

# An Approach for Quantifying and Correcting Sample Size-Related Bias in Population Estimates of Climate-Tree Growth Relationships

Pierre Mérian, Didier Bert, and François Lebourgeois

**Abstract:** Dendroecology is based on the estimation of target population climate sensitivity from a finite number of trees ( $N$ ). Recent studies showed a sample size-related bias in the estimations of climate-tree growth relationships, decreasing sample size leading to a weakening of the bootstrapped correlation coefficients. The present analysis points out that the bias equals the squared root of the expressed population signal of the growth chronology built from  $N$  trees and then proposes a correction factor to accurately estimate the population sensitivity to climate. The interests, limits, and implications of this correction are illustrated from 504 individual growth chronologies of silver fir (*Abies alba* [Mill.]) sampled in the Jura Mountains (France) along an altitudinal gradient of increasing climate forcing. This data set was split into three groups of 168 trees (low, medium, and high elevation). Our results show that the signal common to all trees strengthened with increasing climate forcing and that the accuracy of the correction slightly decreased with both decreasing sample size and climate forcing. Corrected bootstrapped correlation coefficients still underestimated the strength of the population climate-tree growth relationships when less than 10 trees were used at low elevation against 4 at high altitude. FOR. SCI. 59(4):444–452.

**Keywords:** tree sampling bias, expressed population signal, chronology variance, correlation function, *Abies alba*

TREE-RING CHRONOLOGIES HAVE BEEN WIDELY USED in recent decades either for estimating climate sensitivity and its temporal stability (e.g., Wilson et al. 2007, Büntgen et al. 2008b, D'Arrigo et al. 2008, Carrer et al. 2010, Lebourgeois et al. 2011, Mérian et al. 2011) or for reconstructing past climates, particularly temperature (e.g., Büntgen et al. 2008a, 2008b, Briffa et al. 2009, D'Arrigo et al. 2009). Incorrect estimation of climate-tree growth relationships would certainly reduce the validity of both climate reconstructions and projected forest growth and vitality. For that matter, the number of scientific publications dealing with methods in dendrochronology has strongly increased for 10 years to refine the estimation of the climate control of radial growth and provide accurate reconstructions and projections (e.g., Mäkinen and Vanninen 1999, Loehle 2009, Bontemps and Esper 2011, Mérian and Lebourgeois 2011a).

Dendroecological studies aim to estimate the climate sensitivity of a target population from a sample, i.e., a finite number of cored trees accurately selected to be as representative as possible of the population. The sample size often results from a compromise between the precision of the population response estimation and practical constraints (financial, temporal, and other). In a recent plot-scale analysis (0.5 ha), Mérian and Lebourgeois (2011a) gave evidence of

a sample size-related bias in the estimation of climate-tree growth relationships of the dominant trees. Decreasing the number of cored trees per plot led to a general weakening of the bootstrapped correlation coefficients (BCC) (Blasing et al. 1984), implying an underestimation of the climate sensitivity and a risk of estimating “false” nonsignificant correlations (Mérian et al. 2012).

Mérian and Lebourgeois (2011a) quantified this bias through the slope  $S$  of the linear regression between the BCC established with a growth chronology built from the maximum sample size (28 trees) and  $N$  trees ( $N < 28$ ). As a consequence of the sensitivity weakening,  $S$  was systematically  $< 1$  and was found to exponentially decrease with decreasing  $N$ . Because the climatic series used to calculate the BCC remained the same among the sample sizes, the variation in the correlation strength can be attributed to changes in the statistical properties of the growth chronology. For that matter, Shiyatov et al. (1990) reported a nonuniform variance within the growth chronology owing to changing sample size along the covered period, the highest variance being related to the smallest size.

In the present study, we sought to mathematically quantify the bias  $S$  to propose a correction of the BCC and improve the estimation of the population response to climate from a finite sample. Based on previous studies

Manuscript received May 2, 2012; accepted August 17, 2012; published online October 11, 2012; <http://dx.doi.org/10.5849/forsci.12-047>.

Pierre Mérian (merianpierre@gmail.com), AgroParisTech, ENGREF, National Institute for Agronomic Research/AgroParisTech, Laboratoire d'Etude des Ressources Forêt-Bois (LERFoB), Nancy, France. Didier Bert (bert@pierroton.inra.fr), INRA, BIOGECO, University of Bordeaux, Bordeaux, France. François Lebourgeois (francois.lebourgeois@agroparistech.fr), AgroParisTech, ENGREF, National Institute for Agronomic Research/AgroParisTech Laboratoire d'Etude des Ressources Forêt-Bois (LERFoB), Nancy, France.

**Acknowledgments:** The ring-width data come from a dendroecological study focused on silver fir declining in the Jura Mountains. It was funded by the “Direction de l'Espace rural et de la Forêt,” in the framework of the DEFORPA program and the National Institute for Agronomic Research. The first author was funded by a PhD grant from the French Ministry of High Education and Scientific Research. The authors gratefully thank L. Bergès, J.D. Bontemps, and R. Bertrand for comments and advice on statistical procedures, R. Schippfer for his helpful technical contribution on the field, and also M. Becker and F. Gérémia.

Copyright © 2013 by the Society of American Foresters.

(Schulman 1954, Shiyatov et al. 1990), we hypothesized that decreasing the number of trees used to build the growth chronology led to a systematic increase of the growth chronology variance, which induced an artificial weakening of the BCC. The accuracy and implications of such correction on the climate sensitivity estimation was then illustrated through the calculation of correlation functions from various sample sizes (3–168 trees) for three populations of silver fir (*Abies alba* [Mill.]) established along an altitudinal gradient of an increasing climate forcing (Bert 1993). This sampling design allowed testing of the correlation-correction method under various climatic contexts to confirm its universality. We hypothesized that the strength of the signal common to all trees increased with increasing climate forcing (Schulman 1937, Fritts 1976), implying both a lower sample size-related bias (Mérian and Lebourgeois 2011a) and a more accurate correlation-correction under limiting climate.

