur la qualité de la chronologie et de l'estimation des relations cerne–climat, et (ii) sa variabilité sur cinq essences européennes à autécologies contrastées. Cinquante-huit forêts pures et régulières ont été échantillonnées à travers la France. A chaque placette, les études dendroécologiques ont été menées avec des chronologies construites à partir de 28 à trois arbres. La qualité de la chronologie a été étudiée au travers de la corrélation inter-arbre moyenne (r_{bt}) et de l'« expressed population signal » (EPS), alors que les relations cerne–climat ont été évaluées par le calcul des coefficients de corrélation « bootstrapped ». La justesse des analyses dendroécologiques a diminué avec la baisse de N : l'EPS et les BCC se sont rapprochés de zéro, impliquant que le signal commun à tous les arbres s'était affaibli. Par conséquent, la plupart des corrélations significatives sont devenues non-significatives quand la taille de l'échantillon a diminué de 28 à trois arbres par placette. Des différences ont été observées entre les espèces. Pour une taille d'échantillon donnée, les espèces héliophiles *Quercus petraea* et *Pinus sylvestris* ont montré de plus faibles différences inter-arbres dans les séries d'indices de croissance (r_{bt} plus élevés) et de plus forts EPS que les espèces tolérantes à l'ombre *Abies alba*, *Fagus sylvatica* et *Picea abies*. Ces dernières espèces ont été plus sensibles à la baisse de la taille de l'échantillon, avec une plus forte diminution des BCC et une plus forte proportion de changement de significativité. Le seuil d'EPS de 0,85 a été atteint pour environ six à 10 arbres carottés pour les espèces héliophiles, contre 20 à 30 pour les espèces tolérantes à l'ombrage. Nos résultats ont également mis en évidence que, quelque soit l'espèce, le seuil d'EPS de 0,85 correspondait à une précision moyenne des BCC d'environ 0,06. Nous proposons enfin une méthode générale pour estimer cette précision.

Introduction

In temperate and northern ecosystems, tree-ring width has been widely used to investigate the environmental influence on tree growth because it easily provides quantitative and annual retrospective information (Fritts 1976). During the last

two decades, there has been a revival of interest in this proxy with the need to clearly assess the climate–growth relationship instability in the context of climatic change (Briffa et al. 2009; D'Arrigo et al. 2008; Moberg and Jones 2005). Incorrect estimation may reduce the validity of projected forest carbon uptake, growth, and vitality (Lindner et al. 2010).

Received 24 July 2011. Accepted 4 October 2011. Published at www.nrcresearchpress.com/cjfr on 18 November 2011.

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Thus, providing methodological advice to improve the assessment of tree-growth response to climate appears to be a crucial aspect in the field of dendroecological studies.

The variation of ring-width results from interannual changes in environmental conditions and tree physiological processes. Cook (1985) proposed a theoretical linear model classifying the numerous signals influencing ring width into five groups: the age-related growth trend (namely A in Cook (1985)), climatic variations (C), disturbances within a forest community (D1), disturbances originating from outside the community (D2), and residual variations related to other signals (E). In even-aged, pure forests, A, C, and D2 are assumed to be broad-scale signals (i.e., of the same magnitude for all trees), whereas signal D1 is expected to vary among trees due to small-scale heterogeneities in the environmental conditions. At the plot scale (generally less than 1 ha), these local variations are mainly related to stand characteristics such as canopy stratification (Mäkinen and Vanninen 1999; Martín-Benito et al. 2008; Mérian and Lebourgeois 2011) and proximity to the closest stems (Martín-Benito et al. 2010; Misson et al. 2003). As a consequence, it is generally recommended to sample many trees per plot to minimize the strength of the tree-specific signals (D1 and E) and thus emphasize the broad-scale climatic signal (C) when building the growth chronology.

As the chronology accuracy increases with the sample size (Briffa and Jones 1990; Mäkinen and Vanninen 1999), one of the main goals of the sampling strategy is to find the best compromise between limiting the amount of fieldwork and building a reliable chronology, with the level of reliability depending on the purpose of the study and the error margin that researchers are willing to accept. Previous works in this direction have provided useful statistics that are routinely used to quantify the robustness of the chronology such as the mean intertree correlation (r_{bt}) and the expressed population signal (EPS) (Cook 1985; Cook and Kairiukstis 1990; Wigley et al. 1984).

The quality of the climatic signal (C) contained in the rings of trees is expected to increase when coring trees likely to yield good climatic records (Douglass 1939; Cook 1985; Fritts 1976). The most common strategy consists of sampling forest stands growing under limiting climatic conditions, as it permits an accurate chronology to be built from a reduced sample size (Cook and Kairiukstis 1990; Douglass 1939; Fritts 1976; Schulman 1937). For that matter, under temperate climate, a total of 20–30 trees per plot is usually recommended, but this number can be reduced to five to 10 in regions and plots where tree growth depends very much on one limiting factor (Cook and Kairiukstis 1990; Fritts 1976). However, the strength of the climatic signal recorded in the tree rings (C) may also vary among species in relation to differences in their ecophysiological pattern. Species displaying great ability to cope with various local environmental conditions could be assumed to show greater intertree heterogeneity in ring-width series. In a recent plot-scale multispecies analysis, Mérian and Lebourgeois (2011) pointed out that this intertree heterogeneity was related to the ability of tree species to cope with differentiated light levels. Shade-tolerant species are able to grow and survive in low to high levels of

shade, whereas shade-intolerant species grow under low levels of competition for light (Wright et al. 1998). As a consequence, it has been hypothesized that the sample size required to reach a given level of chronology reliability could be lower when studying shade-intolerant species due to a greater homogeneity of canopy structure (Niinemets 2010; Wright et al. 1998). Such specific differences may have strong implications on the sampling strategy, which would have to be adapted to the ecophysiological pattern of the objective species.

This study sought to quantify how the decrease of sample size influenced (i) the chronology reliability and (ii) the assessment of climate–growth relationships for five major European forest tree species characterized by different ecophysiological patterns and growing under temperate conditions. The five studied species were silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and Sessile oak (*Quercus petraea* (Matt.) Liebl.). *Abies alba* and *F. sylvatica* are shade-tolerant species with high sensitivity to summer drought, precipitation, and atmospheric humidity (Becker 1970; Pinto and Gégout 2005). In contrast, *Q. petraea* and *P. sylvestris* are more xerophytic, shade-intolerant species (Misson et al. 2004). Lastly, *P. abies* presents an intermediate shade tolerance and response to summer drought (Lebourgeois et al. 2010; Pinto and Gégout 2005). Previous dendrochronological studies pointed out higher expressed population signal for the shade-intolerant species *Q. petraea* and *P. sylvestris* (Lebourgeois et al. 2005, 2010; Mérian et al. 2011; Mérian and Lebourgeois 2011). The starting hypotheses were that (i) decreasing sample size led to a less accurate estimation of both the climatic signal contained in the chronology and the climate–growth correlations and (ii) ecophysiological traits induced significant differences between species, with a lesser effect of the sample size variation for the shade-intolerant species *Q. petraea* and *P. sylvestris*.

