Agricultural and Forest Meteorology 180 (2013) 132–141

Contents lists available at SciVerse ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Divergence in latewood density response of Norway spruce to temperature is not resolved by enlarged sets of climatic predictors and their non-linearities

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ARTICLE INFO

Article history:
Received 3 September 2012
Received in revised form 22 May 2013
Accepted 24 May 2013

Keywords:
Latewood density
Divergence
Climatic change
PLS regression
Norway spruce

ABSTRACT

In softwoods, latewood density (LWD) is strongly correlated with temperature, and serves as a basis for climatic reconstructions. However, an unexplained decline in the strength of this relationship has been reported from 1970 to 2000, which has been termed the 'divergence' problem. We inquired whether 'divergence' may be resolved by (i) the relationships between LWD and an enlarged set of climatic factors unaccounted for in traditional approaches or (ii) non-linearities in the relationships between climatic variables and LWD. We developed multi-factorial climatic models of LWD historical variations in tree-ring series of Norway spruce in north-eastern France, where divergence has been observed. The relationships between these LWD variations and 38 climatic variables were analysed. Climatic variables were obtained from homogenised climatic series and included monthly maximum and minimum temperature, potential evapotranspiration and water balance. Two climatic models of LWD were built, using projection to latent structure (PLS) regression analysis: (i) a model including linear responses to climatic variables (M1) and (ii) a model including linear and quadratic responses to climatic variables (M2). Models M1 and M2 accounted for 68.9% and 70.4% of LWD variations, respectively. Model predictions still revealed a divergence from 1965 to 1980, a period where LWD strongly decreased. When using both linear and quadratic forms of climatic variables (model M2), model predictions revealed a less acute divergence phenomenon. We concluded that our hypotheses were infirmed and that the divergence phenomenon neither fully resulted from multi-factorial, nor non-linear, climatic control of LWD, and that it may be caused by non-climatic factors, of which atmospheric pollution that remains untested.

1. Introduction

Wood structure and density result from cambial activity (Larsson, 1994; Deleuze and Houllier, 1998), through the mechanisms of cell division, enlargement, wall thickening, and lignification (Fritts, 1976). In all tree species, the onset and duration of cambial activity is under strong temperature control (Rossi et al., 2008). In coniferous species, tree rings further show an intra-annual variation from low-density earlywood to high-density latewood (Larsson, 1994). Latewood density (LWD), particularly maximum latewood density, is often found to correlate positively with summer temperature (Gindl et al., 2000; Wang et al., 2002) and negatively with summer precipitation (Levanic et al., 2009; Wimmer and Grabner, 2000). Similar correlations have been reported for earlywood density, but are usually of a lower magnitude, or non-significant, compared to latewood density (Wang et al., 2002; Wimmer and Grabner, 2000).

In dendroclimatological research, the relationship between LWD and temperature is assumed to be constant over time in a given tree population (Hughes, 2002). This assumption is termed the 'uniformitarian principle', and serves as a basis for climatic reconstructions (Fritts, 1976). However, this principle has been shown to be violated in several recorded declines in the strength of the relationship between LWD and temperature in the second part of the 20th century, at circumpolar northern latitudes (Briffa et al., 1998a; Conkey, 1988), under Alpine conditions (Buntgen et al., 2008; Leonelli et al., 2009) and in the temperate Northern hemisphere (Wilson et al., 2007; Franceschini et al., 2012). This decline in the strength of the relationship between LWD and temperature has been termed the 'divergence' problem (D'Arrigo et al., 2008). Together with divergence, simultaneous unusual declines in wood density have often demonstrated in conifers and broadleaves, as

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http://dx.doi.org/10.1016/j.agrformet.2013.05.011

reported for maximum ring densities in the boreal zone (Briffa et al., 1998a; Conkey, 1988) and for latewood densities in temperate conditions (Franceschini et al., 2012; Bontemps et al., 2013).

The origin of the divergence phenomenon remains unclear, and several non-exclusive causes have been proposed (D'Arrigo et al., 2008; Visser et al., 2010). Most studies rely on simple linear correlation coefficients – or response functions – between wood density indicators and monthly temperature or precipitation (Gindl et al., 2000; Wang et al., 2002; Wimmer and Grabner, 2000). For the purpose of climate reconstruction, the selection of a single climatic predictor of wood density is essential, to allow the inversion of this relationship and reconstitution of past temperature (Briffa et al., 1998b). However, there are several limitations to such traditional approach that may explain the divergence phenomenon. First, they ignore the possibility that environmental factors other than temperature may have a negative effect on latewood density, such as climatic (*e.g.* water availability, Bouriaud et al., 2005) or non-climatic factors (*e.g.* air pollution, Wilson and Elling, 2004); this is termed the 'multi-factor hypothesis'. Second, traditional approaches are linear in essence, and neglect possible non-linear responses to environmental factors (Fritts et al., 1991). The effect of non-linear responses has been emphasised as a cause of apparent divergence during particularly warm periods, of which temperature range is usually poorly covered in calibration datasets (Loehle, 2009); this is termed the 'non-linear response hypothesis'. Third, changes in the timing of the growing season in relation to global change (Buntgen et al., 2010; Chmielewski and Rötzer, 2001) may cause seasonal shifts in climatic control (Lebourgeois et al., 2012), suggesting variation in the accuracy of climatic predictors over long study periods; this is termed the 'phenologic hypothesis'. To date, these hypotheses remain untested.