## Methods

### Mathematical Formulation of the Sample Size-Related Bias

In this section, we present the steps to formulate the bias and the resulting correction factor. When a growth chronology is built from  $N$  trees, the variance of each individual indexed series is composed of the variance of the signal common to all trees within the sampled population ( $\sigma_{\text{POP}}^2$ ) and the variance of the individual signals is considered as noise in dendrochronological studies ( $\sigma_{\text{NOS}}^2$ ) (Fritts 1976, Cook 1985). When the individual series is averaged, the variance of noise is reduced to  $\sigma_{\text{NOS}}^2/N$ , whereas the common variance remains unaffected (Wigley et al. 1984, Briffa and Jones 1990). Thus, the variance of a growth chronology ( $\sigma_{\text{CHR}}^2$ ) can be expressed as

$$\sigma_{\text{CHR}}^2 = \sigma_{\text{POP}}^2 + \frac{\sigma_{\text{NOS}}^2}{N} \quad (1)$$

Let POP be the theoretical growth chronology of the target population, i.e., the growth chronology built from the individual series of all trees of the population. By definition, as  $N$  is close to infinite, the chronology signal is free from any noise and strictly reflects the growth variation common to all trees (Fritts 1976, Wigley et al. 1984). The variance of POP is thus  $\sigma_{\text{POP}}^2$ . Let CHR be the growth chronology built from a representative sample of  $N$  trees within the target population. The variance of CHR is composed of the variances of the signal common to all trees and the residual noise (Wigley et al. 1984, Briffa and Jones 1990). Its variance ( $\sigma_{\text{CHR}}^2$ ) is equivalent to Equation 1. The hypothesized sample size-related increase in the CHR variance with decreasing  $N$  ( $\Delta_{\sigma^2}$ ) can be formulated with the ratio

$$\Delta_{\sigma^2} = \frac{\sigma_{\text{CHR}}^2}{\sigma_{\text{POP}}^2} \quad (2)$$

From Equation 1, Equation 2 becomes

$$\Delta_{\sigma^2} = \frac{\sigma_{\text{POP}}^2 + \frac{\sigma_{\text{NOS}}^2}{N}}{\sigma_{\text{POP}}^2} = 1 + \frac{\sigma_{\text{NOS}}^2}{\sigma_{\text{POP}}^2 \times N} \quad (3)$$

The signal/noise ratio of CHR ( $\text{SNR}_{\text{CHR}}$ ) is one of the most common statistics used in dendrochronology to measure the signal strength relative to noise (Fritts 1976, Wigley et al. 1984). Its formula, previously described and discussed in Fritts (1976) and Briffa and Jones (1990), is defined as the ratio between the variances of the signal common to all trees of the sampled population and the reduced noise

$$\text{SNR}_{\text{CHR}} = \sigma_{\text{POP}}^2 \times \frac{N}{\sigma_{\text{NOS}}^2} \quad (4)$$

According to Equation 4, Equation 3 is equivalent to

$$\Delta_{\sigma^2} = 1 + \frac{1}{\text{SNR}_{\text{CHR}}} \quad (5)$$

$\Delta_{\sigma^2}$  can also be formulated in terms of the expressed population signal ( $\text{EPS}_{\text{CHR}}$ ), another widely used statistic to quantify the growth chronology quality (Wigley et al. 1984). As reported by Briffa and Jones (1990),  $\text{EPS}_{\text{CHR}}$  is formally equivalent to

$$\text{EPS}_{\text{CHR}} = \frac{\text{SNR}_{\text{CHR}}}{1 + \text{SNR}_{\text{CHR}}} \quad (6)$$

Using Equation 6, Equation 5 becomes

$$\Delta_{\sigma^2} = \frac{1}{\text{EPS}_{\text{CHR}}} \quad (7)$$

According to Equation 2, we suggest the following factor for correcting the artificial increase of the CHR variance built from  $N$  trees sampled within the target population

$$\sigma_{\text{POP}}^2 = \sigma_{\text{CHR}}^2 \times \text{EPS}_{\text{CHR}} \quad (8)$$

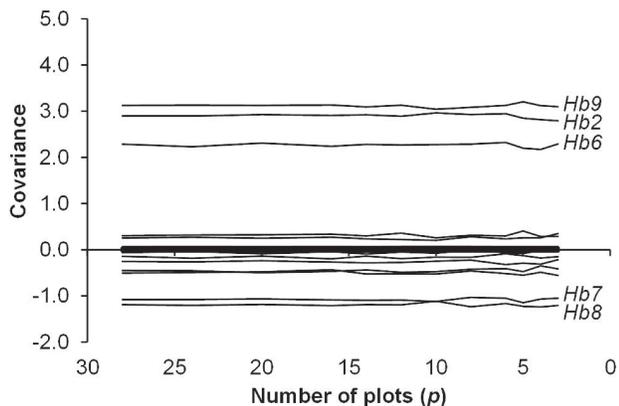
This bias in chronology variance can also be transposed to BCC values. Let CLM be a climate series with a variance  $\sigma_{\text{CLM}}^2$ . As exposed in Mérian and Lebourgeois (2011a), the variation in BCC strength between the population and the sample of  $N$  trees can be quantified with the ratio

$$S = \frac{\text{BCC}_{\text{CHR}}}{\text{BCC}_{\text{POP}}} \quad (9)$$

Because BCC are estimated with Pearson's method (Blasing et al. 1984), Equation 9 equals

$$S = \frac{\sigma_{\text{CHR,CLM}}}{\sigma_{\text{CHR}} \times \sigma_{\text{CLM}}} \times \frac{\sigma_{\text{POP}} \times \sigma_{\text{CLM}}}{\sigma_{\text{POP,CLM}}} \quad (10)$$

where  $\sigma_{\text{CHR,CLM}}$  and  $\sigma_{\text{POP,CLM}}$  are the covariances between CHR and CLM, and POP and CLM, respectively. Because the variance of the signal common to all trees ( $\sigma_{\text{POP}}^2$ ) is contained in both POP and CHR and the variance of the reduced noise  $\sigma_{\text{NOS}}^2/N$  contained in CHR is by definition independent of  $\sigma_{\text{CLM}}^2$ ,  $\sigma_{\text{CHR,CLM}}$  is expected to remain constant whatever the sample size (Figure 1). The



**Figure 1.** Covariance between the growth chronology of group H and climatic series plotted as a function of  $p$  for each climatic regressor. The number of sampled trees per plot was fixed at 1. The climatic regressors showing the greatest covariances are indicated on the right side.

covariance ratio can be approximated to 1 and Equation 10 simplified as

$$S = \frac{\sigma_{\text{POP}}}{\sigma_{\text{CHR}}} = \sqrt{\text{EPS}_{\text{CHR}}} \quad (11)$$

Thus, the sample size-related bias in BCC is equivalent to the square root of EPS of the growth chronology. This mathematical formulation confirms that decreasing sample size leads systematically to an underestimation of the climate-tree growth correlations because EPS varies from 0 to 1 and that the bias is independent of the climatic series (Mérian and Lebourgeois 2011a). To provide an accurate estimation of the population BCC ( $\text{BCC}_{\text{POP}}$ ), we suggest correcting BCC obtained from CHR ( $\text{BCC}_{\text{CHR}}$ ). With use of Equations 9 and 11, the correction factor is

$$\text{BCC}_{\text{POP}} = \frac{1}{\sqrt{\text{EPS}_{\text{CHR}}}} \times \text{BCC}_{\text{CHR}} \quad (12)$$

According to the EPS formula (Wigley et al. 1984, Briffa and Jones 1990), the corrected bias is weaker when the sample size is large and the mean intertree correlation ( $r_{\text{tot}}$  in Briffa and Jones 1990) is high. In the case of a growth chronology built from trees cored in several plots, researchers can limit the magnitude of the bias by increasing the numbers of sampled plots and sampled trees per plot and coring trees with great within- and between-plot correlations in indexed series ( $r_{\text{wp}}$  and  $r_{\text{bp}}$  in Mérian et al. 2012).