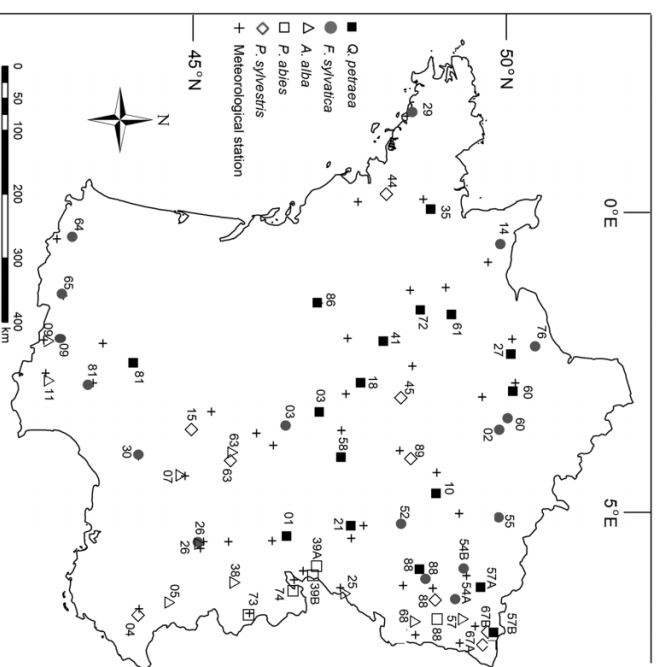
Materials and methods

Study area and climatic data

The 58 plots were sampled between 42°51'52"N and 49°42'39"N and 3°32'34"W and 7°43'46"E in the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR) (Fig. 1). The forests were composed of pure, even-aged, healthy stands. The sample covered a wide range of bioclimatic conditions: oceanic climate in the west ($n = 16$ plots), semicontinental climate in the northeast ($n = 19$), temperate Mediterranean climate in the south ($n = 3$), and mountainous climate ($n = 21$). The variability of climatic conditions and soil properties as previously detailed in Mérian and Lebourgeois (2011) (Supplemental Table S1)¹ are summarized in Table 1. For each stand, climatic data obtained from the nearest meteorological stations of the French National Climatic Network (Météo-France) were considered as representative as possible of the stand weather conditions (Fig. 1). The mean distance between sampled plots and meteorological stations was 23.5 km (standard deviation (SD), 13 km). The difference

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/10.1139/x11-149>.

Fig. 1. Geographical location of the 58 stands of the French network RENECOFOR and the 57 meteorological stations of Métiéo-France. Solid squares, *Q. petraea*; shaded circles, *F. sylvatica*; open triangles, *A. alba*; open squares, *P. abies*; open diamonds, *P. sylvestris*. Each number indicates the administrative French department in which sampling was done. Plus signs, meteorological stations of Métiéo-France.



in altitude was less than 150 m for 71% of the cases and averaged 200 m.

Mean monthly temperature (T) and climatic hydric balance (Hb) were computed for the period 1947–1994. Hb was calculated using the following equation:

$$[1] \quad \text{Hb} = P - \text{PET}$$

where P is the sum of monthly precipitation and PET is the potential evapotranspiration calculated using Turc's formula (Lebourgeois and Piedallu 2005; Turc 1961), defined as

$$[2] \quad \text{PET} = d \times 0.013 \times (\text{Rg} + 50) \times \left(\frac{T}{T + 15} \right)$$

where d is the number of days of the considered month (28, 29, 30, or 31), Rg is the mean daily solar radiation of the considered month (in calories·cm⁻²), and T is the mean monthly temperature.

Tree-ring measurement and standardization

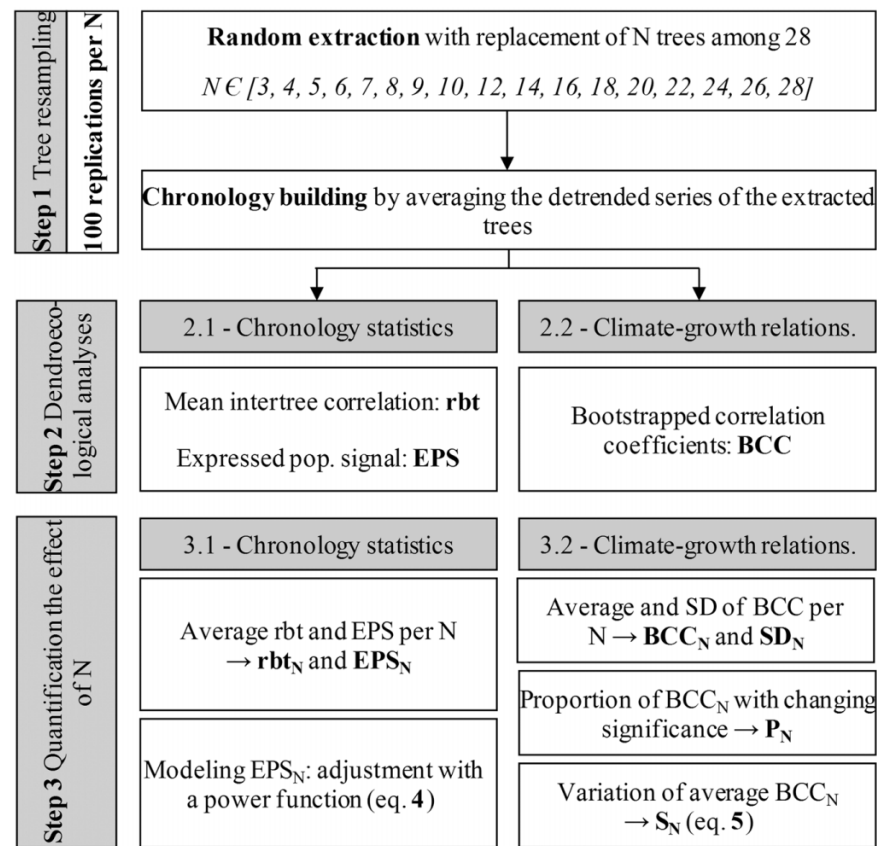
The plot size was 0.5 ha. In 1995, at each plot, 28 dominant trees were cored to the pith at breast height with an incremental borer (one core per tree of 5 cm in diameter; Mäkinen and Vanninen 1999). The ring widths of the 1624 trees were measured, to the nearest 0.01 mm, using a stereo-microscope connected to a microcomputer and the tree-ring program SAISIE (Becker 1989). The individual ring-width series were carefully cross-dated by progressively detecting regional pointer years, defined as those calendar years in

Table 1. Summarized plots characteristics per species.