The objective of the present study was to test whether the apparent divergence phenomenon detected in the relationship between temperature and LWD may be attributed to multi-factorial or non-linear climatic determinism of wood density. We considered the 20th-century chronology of LWD for Norway spruce in north-eastern France, in which a steep decrease in LWD was identified from 1950 to 1980, as well as a loss of sensitivity to summer temperature from 1965 to 1980 (Franceschini et al., 2012). This divergence pattern occurred during a cool period (Moisselin et al., 2002); therefore, we discarded the hypothesis that a possible optimum in the response of latewood density to summer temperature would have been exceeded during a particularly warm period (Loehle, 2009). However, the non-linear response hypothesis may concern other climatic drivers. To perform our analyses, we used the PLS (projection to latent structure, Wold, 1975) regression analysis framework, which is gaining recognition as a useful tool in environmental studies (Carrascal et al., 2009; Gordo et al., 2008; Luedeling and Gassner, 2012). This technique combines features from principal component analysis and multiple linear regression, and facilitates multi-factorial modelling in the context of high dimensionality and multi-collinearity in the set of predictors.

2. Materials and methods

2.1. Tree sampling

We sampled 105 dominant Norway spruce (*Picea abies* Karst. L.) trees at 13 sites in north-eastern France. The sites were located in pure and even-aged plantations in State forests at various altitudinal positions (from 230 to 1000 m a.s.l.). On each site, at least two stands of sufficiently different ages growing in the same site conditions were selected according to the paired-plots method (Bontemps et al., 2009), allowing us to distinguish between the effects of ageing and calendar year on LWD. On each stand, three dominant trees were selected following (Duplat and TranHa, 1997). More information on this sampling approach is available in Franceschini et al. (2010).

2.2. Wood density measurements

Discs at a height of 1.30 m were sampled on each tree, and four orthogonal radial strips were sawn. Wood density was measured using X-ray microdensitometry using the method of Polge and Nicholls (1972) and measurement software of Mothe et al. (1998) and is fully described in Franceschini et al. (2010).

Annual ring density and ring width series were cross-dated after visual superimposition. Earlywood and latewood were separated at the median of within-ring density range (Mothe et al., 1998). For each cambial age, the average ring width, mean ring density and early- and latewood density (respectively EWD and LWD) were computed over the four strips. The regional 20th century chronology of LWD was estimated from a statistical modelling approach presented in Franceschini et al. (2012). From these data, we obtained an annual chronology of LWD filtered out from the effects of ontogeny, growth rate, between-site and -tree variations (Fig. 1a). In the following, historical variations of LWD will refer to this estimated chronology. These historical variations had a standard deviation of 45.3 kg m^{-3}. Summer temperature alone (July, August and September) has been evidenced to be insufficient to account for the variations of this chronology (Franceschini et al., 2012, Fig. 1b).

2.3. Climatic data

Since the 20th-century chronology of LWD was regional, average climatic series for each climatic variable studied had to be built, from individual climatic series representative of each site. Climatic data were extracted from the homogenised centennial time series produced by Météo-France (Caussinus and Mestre, 2004; Moisselin et al., 2002). These chronologies are free from historical shifts which may result from changes in the measurement instruments or in the location of stations, and were developed to assess climatic trends over the 20th century.

The objectives of our study were to identify the relationship between climatic variables and LWD during the twentieth century at the regional scale (Lorraine region) and not at the stand scale. Therefore, the climatic data had to be (i) available for the whole century and (ii) free from historical temporal bias. The homogenised climatic chronologies were therefore well-adapted to our objectives since these chronologies are corrected from historical shifts which may result from the meteorological instruments or in the location of the measurement stations over time. Such data were successfully used in previous works to assess the effects of climatic variables over time on several biological phenomena (Daux et al., 2011; Franceschini et al., 2013; Julliard et al., 2004). For a given location, the climatic data consisted of annual series containing the monthly mean maximum temperature (T_X, °C), monthly mean minimum temperature (T_N, °C) and monthly precipitation sum (P, mm). The climatic series from the closest available station was attributed to each sampled site. The same climatic series could be attributed to more than one site. Hence, climatic series from six stations were used for monthly precipitation sum (mean distance between station and site: 20.7 km) and climatic series from five stations were used for monthly minimum and maximum temperature (mean distance between station and site: 34.1 km) for the 13 sites. For each month and year, mean temperature was computed as the average of minimum and maximum temperatures (Moisselin et al., 2002). Additional climatic variables were computed from these primary data, including: (i) monthly potential Turc evapotranspiration (PET, mm, Turc, 1955) using monthly solar radiation