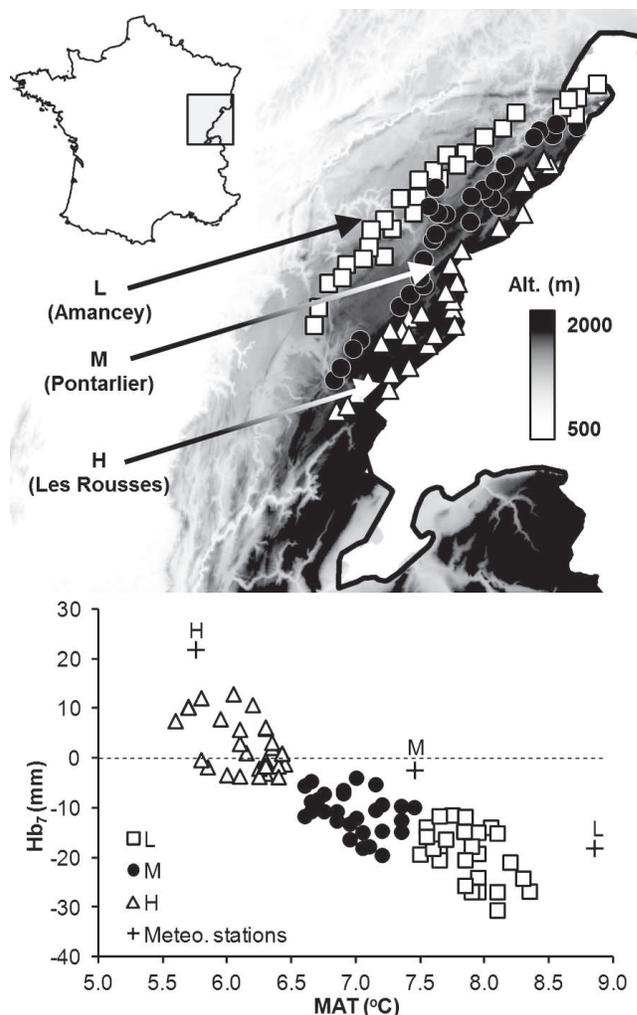
### Illustration of the Sample Size-Related Bias Correction

In this section, we illustrate the accuracy of the sample size-related bias correction from a data set of 504 individual chronologies of *Abies alba* [Mill.] sampled in the Jura Mountains (France) along an altitudinal gradient (Bert 1993).

### Sample Characteristics, Tree-Ring Measurement, and Standardization

The study was conducted in the Jura Mountains on the border with Switzerland, from 46°30' to 47°23' N and 5°48' to 6°58' E (Figure 2). A total of 84 plots were established in pure, mature, and even-aged forests. At each plot, 6 dominant trees were cored to the pith at breast height with an incremental borer in 1989 (one core per tree [Mäkinen and Vanninen 1999]). The mean tree age and diameter reached 107 years and 44 cm, respectively (SD: 37 and 3.3, respectively) (Table 1).

The ring widths of the 504 trees were measured with a stereomicroscope connected to a microcomputer and the tree-ring program SAISIE (Becker 1989) to the nearest 0.01 mm. The individual series were carefully cross-dated by progressively detecting regional pointer years. Absolute dating was checked by the application INTERDAT (Becker



**Figure 2.** Geographical location of the 84 plots and the 3 meteorological stations of Météo-France (Amancey, Pontarlier, and Les Rousses) together with their distribution along the two climatic gradients of stratification. MAT, mean annual temperature in °C; Hb<sub>7</sub>, climatic hydric balance of July in mm; □, low (L); ●, medium (M); △, high (H); +, meteorological stations. Climatic means for the period 1961–1990 were extracted per plot from the AURELHY map at a 1-km<sup>2</sup> resolution (Bénichou and Le Breton 1987).

**Table 1. Summarized plots characteristics per altitude group.**

| Group | Stand characteristics |             |               |             |              |                          | Meteorological series (1961–1990) |         |      |       |      |       |      |
|-------|-----------------------|-------------|---------------|-------------|--------------|--------------------------|-----------------------------------|---------|------|-------|------|-------|------|
|       | Age<br>(yr)           | dbh<br>(cm) | Height<br>(m) | Alt.<br>(m) | MAT<br>(°C)* | Hb <sub>7</sub><br>(mm)* | T                                 |         |      | Prec. |      | Hb.   |      |
|       |                       |             |               |             |              |                          | Year                              | January | July | Year  | July | Year  | July |
| L     | 97 (31)               | 44.9 (3.4)  | 28.6 (6.2)    | 802 (71)    | 7.9 (0.26)   | -19.2 (5.6)              | 8.9                               | 0.9     | 17.4 | 1,364 | 100  | 733   | -18  |
| M     | 109 (36)              | 44.8 (3.6)  | 30.3 (3.6)    | 951 (104)   | 7.0 (0.27)   | -10.9 (4.2)              | 7.5                               | -0.7    | 15.8 | 1,471 | 110  | 911   | -3   |
| H     | 115 (47)              | 43.4 (2.9)  | 28.1 (3.9)    | 1,080 (95)  | 6.1 (0.30)   | 2.5 (5.3)                | 5.8                               | -1.9    | 14.1 | 1,887 | 128  | 1,419 | 22   |

Values are expressed as mean (SD). Alt., altitude; Prec., precipitation. Age, dbh, and height are from 1988. Climatic means are from 1961 to 1990.

\* Climatic values for the period 1961–1990 were extracted per plot from the AURELHY map at a 1-km<sup>2</sup> resolution (Bénichou and Le Breton 1987).

1989), which identifies locations within each series that may have erroneous cross-dating. With use of R freeware (R Development Core Team 2010) and the “dplR” package (Bunn 2008), tree-ring chronologies were computed and standardized to emphasize the interannual climatic signal in each series. A double-detrending process was then applied, based on an initial negative exponential or linear regression followed by a fitting of a cubic smoothing spline with 50% frequency response cutoff and with a rigidity of 25 years (Cook and Peters 1981). Dimensionless indices were obtained by dividing the observed ring width by the predicted value.

### Climate Variability and Plots Stratification

The altitude of plots varied between 620 and 1,310 m above sea level (Bert 1993). The mean climate conditions for the period 1961–1990 were precisely quantified per plot by extracting the mean monthly temperature and monthly sum of precipitation from the Analyse Utilisant le Relief pour l’Hydrométéorologie (AURELHY) map at a 1-km<sup>2</sup> resolution (Bénichou and Le Breton 1987). The AURELHY method allows mean monthly climatic conditions for the period 1961–1990 to be estimated from the thermo-pluviometric series recorded by the meteorological stations. This method first describes the meteorological field as a function of relief descriptors through multiple linear regression equations. Second, the resulting surface of differences between the calculated and measured meteorological values is smoothed by ordinary kriging. The mean annual temperature and sum of precipitation ranged from 5.8 to 9.0 °C and from 1,200 to 1,950 mm, respectively. The climatic hydric balance was also calculated per month using Turc’s formula (Lebourgeois and Piedallu 2005, Mérian and Lebourgeois 2011a). The annual hydric balance was always positive, with values ranging from 500 to 1,350 mm.