Species	Altitude (m)	pH	SWC (mm)	Height (m)	Density (no.·ha ⁻¹)	Age	Diameter (cm)	Temperature (°C)			Precipitation (mm)		Hydric balance (mm)	
								Year	January	July	Year	July	Year	July
<i>Quercus petraea</i> (n = 17)	209 (86)	4.4 (0.2)	137 (42)	26.6 (2.2)	561 (175)	85 (22)	39 (6.9)	10.2 (0.7)	2.4 (1.3)	18.4 (0.8)	803 (113)	55 (8)	114 (112)	-69 (10)
	55/330	4.0/4.8	75/200	22.9/30.4	296/892	53/126	22/70	9.0/11.3	0.3/5.0	17.3/20.3	608/1047	46/70	-37/325	-87/-51
<i>Fagus sylvatica</i> (n = 17)	526 (436)	4.9 (0.8)	97 (40)	26.8 (3.4)	408 (185)	91 (29)	40 (7.2)	9.4 (1.8)	2.2 (2.2)	17.2 (1.4)	1085 (346)	65 (11)	419 (353)	-57 (10)
	50/1400	4.2/6.7	45/200	19.4/30.2	203/811	51/157	23/67	4.5/12.8	-2.0/6.6	12.8/19.8	696/2068	43/85	47/1520	-82/-43
<i>Abies alba</i> (n = 10)	1008 (284)	4.8 (0.6)	85 (24)	26.8 (2.1)	460 (77)	97 (30)	50 (8.2)	7.8 (1.4)	0.2 (1.8)	16.3 (1.2)	1268 (197)	80 (17)	673 (194)	-41 (20)
	400/1360	4.2/5.8	53/120	22.4/29.3	364/578	53/166	29/73	5.8/10.3	-1.4/4.0	14.2/18.1	865/1524	55/108	331/896	-70/-10
<i>Picea abies</i> (n = 5)	1148 (381)	4.9 (0.5)	70 (39)	28.1 (5.2)	499 (174)	101 (48)	48 (6.8)	7.0 (1.2)	-1.3 (1.1)	15.4 (1.4)	1493 (393)	108 (21)	897 (421)	-12 (23)
	660/1700	4.3/5.4	25/125	22.0/34.8	369/798	57/179	37/67	4.9/7.7	-3.2/-0.6	13.1/16.4	1070/1980	82/130	460/1466	-41/18
<i>Pinus sylvestris</i> (n = 9)	521 (537)	4.3 (0.4)	86 (43)	22.9 (3.2)	649 (194)	64 (12)	37 (5.1)	9.4 (1.3)	1.5 (1.8)	17.8 (1)	868 (161)	60 (15)	211 (188)	-63 (21)
	38/1670	3.7/5.0	43/160	17.0/26.9	337/997	52/92	28/54	7.6/11.6	-0.7/5.1	16.0/19.0	687/1170	39/92	2/544	-89/-27

Note: Values are expressed as mean (standard deviation), minimum/maximum; pH, pH of the organomineral horizon; SWC, soil water capacity (in mm) calculated according to textural properties, depth, and coarse element percentages. Height, density, age, and diameter are from 1994. Climatic means are from 1961 to 1990. Characteristics are detailed per plot in Supplemental Table S1.¹

Fig. 2. Flowchart of the methodological process (pop, population; SD, standard deviation).



which at least 75% of the cross-dated trees presented at least 10% narrower or wider rings than the previous one (Becker 1989; Lebourgeois et al. 2000; Mérian and Lebourgeois 2011). Absolute dating was checked by the application INTERDAT (Becker 1989; M. Becker and J.L. Dupouey, unpublished), which identifies locations within each ring series that may have erroneous cross-dating.

Using the R freeware (R Development Core Team 2010) and the dplR package (Bunn 2008), tree-ring chronologies were computed and standardized on the maximum period common to all chronologies (1948–1994; 47 years) to emphasize the interannual climatic signal in each individual series. A double-detrending process was thus applied based on an initial negative exponential or linear regression followed by a fitting of a 31-year cubic smoothing spline with 50% frequency response cutoff (Blasing and Duvick 1983; Cook and Peters 1981).

Tree resampling and chronology building

To investigate the effect of the number of cored trees per plot (N), 17 sample sizes were defined, ranging from 28 to three trees (Fig. 2, step 1). For each plot and N modality, the tree resampling consisted of a random extraction with replacement of N trees among 28 (Efron 1979). The detrended series of the extracted trees were averaged by year using a biweighted robust mean to develop a chronology that represented the common high-frequency variation of the individual series (Cook 1985; Fritts 1976). The resampling

procedure was replicated 100 times per sample size modality to obtain a great number of estimates. This method was based on the concept of “chronology saturation” developed in Boucher et al. (2009), which aims to quantify the stability of the objective signal contained in the chronology along with the sample size decrease.

Quantification of the sample size effect

Chronology statistics

For each chronology, rbt and EPS were calculated to quantify, respectively, the strength of the signal common to all trees (Briffa and Jones 1990) and the degree to which the chronology expressed the population chronology (Wigley et al. 1984) (Fig. 2, step 2.1). The EPS was defined as

$$[3] \quad EPS = \frac{rbt}{rbt + \frac{1-rbt}{N}}$$

where N is the number of cored trees per plot, and rbt is the mean intertree correlation. EPS estimates the proximity between the theoretical population chronology and the chronology obtained by averaging the N sampled individual chronologies by reducing the uncommon variability of the N chronologies from $(1 - rbt)$ to $(1 - rbt)/N$ (Briffa and Jones 1990). Thus, EPS ranges from 0 to 1 and yields 1 when the chronology mirrors the population signal.

For each plot and sample size, average rbt and EPS were calculated from the 100 estimates, namely rbt_N and EPS_N

(Fig. 2, step 3.1). To provide EPS values for sample sizes greater than 28, EPS_N was modeled per plot as a function N using the following power function:

$$[4] \quad EPS_N = (a \times N^b + 1)^c$$

The EPS values were then predicted for each plot up to 80 trees (Fig. 2, step 3.1), because greater sample sizes were not found in the literature. Because of the progressive EPS increase with sample size, any threshold must be a subjective choice. However, the value of 0.85 suggested in Wigley et al. (1984) has been and is still widely used by the dendroecologists to assume the chronology reliability. Thus, the minimum sample size that rated an EPS value of 0.85 (*i*) on average over the 100 estimates ($N_{0.85}$) and (*ii*) for 95% of the estimates (N_{95}) was determined for each plot (Table 2).

Climate–growth relationships

Climate–growth relationships were investigated over the period 1948–1994 using the calculation of bootstrapped correlation coefficients (BCC), with chronologies as dependant variables (Guiot 1991) and using the 24 monthly climatic regressors (12 *T* and 12 *Hb* values) organized from September of the previous growing season to August of the current year (Fig. 2, step 2.2). The statistical significance of the BCC was assessed with the package “bootRes” (Zang 2009) by calculating the 95% confidence level based on 1000 bootstrap re-samples of the data (Guiot 1991). For each plot and sample size, climate–growth relationship statistics were calculated per climatic regressor from the 100 estimates of BCC (Fig. 2, step 3.2): mean value (BCC_N) and standard deviation (SD_N). SD_N quantified the mean difference between two sets of BCC obtained from two samples of *N* trees and thus was used as an indicator of the precision of the BCC estimation. BCC_N was considered significant when at least 50% of the estimates were significant.

