Size-mediated climate–growth relationships in temperate forests: A multi-species analysis

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ABSTRACT

In most dendrochronological studies, climate–growth relationships are established on dominant trees to minimize non-climatic signals. However, response to environmental factors may be affected by tree-size, which begs the question of the representativeness of dominant trees on the stand level. To highlight the variations in climate–growth relationships among sizes and species, under a wide range of ecological conditions (climate and soil properties), 61 pure even-aged stands were sampled across France. At each stand, two tree-ring chronologies were established from 10 big- to 10 small-diameter trees. Our objectives were, (1) to assess variations in climate sensitivity between the two size-diameter classes, and (2) to investigate the role of species and ecological conditions on these variations. The climate-growth relationships were evaluated from 122 tree-ring chronologies (1 220 trees) through extreme growth years and correlation function analyses. Sensitivity to climate of shade-intolerant and moderately shade-tolerant species (*Picea abies* (L.) Karst., *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl.) remained constant between the size-diameter classes for both temperature and hydric balance, while the shade-tolerant species *Abies alba* Mill. and *Fagus sylvatica* L. displayed significant differences, with larger trees being more sensitive to summer drought than smaller trees. This difference increased with increasing climatic xericity. Our results suggest that, for shade-tolerant species, (1) big trees could be more sensitive to climatic change especially under xeric climate, and (2) future tree ring studies should include trees stratified by size to produce unbiased estimation of sensitivity to climate.

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1. Introduction

In dendroclimatology, sampling procedures have been developed to minimize non-climatic signals through the selection of trees not affected by severe competition, such as isolated or dominant trees (Fritts, 1976; Schweingruber, 1990). However, eco-physiological studies have shown that functional processes vary as tree age and size increase (Mencuccini et al., 2005; Rossi et al., 2008). The photosynthetic performance generally decreases with increasing size and age (Thomas and Winner, 2002) due to a decreasing light capture efficiency (Niinemets, 2010) and increasing path length for water transport (Becker et al., 2000; Niinemets, 2002). Size and age also affect stomatal conductance (Hubbard et al., 1999) and thus water-use efficiency (Bert et al., 1997). Despite the difficulty to clearly separate the effects of both factors, tree-size seems to account for more in tree vigor than age (Penuelas, 2005). Such size-related changes in tree physiol-ogy could induce a heterogeneous sensitivity to climate between trees.

Tree-ring width has been the most frequently proxy used to assess climate–growth relationships and the effect of the global warming on forest growth and vitality (D'Arrigo et al., 2008). Significant links between current climatic trends and changes in sensitivity to climate have been pointed out under temperate (Friedrichs et al., 2009) and Mediterranean contexts (Macias et al., 2006; Andreu et al., 2007). Increase in drought frequency and sever-ity profoundly altered the growth and vigor of tree populations under dry climate during the last decades (Jump et al., 2006; Sarris et al., 2007) and recently under temperate regions (Charru et al., 2010). Drought-induced dieback of trees also increased with the global warming, but only few studies analyzed the effect of tree-size on the ability of trees to cope with increases in drought frequency and severity (Bigler et al., 2007; Koepke et al., 2010). However, Galiano et al. (2010) highlighted the key role of stand structure on mortality, and tree-size has been found to modulate the magni-tude of growth decline and release in North America (Gavin et al., 2008) and in Southern Europe (Martin-Benito et al., 2008): big trees undergo more severe decline than small trees, but the causes still remained unclear. Thus, testing the hypothesis of size-mediated

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sensitivity to climate could give valuable information on the ability of trees to cope with climate change. Such insights may have important consequences on sampling strategies and validity of observed changes in growth sensitivity and vitality.

Trees of different sizes compete differently for resources (Orwig and Abrams, 1997; Niinemets, 2010), and are also affected by micro-climatic variations at the canopy level (Aussenac, 2000). Studies on size-modulation of climate–growth relationships in deciduous species are scarce and contradictory (Orwig and Abrams, 1997; Piutti and Cescatti, 1997). In coniferous species, results are more consistent, especially on drought, with higher sensitivity in small-diameter trees (Pichler and Oberhuber, 2007; De Luis et al., 2009; Linares et al., 2010). Under cold climate, conifers were found to respond in the same way among size-diameter classes (Meyer and Braker, 2001; Chhin et al., 2008). This tends to prove that tree-size effect on sensitivity to climate is complex and probably modulated by species-specific ecological patterns (Wright et al., 1998; Dekker et al., 2009) and local conditions (Orwig and Abrams, 1997). Most of these studies were led at small regional scales, on one or two species, and on restricted ecological gradients, leading to a partial understanding of the variation of response to climate with tree-size. A multi-species analysis on a wide range of ecological conditions could be relevant for verifying the accuracy of the general implicit extrapolation from climatic sensitivity of dominant trees to stand-level sensitivity.