To analyze the variation of the sample size-related bias along this altitudinal climatic gradient, the 84 plots were stratified based on their climatic characteristics for the period 1961–1990 to define groups with contrasted intergroup climatic conditions. The selected stratification criteria were the mean annual temperature (MAT) and the climatic hydric balance of July (Hb<sub>7</sub>) (Figure 2); indeed, MAT was a synthetic thermal variable that did not favor either summer heats or winter frosts, whereas Hb<sub>7</sub> focused on the intensity of the major water limitation during the growth year. The plot distribution along these two gradients allowed defining three groups of 28 plots with contrasted climates and alti-

tudes (Figure 2; Table 1): low (L, mean altitudinal value: 802 m), medium (M, 950 m), and high elevation (H, 1080 m). Both MAT and Hb<sub>7</sub> were significantly different among the three groups (Newman-Keuls test,  $q < 10^{-7}$ ). MAT decreased with increasing altitude, with values of 7.9, 7.0, and 6.1 °C for L, M, and H, respectively, whereas Hb<sub>7</sub> increased (-19.2, -10.9, and 2.5 mm). The within-group climate variability was rather constant among the groups, with SDs of MAT and Hb<sub>7</sub> of approximately 0.27 °C and 5 mm, respectively.

Long-term series of mean monthly temperature (T) and climatic hydric balance (Hb) were obtained from meteorological stations of the French National Climatic Network (Météo-France). For each group, one station was selected based on its representativeness of the climate conditions and the length of the recordings (Figure 2; Table 1). The stations of Amancey (L), Pontarlier (M), and Les Rousses (H) were the only sources of long-term data within the study area, with series covering at least the period 1936–1988.

### Resampling Procedure and Growth Chronology Building

For each group, the effect of the number of sampled plots ( $p$ ) and trees per plot ( $t$ ) was investigated through 12 modalities of  $p$  (28 to 3 plots) and 6 modalities of  $t$  (6 to 1 trees). The flow chart of the methodological process is detailed in Mérian et al. (2012) and is thus briefly presented below. For each combination ( $p, t$ ),  $p$  plots among 28 were randomly extracted with replacement; then, within each plot,  $t$  trees among 6 were also randomly extracted with replacement. The indexed series of the extracted trees were averaged by year using a bi-weighted robust mean to develop a growth chronology, which represented the common high-frequency variation of the individual series (Cook and Peters 1981, Cook 1985). The resampling procedure was replicated 500 times per combination to avoid sampling bias (Efron 1979). All the growth chronologies covered the period 1937–1988 (52 years).

### Dendroecological Analyses and Bias Quantification

The characteristics of the common signal contained in the growth chronologies were assessed through classic dendrochronological statistics (Wigley et al. 1984, Briffa and Jones 1990, Mérian et al. 2012). For each chronology, we

calculated the following: the mean within-plot correlation ( $r_{wp}$ ), estimated by averaging the correlation coefficients between series from the same plot over all plots; the mean between-plot correlation ( $r_{bp}$ ), defined as the mean value of the correlations calculated between all possible pairs of series from different plots; the mean effective chronology correlation ( $r_{eff}$ ), which incorporated both within- and between-plot correlation strengths, and the expressed population signal (EPS). Climate-tree growth relationships were analyzed over the period 1937–1988 using the calculation of bootstrapped correlation coefficients (Blasing et al. 1984). The growth chronologies were introduced as dependant variables and then fitted with 24 successive monthly climatic regressors (12 T and 12 Hb values) organized from September of the previous growing season to August of the current year. These analyses were achieved with the “bootRes” package (Zang 2009).

For each altitudinal group and combination ( $p, t$ ), mean value, SD, and confidence interval at the 95% level of the statistics ( $r_{wp}$ ,  $r_{bp}$ ,  $r_{eff}$ , and EPS) and sets of BCC were computed from the 500 estimates. The variation of the strength of the signal common to all trees, attributable to broad-scale environmental influences such as regional climatic forcing (Briffa and Jones 1990, Mérian et al. 2012), was investigated among altitudinal groups through differences in growth chronology statistics. Then, the slope  $S_{(p, t)}$

of the linear regression between the BCC established from the combinations (28, 6) and ( $p, t$ ) was calculated as

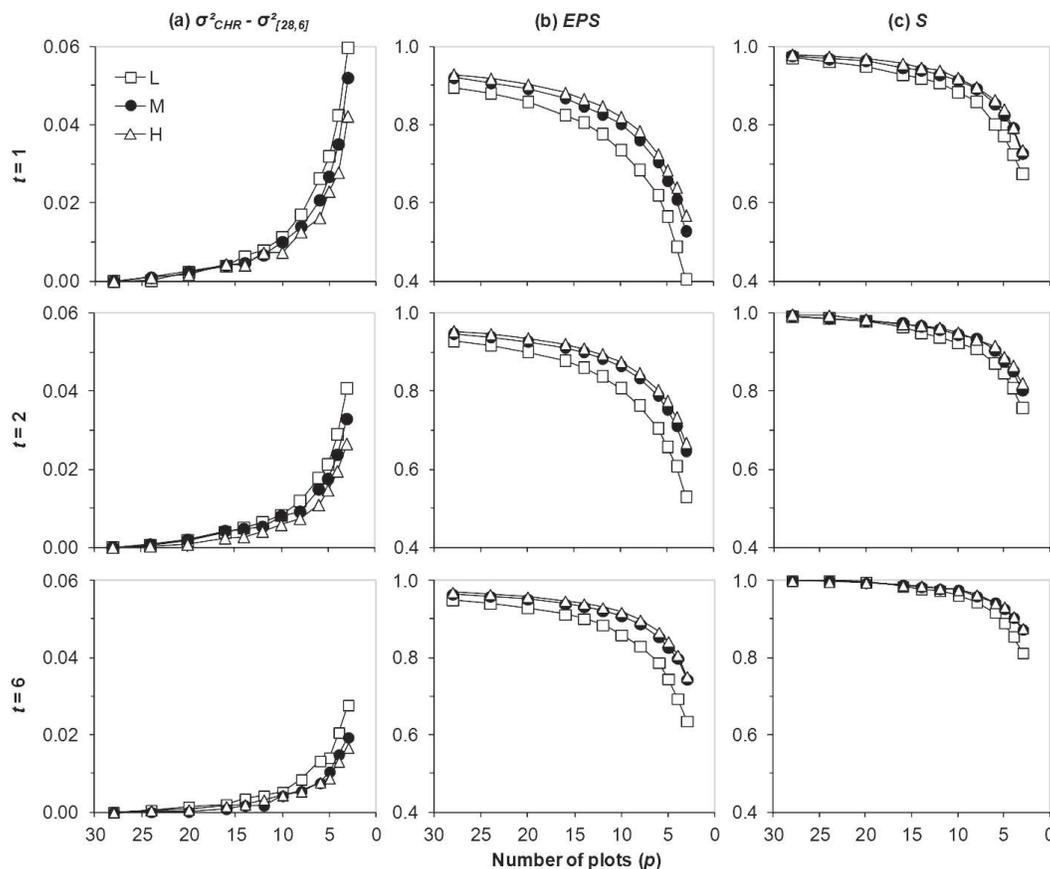
$$BCC_{(p, t)} = S_{(p, t)} \times BCC_{(28, 6)} \quad (13)$$