The effect of decreasing *N* on BCC_N was refined per species by the calculation of the proportion of BCC_N with changing significance between 28 and *N* trees (P_N). Two cases were observed: (*i*) from significant to nonsignificant values (Fig. 3, areas 1) and (*ii*) from nonsignificant to significant values (Fig. 3, areas 2). The sample size related bias in the BCC_N estimation was quantified with the slope S_N of the linear regression, defined as

$$[5] \quad BCC_N = S_N \times BCC_{28}$$

S_N values lower than 1 indicate that BCC approached zero with decreasing *N* (Fig. 3). The *y* intercept was nonsignificant regardless of the species and was thus voluntarily omitted in eq. 5 and the analysis.

Results

Sample size effect on chronology statistics

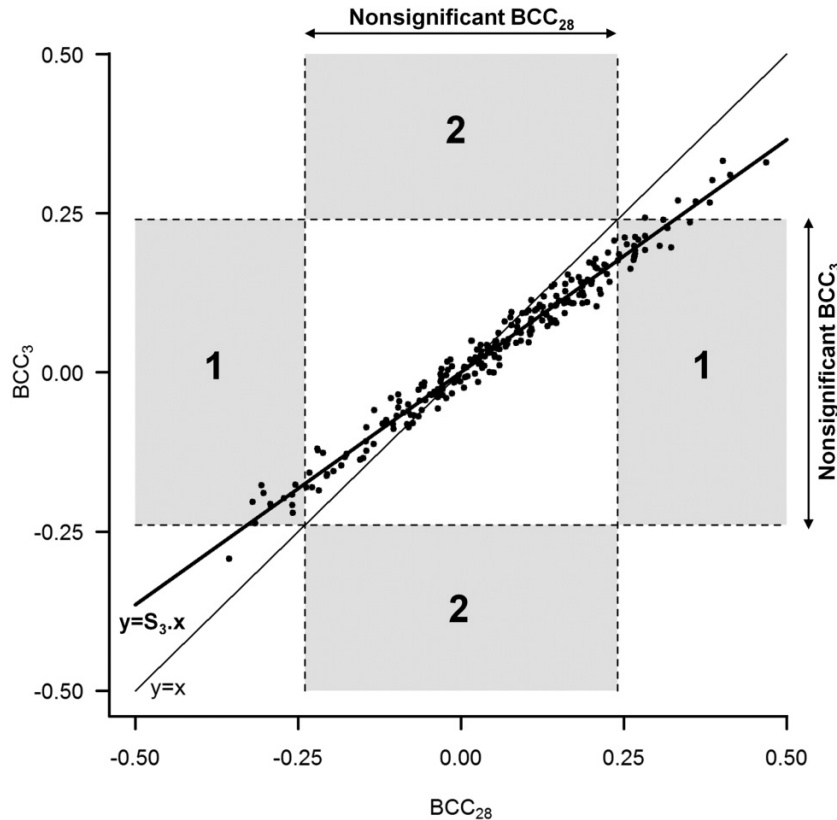
Regardless of the species, the mean intertree correlation (rbt_N) was estimated without sample size related bias, whereas the expressed population signal (EPS_N) decreased exponentially with decreasing *N* (Table 2; Fig. 4). This weakening was more rapid with small sample size and low rbt_N . Strong differences were evident among the five species. *Quercus petraea* and *P. sylvestris* showed the highest rbt_N ,

Table 2. Summarized master chronology statistics and EPS_N model parameters per species.

Species	rbt_N			EPS_N					EPS_N model		
	rbt_3	rbt_{10}	rbt_{38}	EPS_3	EPS_{10}	EPS_{28}	$N_{0.85}$	N_{95}	<i>a</i>	<i>b</i>	<i>c</i>
<i>Quercus petraea</i> (<i>n</i> = 17)	0.54 (0.07)	0.54 (0.07)	0.54 (0.07)	0.77 (0.05)	0.92 (0.02)	0.97 (0.01)	5.6 (1.4)	7.6 (1.9)	-0.252 (0.292)	-0.94 (0.024)	7.697 (5.451)
<i>Fagus sylvatica</i> (<i>n</i> = 17)	0.40/0.70	0.41/0.70	0.41/0.70	0.65/0.87	0.87/0.96	0.95/0.98	3/9	4/12	-1.086/-0.032	-0.976/-0.896	0.504/12.847
<i>Abies alba</i> (<i>n</i> = 10)	0.22 (0.08)	0.22 (0.08)	0.22 (0.08)	0.41 (0.12)	0.71 (0.09)	0.85 (0.08)	26.2 (11.9)	NA	-0.173 (0.046)	-0.847 (0.037)	13.634 (0.487)
<i>Picea abies</i> (<i>n</i> = 5)	0.10/0.45	0.11/0.44	0.12/0.45	0.20/0.70	0.54/0.89	0.78/0.96	7/50	NA	-0.255/-0.078	-0.934/-0.794	12.692/14.539
<i>Pinus sylvestris</i> (<i>n</i> = 9)	0.27 (0.07)	0.27 (0.06)	0.27 (0.06)	0.49 (0.10)	0.77 (0.06)	0.93 (0.02)	18 (6.8)	NA	-0.271 (0.276)	-0.864 (0.041)	10.64 (4.516)
	0.17/0.41	0.16/0.39	0.16/0.39	0.32/0.66	0.65/0.86	0.84/0.95	9/33	NA	-0.881/-0.094	-0.929/-0.8	2.505/13.881
	0.20 (0.05)	0.20 (0.05)	0.20 (0.05)	0.37 (0.09)	0.69 (0.07)	0.83 (0.05)	27 (9.1)	NA	-0.182 (0.035)	-0.841 (0.029)	13.632 (0.339)
	0.15/0.28	0.14/0.27	0.14/0.28	0.26/0.51	0.60/0.78	0.81/0.91	16/41	14.3 (4.4)	-0.231/-0.133	-0.875/-0.812	13.217/14.158
	0.39 (0.10)	0.39 (0.10)	0.39 (0.10)	0.63 (0.09)	0.85 (0.05)	0.95 (0.02)	10.9 (3.8)	7/22	-0.101 (0.026)	-0.927 (0.042)	12.884 (0.202)
	0.27/0.60	0.26/0.60	0.27/0.60	0.48/0.81	0.77/0.94	0.91/0.98	5/16		-0.142/-0.051	-0.982/-0.858	12.546/13.226

Note: Values are expressed as mean (standard deviation), minimum/maximum; *N*, number of trees per plot (17 modalities); *rbt*, mean intertree correlation; EPS_N , expressed population signal; $N_{0.85}$, sample size that yielded the EPS value of 0.85 on average; N_{95} , sample size that yielded the EPS value of 0.85 for 95% of the estimates; *a*, *b*, and *c*, parameters of eq. 4 (see text for details); NA, when N_{95} was > 28 trees per plot. Characteristics are detailed per plot in Supplemental Table S2.