In this study, we seek to highlight how climate affects radial growth of trees for two size-diameter classes. The analysis was led on five temperate species with contrasting ecological patterns, widely spread in Europe (distribution maps EUFORGEN 2009, www.euforgen.org): *Abies alba* Mill., *Fagus sylvatica* L., *Picea abies* (L.) Karst., *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl. *A. alba* and *F. sylvatica* are shade-tolerant species, with a high need of precipitation or atmospheric humidity, and rather sensitive to summer drought (Becker, 1970; Pinto and Gégout, 2005). In contrast, *Q. petraea* and *P. sylvestris* are shade-intolerant and more xerophytic. Lastly, *P. abies* presents an intermediate shade-tolerance and response to summer drought (Pinto and Gégout, 2005; Lebourgeois et al., 2010b). Forests were sampled across France under a wide range of climatic and pedological conditions. The starting hypotheses were that (1) contrasting diameter-sizes contribute to the occurrence of differing tree-growth responses to climate, (2) ecophysiological traits lead to significant differences between species in response to size variation, and (3) contrasting ecological conditions (climate, acidity, soil water capacity) modulate these species-specific relationships. Climatic factors influencing tree-growth were identified with two complementary methods: (1) the identification of tree-growth response to extreme climatic events using the calculation of pointer years (Schweingruber and Nogler, 2003) and, (2) the establishment of mean relationships between tree ring and climate using correlation function analysis (Fritts, 1976; Guiot, 1991).

2. Materials and methods

2.1. Study area and variability of ecological conditions

The 61 stands were sampled between 42°51′52″N and 49°42′39″N, and 3°32′34″W and 7°43′46″E (Fig. 1) in the French permanent plot network for the monitoring of forest ecosystems (RENECOFOR). The sampled forest stands covered a wide range of bioclimatic conditions: oceanic climate in the western part of the area (*n* = 17 stands), semi-continental in the North-East (*n* = 21), temperate Mediterranean in the South (*n* = 3) and mountain (*n* = 20). Oceanic climate is firstly characterized by medium mean annual temperature with low thermal amplitude due to mild winters and fresh summers, and intermediate precipitation level,

with rather dry summers (Fig. 2a). Semi-continental climate corresponds to higher precipitation, lower mean annual temperature, and higher thermal amplitude with cold winters (Fig. 2b). Temperate Mediterranean climate is defined by dry and warm conditions, especially in summer (Fig. 2d), and mountain climate by low temperature and high precipitation, especially in winter (Fig. 2c).

The slope of the stands ranged from 0 to 66%, and elevation from 38 to 1700 m above sea level. Stands sampled above the altitude of 800 m were mainly *A. alba* (*n* = 8), *P. abies* (*n* = 4) and *F. sylvatica* stands (*n* = 4) (Table 1). *Q. petraea* and *P. sylvestris* were mostly sampled in the lowlands. Soil properties were observed through two trenches per stand. According to textural properties (Bruand et al., 2003), depth and coarse element percentages of each soil horizon, we calculated the soil water capacity (SWC) (Lebourgeois et al., 2005). Soil fertility was estimated through the pH of the organo-mineral horizon (pH). SWC ranged from 25 to 200 mm (mean value: 102), and pH from 3.7 to 6.7 (mean value: 4.7). *Q. petraea* stands generally presented high SWC (mean: 130), while SWC of other species averaged from 73 to 98 mm (Table 1).

2.2. Selected trees, ring-width measurements and analysis

At each stand, 23–30 trees were cored at breast height as close as possible to the pith with an incremental borer in 1995 (one core per tree). The sampled forests were composed of pure and even-aged stands. To highlight the variations in sensitivity to climate depending on size, two groups of trees were defined, reflecting two levels of competition within stand. As diameter growth is closely linked with the canopy position (Klopcic and Boncina, 2010), we selected the 10 biggest and 10 smallest trees at each stand, respectively called big- and small-diameter classes (BD and SD). The age difference between BD and SD was not significant at the level of 5%, except for 2 stands with BD older than SD (Table 1). The diameters of BD were from 18 to 49% higher than those of SD (mean: 28) (Table 2).

The ring widths of the 1 220 trees were measured with a stereo-microscope connected to a micro-computer and the tree ring program SAISIE (Becker, 1989), to the nearest 0.01 mm. We carefully cross-dated the individual ring widths series by progressively detecting regional pointer years, which were defined as those calendar years when at least 75% of the cross-dated trees presented an absolute value of radial growth variation higher than 10% (Becker et al., 1994; Lebourgeois et al., 2005). The radial growth variation expresses to which extend the ring of the current year is narrower (negative value) or wider (positive value) than the previous one. The radial growth variation was calculated using the following equation:

$$RGV_n = 100 \times \frac{(RW_n - RW_{n-1})}{RW_{n-1}} \tag{1}$$

where RW_n is the ring width of the year *n*, and RW_{n-1} the ring width of the previous year.

Absolute dating was checked by the application INTERDAT (Becker and Dupouey unpublished) which identifies locations within each ring series that may have erroneous cross-dating. Using the program ARSTAN v6.05P (Cook, 1985), we computed and standardized the tree ring chronologies on the maximum period common to all chronologies (1948–1994; 47 years) to remove non-climatic and tree-age-related growth trends in each individual ring widths series. A double-detrending process based on an initial negative exponential or linear regression, followed by a fitting of a 30-year cubic smoothing spline with 50% frequency response cut-off was applied for each raw measurement series (Cook and Peters, 1981). Then, for each stand and population, the growth indexes were averaged by year using a bi-weighted robust mean to develop a stand chronology which represented the common high-