where  $BCC_{(p, t)}$  and  $BCC_{(28, 6)}$  are the sets of 24 BCC of the combinations ( $p, t$ ) and (28, 6), respectively. Finally, EPS and  $S_{(p, t)}$  were compared to verify the accuracy of the mathematical formulation of the bias, and all of the BCC were finally corrected using Equation 12 ( $BCC_{COR}$ ).

## Results

### Sample Size Effect on Dendroecological Investigations

Decreasing sample size did not affect the estimation of either the mean within-plot or between-plot correlations ( $r_{wp}$  and  $r_{bp}$ ), whereas it strongly reduced the expressed population signal. As expected, both the chronology variance increase and the EPS weakening were related to the sample size decrease, with stronger trends with small samples (Figure 3a and b). For example, at low elevation and for  $t = 1$ , the EPS decrease rate 0.16 when  $p$  was reduced from 28 to 6 or from 6 to 3 (Figure 3b). Likewise, for a given number of plots, diminishing  $t$  from 6 to 2 or from 2 to 1 resulted in similar EPS drops. Based on confidence intervals, the EPS decrease with sample size was significant at



**Figure 3.** Chronology variance increase (a,  $\sigma^2_{CHR} - \sigma^2_{(28, 6)}$ ), expressed population signal (b, EPS), and slope of Equation 13 (c,  $S$ ) plotted as a function of  $p$  for three modalities of number of trees per plot ( $t = 1, 2, \text{ and } 6$ ).  $\square$ , low (L);  $\bullet$ , medium (M);  $\triangle$ , high (H).

the 95% level among the combinations ( $p, t$ ) (Table 2). As a consequence of Equation 12, BCC approached 0 with decreasing  $p$  and  $t$ .

Differences in both statistics of growth chronology and climate-tree growth relationships were seen along the altitudinal gradient of increasing climate limitation (Figure 3). Whatever the statistic, the classification of the three groups remained the same and was consistent with their respective position along the altitudinal gradient.  $r_{wp}$  remained rather constant (approximately 0.52), whereas  $r_{bp}$  increased with altitude (respective values of 0.236, 0.295, and 0.323 for the groups L, M, and H), which induced higher EPS at high elevation for a given combination ( $p, t$ ). For instance, EPS of the combination (3, 1) rated 0.41, 0.53, and 0.57 for the groups L, M, and H. Whatever the combination ( $p, t$ ), the EPS value was significantly higher for group H compared with that for group M and also for group M compared with that for group L (Figure 3b; Table 2). Likewise, the BCC weakening between (28, 6) and ( $p, t$ ) was stronger for L than for M and H, with higher  $S_{(p, t)}$  values (Figure 3c).

### Sample Size-Related Bias Estimation and Correction

The sample size-related bias in climate-tree growth relationships was mathematically formulated as the squared root of EPS (cf. Equation 12) and empirically quantified with the slope  $S$  (cf. Equation 13). These two bias estimators displayed a very high consistency whatever the combination ( $p, t$ ) since the linear regressions showed  $R^2$  closed to 1 (0.9940, 0.9936, to 0.9929 for the groups L, M, and H, respectively).

Thus, BCC were corrected for each group and combination using the correction factor of Equation 12. The correction is illustrated in Figure 4, based on the combination (3, 1). This example was chosen because it was associated to the worse EPS value (0.41) (Table 2) and thus the highest bias. The corrected BCC [ $BCC_{COR(3, 1)}$ ] were systematically closer to the most accurate estimation of the population response, defined as  $BCC_{COR}$  of the combination (28, 6), i.e.,  $BCC_{COR(28, 6)}$ . However,  $BCC_{COR(3, 1)}$  did not strictly mirror  $BCC_{COR(28, 6)}$  with still a slight underestimation of the correlation strength (Figure 4b). The accuracy of the

**Table 2.** Detailed values of EPS per zone for 16 combinations of ( $p, t$ ).

| Group | $t/p$ | 3           | 5           | 10          | 28          |
|-------|-------|-------------|-------------|-------------|-------------|
| L     | 1     | 0.41 (2.02) | 0.57 (1.31) | 0.74 (0.61) | 0.90 (0.18) |
|       | 2     | 0.53 (1.75) | 0.66 (1.05) | 0.81 (0.44) | 0.93 (0.09) |
|       | 4     | 0.61 (1.58) | 0.73 (0.88) | 0.85 (0.35) | 0.94 (0.09) |
| M     | 6     | 0.64 (1.49) | 0.75 (0.88) | 0.86 (0.35) | 0.95 (0.09) |
|       | 1     | 0.53 (1.58) | 0.66 (0.96) | 0.80 (0.44) | 0.92 (0.09) |
|       | 2     | 0.65 (1.14) | 0.75 (0.70) | 0.86 (0.26) | 0.95 (0.09) |
| H     | 4     | 0.71 (0.88) | 0.81 (0.44) | 0.90 (0.18) | 0.96 (0.09) |
|       | 6     | 0.74 (0.79) | 0.83 (0.44) | 0.91 (0.18) | 0.96 (0.09) |
|       | 1     | 0.57 (1.40) | 0.68 (0.79) | 0.82 (0.35) | 0.93 (0.09) |
|       | 2     | 0.67 (0.96) | 0.77 (0.53) | 0.88 (0.18) | 0.95 (0.09) |
|       | 4     | 0.74 (0.79) | 0.82 (0.44) | 0.91 (0.18) | 0.97 (0.08) |
|       | 6     | 0.75 (0.70) | 0.84 (0.35) | 0.92 (0.09) | 0.97 (0.08) |

Values are expressed as mean value ( $100 \times$  confidence interval at the 95% level) and are calculated from the 500 replications of the plot and tree resampling.

correction increased with sample size whatever the group (Figure 5). For a number of sampled plots less than 6 and one tree sampled per plot,  $BCC_{COR}$  always underestimated the population correlation coefficient. For greater sample sizes ( $t > 1$  and  $P > 6$ ), the difference between  $BCC_{COR(p, t)}$  and  $BCC_{COR(28, 6)}$  almost rated 0. Similarly, the accuracy of the correction increased with altitude, the underestimation of  $BCC_{COR}$  being greater for group L (Figure 5a) than that for groups M and H (Figure 5b and c).