Fig. 3. Illustration of the sample size related bias on the average bootstrapped correlation coefficients (BCC) for *Abies alba*. The thresholds of correlation significance for BCC₃ and BCC₂₈ are indicated by the horizontal and vertical broken lines, respectively; the nonsignificant BCC are located between the broken lines. The shaded areas highlight BCC for which the significance changed when the sample size (N) diminished from 28 to 3 trees: from significant to nonsignificant value in areas 1, and the inverse trend in areas 2. The magnitude of the bias is estimated through the slope S_N of the linear regression $BCC_N = S_N \cdot BCC_{28}$ (eq. 5, see text for details); a slope lower than 1 indicates that BCC approached zero with decreasing N .



with respective values of 0.54 and 0.39, versus 0.20 to 0.27 for the three other species (*A. alba*, *F. sylvatica*, and *P. abies*). As a consequence of the EPS formula (eq. 3), *Q. petraea* and *P. sylvestris* also displayed the highest EPS _{N} , with, for example, an EPS₁₀ of 0.92 and 0.85, whereas *A. alba*, *F. sylvatica*, and *P. abies* rated 0.77, 0.71, and 0.69 (Table 2).

To provide EPS values for sample sizes >28 , EPS _{N} was modeled as a function of N (eq. 4). Regardless of the plots, R^2 was >0.995 (Table 2; Supplemental Table S2)¹ and the parameters a , b , and c were highly significant (p value $< 10^{-7}$, data not shown), which tended to prove that a power function was accurate in describing EPS _{N} trends. The sample size that yielded the EPS threshold of 0.85 on average ($N_{0.85}$) was always <28 trees for *Q. petraea* and *P. sylvestris* but greater than this value in 1 case out of 10 for *A. alba*, 4/17 for *F. sylvatica*, and 2/5 for *P. abies* (Table 2). Nevertheless, $N_{0.85}$ was systematically reached before 50 trees and was set around 6 for *Q. petraea*, 11 for *P. sylvestris*, 18 for *A. alba*, and 27 for both *F. sylvatica* and *P. abies*. In the same way, the sample size that rated an EPS of 0.85 for 95% of the estimates (N_{95}) was >28 trees in 2 cases out of 10 for *A. alba*, 9/17 for *F. sylvatica*, and 4/5 for *P. abies*. When both $N_{0.85}$ and N_{95} were available (i.e., when they were both <28 trees), N_{95} was around 25% greater than $N_{0.85}$.

Sample size effect on climate–growth relationship statistics

Strength and significance of the correlations

The general effect of decreasing sample size consisted of a weakening of the climate–growth correlations. Indeed, S_N (i.e., the slope of the linear regression defined in eq. 5 that quantified the sample size related bias in the BCC estimation when the sample size decreased from 28 to N trees) was systematically <1 , which implied that BCC approached zero (Fig. 3). At the same time, the proportion of BCC with changing significance between 28 and N trees (P_N) increased with decreasing N (Fig. 5b). Because of the BCC weakening, these changes were observed strictly from significant to nonsignificant values (Fig. 3). Both the BCC weakening and the P_N increase were more rapid with small sample size. Focusing on P_N , the augmentation was particularly strong when N was <10 trees (Fig. 5b).

S_N and P_N trends differed among the five species. Two groups were evidenced: *Q. petraea* and *P. sylvestris* displayed a rather low sensitivity to the sample size decrease, with S_N values of 0.89 and 0.85 when coring three trees (Fig. 5a). In contrast, *A. alba*, *F. sylvatica*, and *P. abies* showed greater weakenings, with S_N values around 0.7. This species-specific

Fig. 4. Mean trends in chronology statistics per species. N , number of cored trees per plot; rbt , mean intertree correlation; EPS, expressed population signal; black curve, mean predicted EPS_N per species; dark grey area, standard deviation (SD) of the mean predicted EPS_N ; grey curve, mean observed rbt_N per species; light grey area, standard deviation of the mean observed rbt_N . The horizontal line denotes the EPS threshold of 0.85. The vertical line denotes the maximum number of trees observed per plot (28 trees).

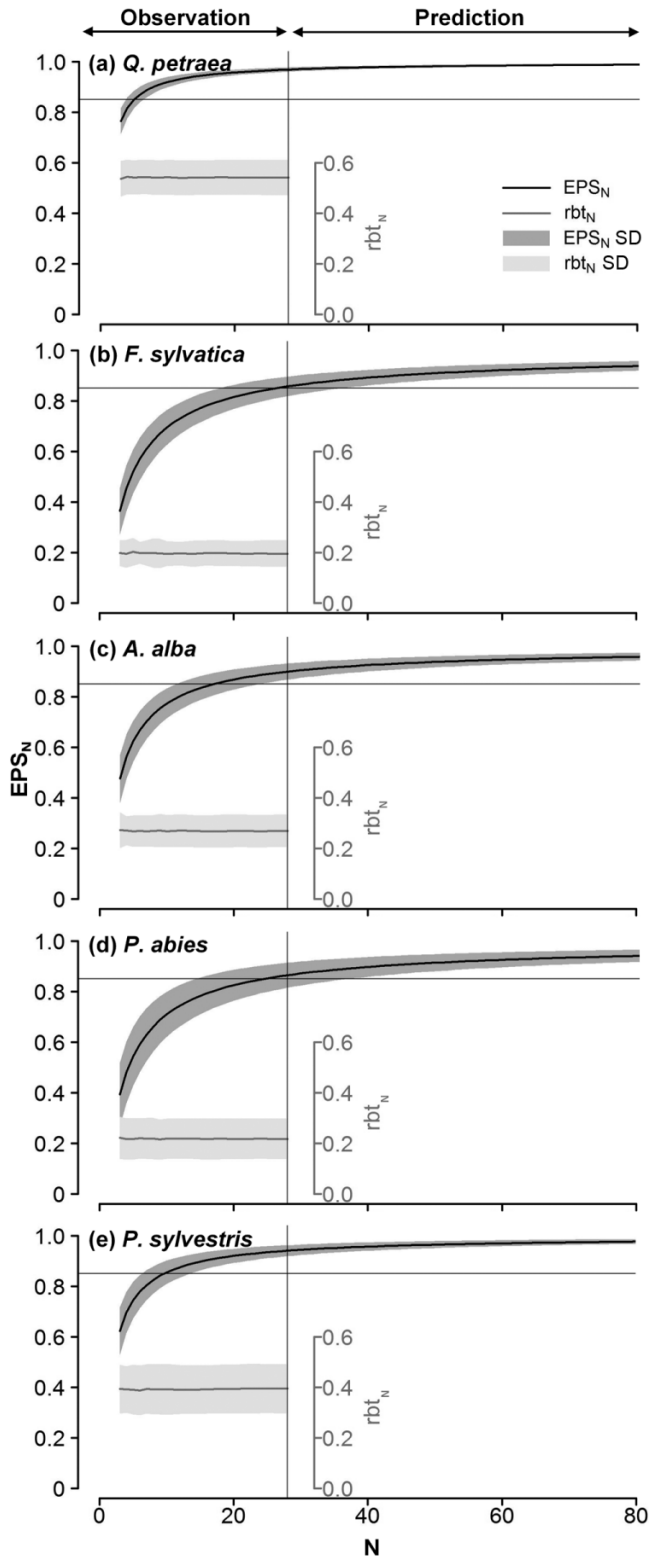
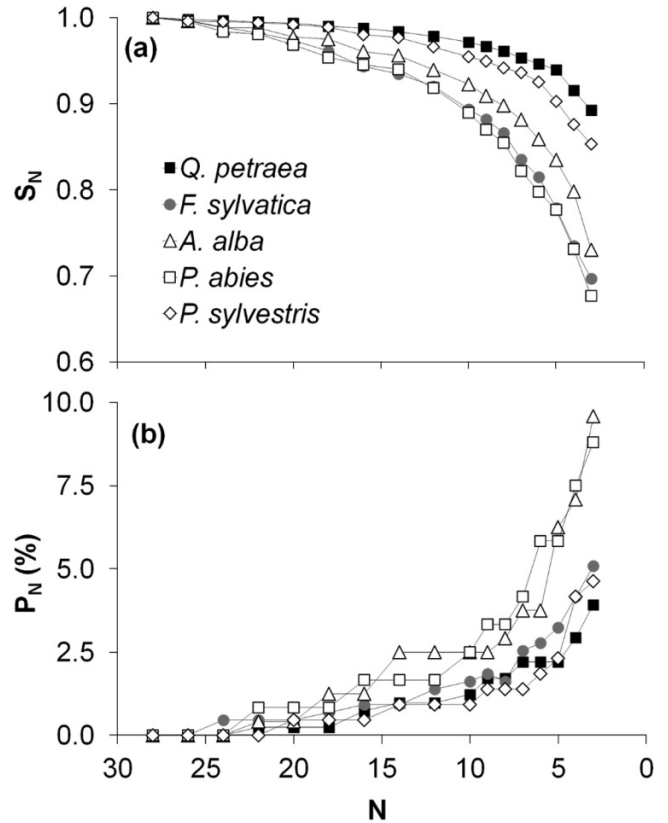