## Discussion

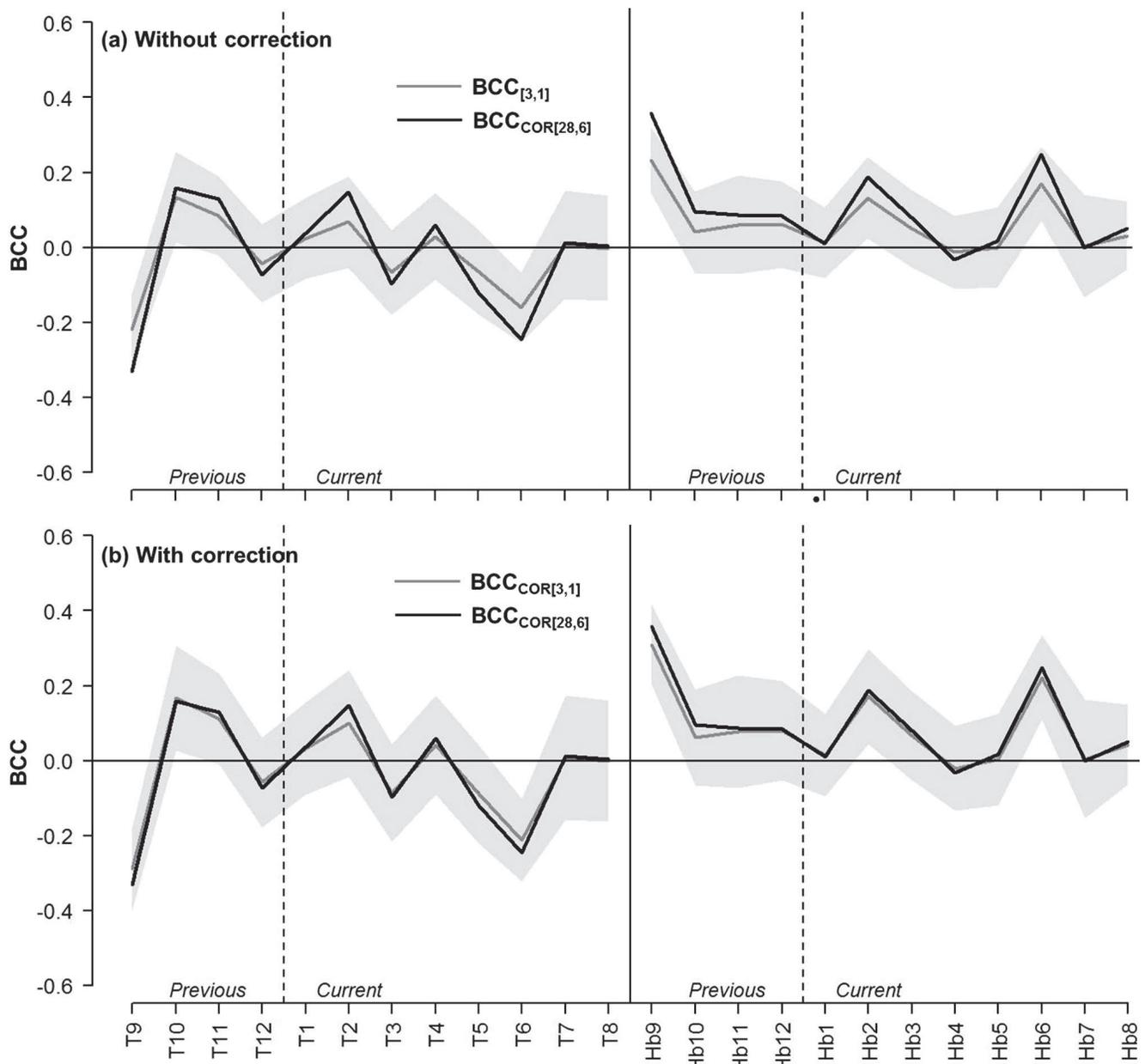
### Unbiased Estimation of the Population Sensitivity to Climate

Decreasing sample size induced an increasing variance of the growth chronology due to increasing variance of the reduced noise (see Equation 1). As a consequence, bootstrapped correlation coefficients weakened with decreasing sample size, which resulted in a general underestimation of the climate sensitivity. Such bias may reduce the validity of correlation function comparisons established on growth chronologies built from various sample sizes or sample characteristics [i.e., different combinations of ( $p, t$ )]. The simulation approach presented in Mérian et al. (2012) allowed the estimation of the magnitude of this bias on BCC, its mathematical formulation, and the related correlation-correction factor of  $1/\sqrt{EPS}$  (cf. Equation 12). Thus, this correction relied on a climate-tree growth correlation strengthening to compensate for the lower reduction of noise variance. Such nonuniform variance in time series due to changing sample size was previously seen within the growth chronology in Shiyatov et al. (1990). Then, these authors proposed a correction factor based on the calculation of the coefficient of variation for the time interval of the maximum sample size ( $m_{max}$ ) to eliminate this sample size-related trend in time series variance. This correction factor can be defined as “the ratio of the coefficient of variation of the  $m_{max}$  time period to that for a sample size  $m < m_{max}$ .”

The main point of this BCC correction factor is that its estimation does not require any information about the variance of the theoretical population growth chronology. Researchers only have to estimate the respective importance of signal and noise through widely used chronology statistics, such as SNR or EPS (Wigley et al. 1984, Briffa and Jones 1990). The second point resulting from the first one is that climate-tree growth relationships obtained from samples of different sizes can be accurately compared after correction. Thus, to avoid sample size-related bias in climate-tree growth relationships estimations, two suggestions are to correct the intrachronology trend in variance to compensate for the change in sample size (Shiyatov et al. 1990), and to correct the BCC values to compensate for partial noise reduction due to sampling effort when individual series are averaged; the aim of both corrections is to approach the population signal variance.

### Limit of the Correction: Does the Sample Signal Mirror the Target Population Signal?

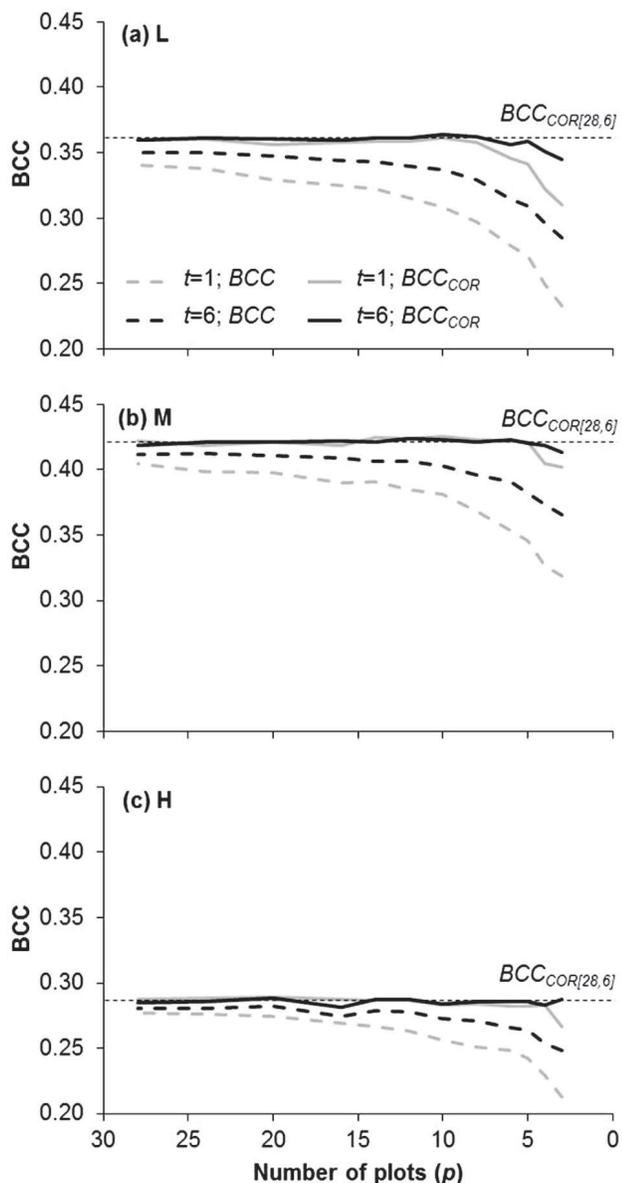
Equation 12 is expected to correct the BCC values estimated with a chronology built from a finite number of trees.



**Figure 4.** Illustration of the sample size-related bias correction for the group L and the combination (3, 1). (a) Comparison of the population response estimated through the corrected BCC of the combination (28, 6) [ $BCC_{COR(28, 6)}$ ] and the response obtained with the combination (3, 1) without correction. (b) Comparison of the population response and the corrected response obtained with the combination (3, 1) [ $BCC_{COR(3, 1)}$ ]. Gray areas indicate the SD range of BCC among the 500 replications for the combination (3, 1). Month is represented by a number (e.g., 1 represents January).

However, such correction implies that the signal common to all of the sampled trees mirrors that of the target population. Indeed, Equation 1 is based on the assumption that the sampling strategy designed by the researchers minimizes sampling bias. In other words, Equation 1 hypothesizes that the sampled trees are representative of the target population variability. However, the robustness of this statement decreases with both sample size and climate forcing. The main implication of estimating the population signal from a small sample is that, whatever the distribution of the sampled trees over the target population, the within-population variability cannot be accurately represented. Similarly, this variability in tree growth pattern is more difficult to sample under low climatic limitation, i.e., at low elevation where significant

lower EPS values were seen (Table 2). Indeed, because the growth chronology variance is composed of the variances of the signal common to all trees, attributable to broad-scale environmental influences, and the residual noise, decreasing climate forcing results in increasing importance of the tree-specific growth pattern induced by local environmental variations. The relative importance of the residual noise variance in the growth chronology variance increases, leading to lower SNR and EPS values and thus higher bias in climate-tree growth relationships estimation. As a consequence, the sampling bias in the estimation of the population signal from that of the growth chronology is greater for low sample sizes and under low limiting climatic conditions (Figure 5). In such cases, the sample size-related bias



**Figure 5.** Illustration of the sample size-related bias correction per group and for the climatic regressor  $Hb_9$  (climatic hydric balance of previous November). Results are presented for the two extreme numbers of trees per plot: 1 (gray lines) and 6 (black lines). Dashed lines, uncorrected BCC; continuous lines, corrected BCC. The BCC values are plotted as a function of  $p$ . The population response was estimated through the corrected BCC of the combination (28, 6) [ $BCC_{COR(28,6)}$ ].

correction of Equation 12 allows approaching the response pattern of the sampled population but not that of the target population.

A second implication resulting from the first one is that two independent small samples will correspond to rather different populations and thus different common signals. Researchers have to keep in mind that the bias correction proposed in this analysis is all the more accurate when the number of cored trees is large, i.e., if the within-population variability is approximated (Figure 5). Sophisticated sampling strategies based on a prior analysis of the population variability can be of interest to optimize the repartition of the  $N$  sampled trees to increase the precision of the climate-

tree growth relationship estimation (e.g., Schreuder et al. 1971, Garcia 1992). The accuracy of the bias correction can also be increased with the definition of a homogeneous target population. The illustration of this study revealed an enhancement of growth synchrony with increasing elevation. This finding implies that the sample size decrease induced both lower biases and between-sample differences in BCC estimation with increasing environmental forcing (Figure 4; Table 2) (Fritts 1976, Wigley et al. 1984, Briffa and Jones 1990). Last, at the plot scale, the variability of the target population can be refined by focusing on a group of trees with homogeneous growth pattern; for instance, a specific age class (Yu et al. 2008, Copenheaver et al. 2011) or tree size (Piutti and Cescatti 1997, Martin-Benito et al. 2008, Mérian and Lebourgeois 2011b).

## Conclusion

The sample-size related bias in population estimates of climate-tree growth relationships shown in a previous analysis (Mérian and Lebourgeois 2011a) was quantified as the squared root of the EPS of the growth chronology built from  $N$  trees. We thus proposed correcting the bootstrapped correlation coefficients resulting from climate-tree growth correlation functions with a factor of  $1/\sqrt{EPS}$  (cf. Equation 12). The accuracy of this correction decreased with decreasing EPS values, i.e., for small sample sizes and for samples collected under low limiting environmental conditions. The main limit of the correlation-correction concerns potential sampling bias in the field, that is, differences between the target and the sampled populations. In such cases, the correction only results in a best estimation of response pattern of the sampled population but not that of the target population.

The magnitude of the bias was investigated through the calculation of correlation functions (Blasing et al. 1984). However, climate-tree growth relationships can also be estimated with response functions (Guiot 1991). Whereas the first method treats each climatic regressor separately to estimate their effect on tree growth, the latter relies on a regression in principal components to avoid problems with intercorrelations among climatic series. Because both methods are widely used in dendrochronological studies, it could be of interest to extend the bias quantification to bootstrapped correlation coefficients obtained with response function calculation.