Fig. 5. Effect of decreasing sample size on bootstrapped correlation coefficient (BCC) statistics per species. S_N , slope of the linear regression $BCC_N = S_N \cdot BCC_{28}$ (eq. 5, see text for details); P_N , proportion of changes in BCC significance between 28 and N trees (in %).



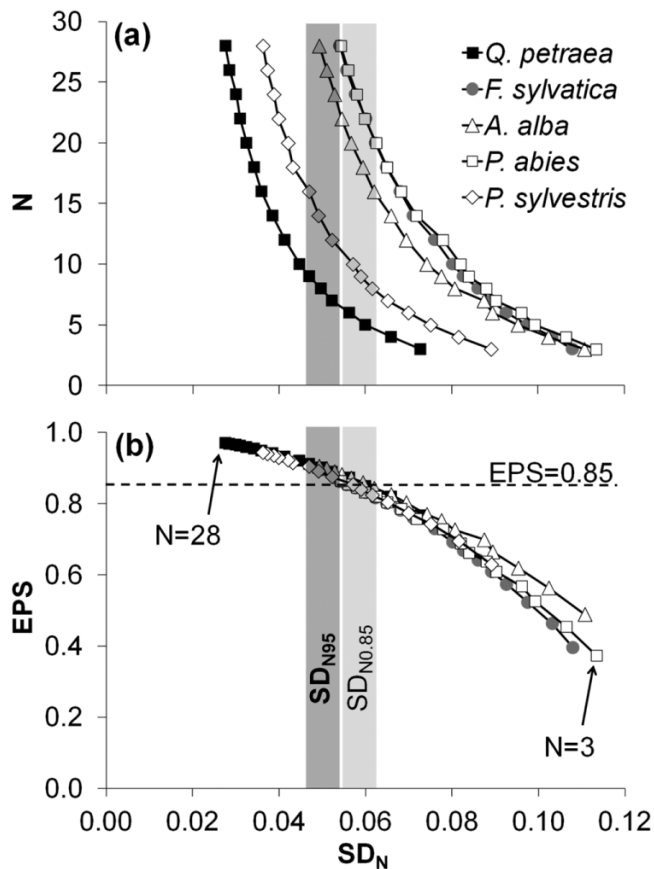
pattern was also pointed out for P_N , albeit the response of *F. sylvatica* was closer to those of *Q. petraea* and *P. sylvestris* (Fig. 5b). For a given sample size, P_N for *A. alba* and *P. abies* was generally twice that of the three other species. For example, P_3 reached around 9% for *A. alba* and *P. abies* versus 4% for the others.

Precision of the correlations

The 100 replications of the tree resampling procedure allowed calculating the standard deviation of the average BCC value from the 100 estimations (SD_N). Decreasing sample size from 28 to three trees led to a SD_N increase of around 0.05 for the five species (Fig. 6a). SD_N ranged from 0.03 to 0.06 when coring 28 trees and increased exponentially up to 0.07–0.11 for three trees. Although the SD_N increase was rather similar among the five species, *A. alba*, *F. sylvatica*, and *P. abies* displayed consistently higher values than *Q. petraea* and *P. sylvestris*. For instance, SD_3 reached 0.110 for *Abies–Fagus–Picea* versus 0.073 for *Q. petraea* and 0.082 for *P. sylvestris*.

Because of the positive relationship between N and EPS, SD_N increased with decreasing EPS (Fig. 6b). For a given EPS, all of the species displayed very similar SD_N values. The precision of the climate–growth correlations established from chronologies rating an EPS of 0.85 on average ($SD_{N0.85}$) varied between 0.056 and 0.062. SD_{N95} corresponded to slightly lower values, ranging from 0.049 to 0.056 (Fig. 6b).

Fig. 6. Relationships between the standard deviation of BCC among the 100 replications (SD_N) and (a) sample size (N) and (b) expressed population signal (EPS). $SD_{N_{0.85}}$ and $SD_{N_{95}}$, standard deviations of BCC among the 100 replications when $N = N_{0.85}$ and $N = N_{95}$, respectively.



Discussion

The interannual ring-width variation depends on numerous environmental signals and tree physiological processes (Cook 1985; Fritts 1976; Schulman 1937). The aim of this study was to analyze the effect of decreasing the number of cored trees per plot on the strength of the signal common to all trees. This signal strength, estimated through the calculation of EPS and rbt, was assumed to be linked to climatic factors (Briffa and Jones 1990; Cook 1985; Mäkinen and Vanninen 1999) and thus was related to the sample size related variations in the climate–growth relationship assessment. However, Mäkinen and Vanninen (1999) reminded us that EPS and rbt “are not capable of providing any information about the real reasons for this [common] variability.”

General sample size effect on accuracy of dendroecological investigations

As expected, decreasing sample size affected the strength of the common signal contained in the chronology (Cook and Kairiukstis 1990; Mäkinen and Vanninen 1999; Wigley et al. 1984). Estimation of rbt was not biased by sample size, which could be expected as the similarity between two trees depended directly on the variability of the biotic and

abiotic conditions within the plot. EPS decreased with decreasing N , with a very rapid diminution below 10–15 trees. Thus, the chronologies established from 28 trees per plot gave the most accurate estimation of the common signal (Fig. 4; Table 2) and were considered as the reference to quantify the effect of decreasing N on climate–growth relationships. However, the analysis provided evidence that the chronologies were not always saturated for a sample size of 28 trees, especially for the shade-tolerant species *A. alba*, *F. sylvatica*, and *P. abies*, which displayed EPS_{28} values below the threshold of 0.85 suggested in Wigley et al. (1984) (Table 2; Supplemental Table S2).¹

Systematic variations in climate–growth relationship statistics were reported throughout the five species. Decreasing sample size led to a weakening of the correlation coefficients (Figs. 3, 5a). BCC approached zero, explaining that the changes in significance were strictly observed from significant to nonsignificant values (Fig. 5b; Supplemental Fig. S1).¹ The slope of the linear regression defined in eq. 5 (S_N) and the proportion of BCC with changing significance (P_N) exponentially increased with decreasing N , with a rather clear threshold around 10 trees for P_N . In relation to the EPS trends, these results tended to confirm that the signal common to all trees was mainly attributable to climate forcing (Briffa and Jones 1990; Fritts 1976). Such sample size related bias might have important consequences when assessing the role of climate on tree growth and vitality. The main implications of dendroecological investigations from small sample sizes are (i) a general underestimation of the climate sensitivity and (ii) a risk of estimating “false” nonsignificant correlations.

Species-specific modulations of the sample size effect

This analysis clearly defined two groups of species. Dendroecological investigations were less sensitive to sample size variations for the shade-intolerant species *Q. petraea* and *P. sylvestris* than for the shade-tolerant species *F. sylvatica*, *A. alba*, and *P. abies*. Indeed, *Q. petraea* and *P. sylvestris* displayed higher rbt and EPS than *F. sylvatica*, *A. alba*, and *P. abies*, which suggested a stronger common signal for the two first species (Fig. 4; Table 1). This lower intertree variability certainly explained that the chronology signal was less affected by tree removal. As a consequence, the climate–growth relationships were also more stable among the sample size modalities for *Q. petraea* and *P. sylvestris* than for *F. sylvatica*, *A. alba*, and *P. abies* (Fig. 5).

Such shade tolerance – shade intolerance opposition in climate–growth relationship stability has already been observed when focusing on tree size (Mérian and Lebourgeois 2011; Niinemets 2010). Size-mediated sensitivity to climate was evidenced for shade-tolerant species (Mérian and Lebourgeois 2011; Piutti and Cescatti 1997), whereas literature gave contradictory results on shade-intolerant species (Chhin et al. 2008; De Luis et al. 2009). In a previous study (Mérian and Lebourgeois 2011), these greater intertree differences in growth pattern for the shade-tolerant species *F. sylvatica*, *A. alba*, and *P. abies* were related to higher canopy stratification and variability in levels of shade. The canopy heterogeneity was assumed to induce microclimatic variations from one tree to another (Leuzinger and Korner 2007; Ma et al. 2010) and decrease the signal-to-noise ratio. For instance,

the most dominant trees, which did not benefit from temperature buffering of the canopy (Aussenac 2000), often displayed a higher sensitivity to summer water under temperate conditions (Martín-Benito et al. 2008; Mérian and Lebourgeois 2011; Piutti and Cescatti 1997). As a conclusion, such interspecific differences in the sample size effect on dendroecological investigations imply that (i) for a given number of trees per plot, the accuracy of the climate sensitivity estimation might strongly vary from one species to another and (ii) the sampling effort has to be adapted to the species autecology.

Sample size related precision in the assessment of bootstrapped correlation coefficients (BCC)

The 100 consecutive random extractions of N trees per plot (Boucher et al. 2009; Efron 1979) allowed estimation of the mean absolute difference between BCC established from two samples of N trees (SD_N). As expected, SD_N increased with decreasing sample size (Fig. 6a) and EPS (Fig. 6b). This resampling method provided evidence that the EPS threshold of 0.85 suggested in Wigley et al. (1984) corresponded to a SD_N of around 0.06, regardless of the species ($SD_{N0.85}$; Fig. 6b). This implied that for a given even-aged, pure stand, two chronologies built from independent samples and rating an EPS of 0.85 would give rather consistent patterns of BCC but would not allow clear assessment of the strength of the climate–growth correlations with potential changes in BCC significance (Supplemental Fig. S1).¹ Such sample size related precision in the assessment of BCC should be taken into account when performing comparisons of climate–growth relationships (among species, climatic contexts, periods, etc.). The dendroecologists must carefully question the minimum number of trees to core per plot to ensure that sample size related imprecisions will be below the expected differences among the compared climate–growth relationships; as a consequence, the SD_N threshold depends greatly on the purpose of the study. The present analysis provides the relationships between this precision and both sample size and EPS for five major European species growing under temperate conditions (Fig. 6). Such curves might help in estimating the minimum sample size required for a given level of precision.

Nevertheless, it has to be kept in mind that (i) these curves were established on individual chronologies of 47-year length and (ii) the sample size can also be questioned in terms of chronology length. For a given number of trees per plot, the precision of the climate–growth relationship estimations can be expected to increase with chronology length. The standard error diminishes with increasing chronology length, leading to significant BCC, despite low values. Because of the inter-annual correlation over a long growth-index series, the correlation significance would be reached for lower BCC values than those observed when the values in the sample are statistical independent.

If the number of cored trees per plot is imposed by others constraints (financial, temporal, etc.), then the precision of the BCC estimation can be assessed with a bootstrap procedure applied on the sampled trees (Efron 1979). The size of each subsample has to be the same as that of the initial sample to avoid bias (Efron 1983). Replicated T times, this resampling procedure yields T sets of BCC from which the

mean of the climate–growth relationship and its SD (i.e., the precision) will be estimated. Even if the estimations of both the BCC and SD did not change significantly beyond 30 replications (data not shown), increasing the number of estimations to ensure the robustness of the findings is recommended. As this method also provides confidence limits for each BCC, statistical significance tests can be applied to explore differences in response to climate among plots.

Acknowledgements

We thank the European Commission, the French Agricultural Ministry, the French National Institute of Forest Research, and the French National Forest Office for providing funds to conduct this research (contract DG VI, n19760FR0030) and Météo France for their helpful technical assistance in selection of the meteorological stations. We sincerely thank the foresters of the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR) who collected and made available the data used in this study.