## Literature Cited

- 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.
- BERT, D. 1993. Impact of ecological factors, climatic stresses, and pollution on growth and health of silver fir (*Abies alba* Mill.) in the Jura mountains: An ecological and dendrochronological study. *Acta Oecol.* 14(2):229–246.
- BÉNICHOU, P., AND O. LEBRETON. 1987. Prise en compte de la topographie pour la cartographie des champs pluviométriques statistiques. *La Météorol.* 7(19):23–34.
- BLASING, T.J., A.M. SOLOMON, AND D.N. DUVICK. 1984. Response functions revisited. *Tree-Ring Res.* 44:1–15.
- BONTEMPS, J.D., AND J. ESPER. 2011. Statistical modelling and

- RCS detrending methods provide similar estimates of long-term trend in radial growth of common beech in north-eastern France. *Dendrochronologia* 29(2):99–107.
- BRIFFA, K.R., AND P.D. JONES. 1990. Basic chronology statistics and assessment. P. 137–152 in *Methods of dendrochronology: Applications in the environmental sciences*, Cook, E.R., and L.A.E. Kairiukstis (eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- BRIFFA, K.R., G. VAN DER SCHRIER, AND P.D. JONES. 2009. Wet and dry summers in Europe since 1750: Evidence of increasing drought. *Int. J. Climatol.* 29(13):1894–1905.
- BUNN, A.G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26(2):115–124.
- BÜNTGEN, U., D. FRANK, H. GRUDD, AND J. ESPER. 2008a. Long-term summer temperature variations in the Pyrenees. *Clim. Dynam.* 31(6):615–631.
- BÜNTGEN, U., D. FRANK, R. WILSON, M. CARRER, AND C. URBINATI. 2008b. Testing for tree-ring divergence in the European Alps. *Glob. Change Biol.* 14(10):2443–2453.
- CARRER, M., P. NOLA, R. MOTTA, AND C. URBINATI. 2010. Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos* 119(9):1515–1525.
- COOK, E.R. 1985. *A time series analysis approach to tree ring standardization*. PhD thesis, Univ. of Arizona, Tucson, AZ. 171 p.
- COOK, E.R., AND K. PETERS. 1981. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Res.* 41:45–53.
- COPENHEAVER, C.A., C.J. CRAWFORD, AND T.M. FEARER. 2011. Age-specific responses to climate identified in the growth of *Quercus alba*. *Trees Struct. Funct.* 25(4):647–653.
- D'ARRIGO, R., G. JACOBY, B. BUCKLEY, J. SAKULICH, D. FRANK, R. WILSON, A. CURTIS, AND K. ANCHUKAITIS. 2009. Tree growth and inferred temperature variability at the North American Arctic treeline. *Glob. Planet Change* 65(1–2):71–82.
- D'ARRIGO, R., R. WILSON, B. LIEPERT, AND P. CHERUBINI. 2008. On the 'Divergence Problem' in Northern Forests: A review of the tree-ring evidence and possible causes. *Glob. Planet Change* 60(3–4):289–305.
- EFRON, B. 1979. 1977 Rietz lecture: Bootstrap methods: Another look at the jackknife. *Ann. Stat.* 7(1):1–26.
- FRITTS, H.C. 1976. *Tree rings and climate*. Academic Press, New York. 567 p.
- GARCIA, O. 1992. Sampling for tree-ring analysis. P. 110–129 in *Proc. of the International IUFRO conference on integrating forest information over space and time*, Turner G., and B. Wood (eds.). NUTECH Pty Ltd., Canberra, Australia.
- GUIOT, J. 1991. The bootstrapped response function. *Tree-Ring Res.* 51:39–41.
- LEBOURGEOIS, F., P. MÉRIAN, F. COURDIER, J. LADIER, AND P. DREYFUS. 2011. Instability of climate signal in tree-ring width in Mediterranean mountains: A multi-species analysis. *Trees Struct. Funct.* 26(3):715–729, 2012.
- LEBOURGEOIS, F., AND C. PIEDALLU. 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.
- LOEHLE, C. 2009. A mathematical analysis of the divergence problem in dendroclimatology. *Climatic Change* 94(3–4):233–245.
- MÄKINEN, H., AND P. VANNINEN. 1999. Effect of sample selection on the environmental signal derived from tree-ring series. *For. Ecol. Manage.* 113(1):83–89.
- MARTIN-BENITO, D., P. CHERUBINI, M. DEL RIO, AND I. CANELLAS. 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees Struct. Funct.* 22(3):363–373.
- MÉRIAN, P., J.D. BONTEMPS, L. BERGÈS, AND F. LEBOURGEOIS. 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.
- MÉRIAN, P., AND F. LEBOURGEOIS. 2011a. Consequences of the decreasing number of cored trees per plot on chronology statistics and climate-growth relationships: A multispecies analysis in a temperate climate. *Can. J. For. Res.* 41:2413–2422.
- MÉRIAN, P., AND F. LEBOURGEOIS. 2011b. Size-mediated climate-growth relationships in temperate forests: A multi-species analysis. *For. Ecol. Manage.* 261(8):1382–1391.
- MÉRIAN, P., J.C. PIERRAT, AND F. LEBOURGEOIS. 2012. Effect of sampling effort on the regional chronology statistics and climate-growth relationships estimation. *Dendrochronologia*. doi: 10.1016/j.dendro.2012.07.001.
- PIUTTI, E., AND A. CESCATTI. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Can. J. For. Res.* 27(3):277–284.
- R DEVELOPMENT CORE TEAM. 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available online at [www.R-project.org](http://www.R-project.org); last accessed July 10, 2012.
- SCHREUDER, H.T., J. SEDRANSK, K.D. WARE, AND D.A. HAMILTON. 1971. 3-P sampling and some alternatives, II. *For. Sci.* 17(1):103–118.
- SCHULMAN, E. 1937. Selection of trees for climatic study. *Tree-Ring Res.* 3(3):22–23.
- SCHULMAN, E. 1954. Dendroclimatic changes in semiarid regions. *Tree-Ring Res.* 20(3–4):26–30.
- SHIYATOV, S., V. MAZEPA, AND E.R. COOK. 1990. Correcting for trend in variance due to changing sample size. P. 133–137 in *Methods of dendrochronology: Applications in the environmental sciences*, Cook, E.R., and L.A.E. Kairiukstis (eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- WIGLEY, T.M., K.R. BRIFFA, AND P.D. JONES. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol.* 23:201–213.
- WILSON, R., R. D'ARRIGO, B. BUCKLEY, U. BÜNTGEN, J. ESPER, D. FRANK, B. LUCKMAN, S. PAYETTE, R. VOSE, AND D. YOUNGBLUT. 2007. A matter of divergence: Tracking recent warming at hemispheric scales using tree ring data. *J. Geophys. Res.* Atmos. 112(D17).
- YU, G.R., Y.B. LIU, X.C. WANG, AND K.P. MA. 2008. Age-dependent tree-ring growth responses to climate in Qilian juniper (*Sabina przewalskii* Kom.). *Trees Struct. Funct.* 22(2):197–204.
- ZANG, C. 2009. *bootRes: Bootstrapped response and correlation functions*. R package version 0.2. Available online at [CRAN.R-project.org/package=bootRes](http://CRAN.R-project.org/package=bootRes); last accessed July 10, 2012.