References

- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Ann. For. Sci.* **57**(3): 287–301. doi:10.1051/forest:2000119.
- Becker, M. 1970. Transpiration et comportement vis-à-vis de la sécheresse de jeunes plants forestiers (*Abies alba* Mill., *Picea abies* (L.) Karsten., *Pinus nigra* Arn. ssp. *laricio* Poir., *Pinus strobus* L.). [Transpiration and drought behaviour of some forest seedlings (*Abies alba* Mill., *Picea abies* (L.) Karsten., *Pinus nigra* Arn. ssp. *laricio* Poir., *Pinus strobus* L.).] *Ann. For. Sci.* **27**(4): 401–420. doi:10.1051/forest/19700404.
- Becker, M. 1989. The role of climate on present and past vitality of silver fir forests in the Vosges Mountains of northeastern France. *Can. J. For. Res.* **19**(9): 1110–1117. doi:10.1139/x89-168.
- Blasing, T.J., and Duvick, D.N. 1983. Filtering the effects of competition from ring-width series. *Tree-Ring Res.* **43**: 19–30.
- Boucher, E., Begin, Y., and Arseneault, D. 2009. Hydro-climatic analysis of mechanical breakups reconstructed from tree-rings, Necopastic watershed, northern Quebec, Canada. *J. Hydrol. (Amst.)*, **375**(3–4): 373–382. doi:10.1016/j.jhydrol.2009.06.027.
- Briffa, K.R., and Jones, P.D. 1990. Basic chronology statistics and assessment. In *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, the Netherlands. pp. 137–152.
- Briffa, K.R., van der Schrier, G., and Jones, P.D. 2009. Wet and dry summers in Europe since 1750: evidence of increasing drought. *Int. J. Climatol.* **29**(13): 1894–1905. doi:10.1002/joc.1836.
- Bunn, A.G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**(2): 115–124. doi:10.1016/j.dendro.2008.01.002.
- Chhin, S., Hogg, E.H.T., Lieffers, V.J., and Huang, S. 2008. Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. *For. Ecol. Manage.* **256**(10): 1692–1703. doi:10.1016/j.foreco.2008.02.046.
- Cook, E.R. 1985. A time series analysis approach to tree ring standardization. Faculty of the School of Renewable Natural Resources, University of Arizona, Tucson, Arizona.
- Cook, E.R., and Kairiukstis, L.A.E. 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Cook, E.R., and Peters, K. 1981. The smoothing spline: a new

- approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bull.* **41**: 45–53.
- D'Arrigo, R., Wilson, R., Liepert, B., and Cherubini, P. 2008. On the 'divergence problem' in northern forests: a review of the tree-ring evidence and possible causes. *Global Planet. Change*, **60**(3–4): 289–305. doi:10.1016/j.gloplacha.2007.03.004.
- De Luis, M., Novak, K., Cufar, K., and Raventos, J. 2009. Size-mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. *Trees Struct. Funct.* **23**(5): 1065–1073.
- Douglass, A.E. 1939. Typical site of trees producing the best crossdating. *Tree-Ring Res.* **6**(2): 10–11.
- Efron, B. 1979. Bootstrap methods: another look at the jackknife. *Ann. Stat.* **7**(1): 1–26. doi:10.1214/aos/1176344552.
- Efron, B. 1983. Model selection and the bootstrap. *Math. Soc. Sci.* **5**(2): 236.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, London, New York, San Francisco.
- Guiot, J. 1991. The bootstrapped response function. *Tree-Ring Bull.* **51**: 39–41.
- Lebourgeois, F., and Piedallu, C. 2005. Appréhender le niveau de sécheresse dans le cadre des études stationnelles et de la gestion forestière à partir d'indices bioclimatiques. *Rev. For. Fr.* **57**(4): 331–356.
- Lebourgeois, F., Becker, M., Chevalier, R., Dupouey, J.L., and Gilbert, J.M. 2000. Height and radial growth trends of Corsican pine in western France. *Can. J. For. Res.* **30**(5): 712–724. doi:10.1139/x00-001.
- Lebourgeois, F., Bréda, N., Ulrich, E., and Granier, A. 2005. Climate–tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees Struct. Funct.* **19**(4): 385–401.
- Lebourgeois, F., Rathgeber, C.B.K., and Ulrich, E. 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *J. Veg. Sci.* **21**(2): 364–376. doi:10.1111/j.1654-1103.2009.01148.x.
- Leuzinger, S., and Korner, C. 2007. Tree species diversity affects canopy leaf temperatures in a mature temperate forest. *Agric. For. Meteorol.* **146**(1–2): 29–37. doi:10.1016/j.agrformet.2007.05.007.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolstrom, M., Lexer, M.J., and Marchetti, M. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manage.* **259**(4): 698–709. doi:10.1016/j.foreco.2009.09.023.
- Ma, S.Y., Concilio, A., Oakley, B., North, M., and Chen, J.Q. 2010. Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *For. Ecol. Manage.* **259**(5): 904–915. doi:10.1016/j.foreco.2009.11.030.
- Mäkinen, H., and Vanninen, P. 1999. Effect of sample selection on the environmental signal derived from tree-ring series. *For. Ecol. Manage.* **113**(1): 83–89. doi:10.1016/S0378-1127(98)00416-2.
- Martín-Benito, D., Cherubini, P., del Río, M., and Canellas, I. 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees Struct. Funct.* **22**(3): 363–373.
- Martín-Benito, D., Del Río, M., Heinrich, I., Helle, G., and Canellas, I. 2010. Response of climate–growth relationships and water use efficiency to thinning in a *Pinus nigra* afforestation. *For. Ecol. Manage.* **259**(5): 967–975. doi:10.1016/j.foreco.2009.12.001.
- Mérian, P., and Lebourgeois, F. 2011. Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. *For. Ecol. Manage.* **261**(8): 1382–1391. doi:10.1016/j.foreco.2011.01.019.
- Mérian, P., Bontemps, J.D., Bergès, L., and Lebourgeois, F. 2011. Spatial variation and temporal instability in climate–growth relationships of sessile oak (*Quercus petraea* [Matt.] Liebl.) under temperate conditions. *Plant Ecol.* **212**(11): 1855–1871. doi:10.1007/s11258-011-9959-2.
- Misson, L., Vincke, C., and Devillez, F. 2003. Frequency responses of radial growth series after different thinning intensities in Norway spruce (*Picea abies* (L.) Karst.) stands. *For. Ecol. Manage.* **177**(1–3): 51–63. doi:10.1016/S0378-1127(02)00324-9.
- Misson, L., Rathgeber, C., and Guiot, J. 2004. Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model. *Can. J. For. Res.* **34**(4): 888–898. doi:10.1139/x03-253.
- Moberg, A., and Jones, P.D. 2005. Trends in indices for extremes in daily temperature and precipitation in central and western Europe, 1901–99. *Int. J. Climatol.* **25**(9): 1149–1171. doi:10.1002/joc.1163.
- Niinemets, U. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol. Res.* **25**(4): 693–714. doi:10.1007/s11284-010-0712-4.
- Pinto, P.E., and Gégout, J.C. 2005. Assessing the nutritional and climatic response of temperate tree species in the Vosges Mountains. *Ann. For. Sci.* **62**(7): 761–770. doi:10.1051/forest:2005068.
- Piutti, E., and Cescatti, A. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Can. J. For. Res.* **27**(3): 277–284. doi:10.1139/x96-176.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org>.
- Schulman, E. 1937. Selection of trees for climatic study. *Tree-Ring Res.* **3**(3): 22–23.
- Turc, L. 1961. Evaluation des besoins en eau d'irrigation. Evapotranspiration potentielle. *Ann. Agron.* **12**(1): 13–49.
- Wigley, T.M., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol.* **23**(2): 201–213. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.
- Wright, E.F., Coates, K.D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Can. J. For. Res.* **28**(6): 871–886. doi:10.1139/x98-055.
- Zang, C. 2009. bootRes: bootstrapped response and correlation functions. R package version 0.2. Available at <http://cran.r-project.org/web/packages/bootRes/index.html>.