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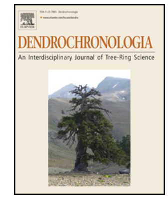

Blue intensity from a tropical conifer's annual rings for climate reconstruction: An ecophysiological perspective

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A R T I C L E I N F O

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A B S T R A C T

We developed Blue Intensity (BI) measurements from the crossdated ring sequences of *Fokienia hodginsii* (of the family Cupressaceae) from central Vietnam. BI has been utilized primarily as an indirect proxy measurement of latewood (LW) density of conifers (i.e., LWBI) from high latitude, temperature-limited boreal forests. As such, BI closely approximates maximum latewood density (MXD) measurements made from soft x-ray. The less commonly used earlywood (EW) BI (EWBI) represents the minimum density of EW and is influenced by the lighter pixels from the vacuoles or lumens of cells. The correlation of our BI measurements with climate, strongest for EWBI, rivals that for total ring width (RW), and we demonstrate that it can be successfully employed as an independent predictor for reconstruction models. EWBI exhibits robust spatial correlations with winter and spring land temperature, sea surface temperature (SST) over the regional domain of ENSO, and the Standardized Precipitation Evapotranspiration Index (SPEI) over Indochina. However, in order to mitigate the effects of color changes at the heartwood – sapwood boundary we calculated ΔBI (EWBI-LWBI), and it too exhibits a significant ($p < 0.05$), temporally stable response to prior autumn (Oct-Nov) rainfall and winter (December to April) dry season temperature. We interpret this response as reflecting a potential cavitation defense by reducing lumen diameter as a means to safeguard hydraulic conductivity in the stem, and to prevent the xylem from imploding due to negative pressure. This study has wide implications for the further use of BI from the global tropics, though it is unclear how many tropical tree species will be appropriate for use. It seems very likely that other wood anatomical measurements can be combined with BI and RW for climate reconstruction.

1. Introduction

In dendroclimatology, the maximum latewood density (MXD, expressed as grams/cm^3) of tree rings is a parameter measured directly by soft X-ray of carefully prepared thin sections of wood (Schweingruber, 2012). MXD, most commonly measured from temperature-limited conifers of the Northern Hemisphere high latitudes, often expresses a stronger correlation with current growing season temperature than does total ring width (RW). This is in part because RW of conifers exhibits a strong autocorrelation that reflects the carry-over effects from the previous year's growth that are often the result of non-climatic signals related to stand dynamics and endogenous disturbances (Cook and Kairiukstis, 1990; Fritts, 1976). Conversely, the autocorrelation of MXD is much more closely aligned to what is exhibited by temperature data (Briffa et al., 2002; Rydval et al., 2014), owing to a more direct current-season response to temperature than is expressed for RW. Therefore MXD is more reflective of the secondary process of cell lignification of the latewood, a process that is largely controlled by late growing season temperature (Mork, 1960). Accordingly, including MXD with RW for reconstruction of growing season temperature often increases the skill and spectral fidelity of reconstruction models (e.g., D'Arrigo et al., 2003; Wilson and Luckman, 2003; Wilson et al., 2016).

Blue reflectance or blue intensity (BI) is an image analysis based measurement that is interpreted as a proxy for the density of tree rings

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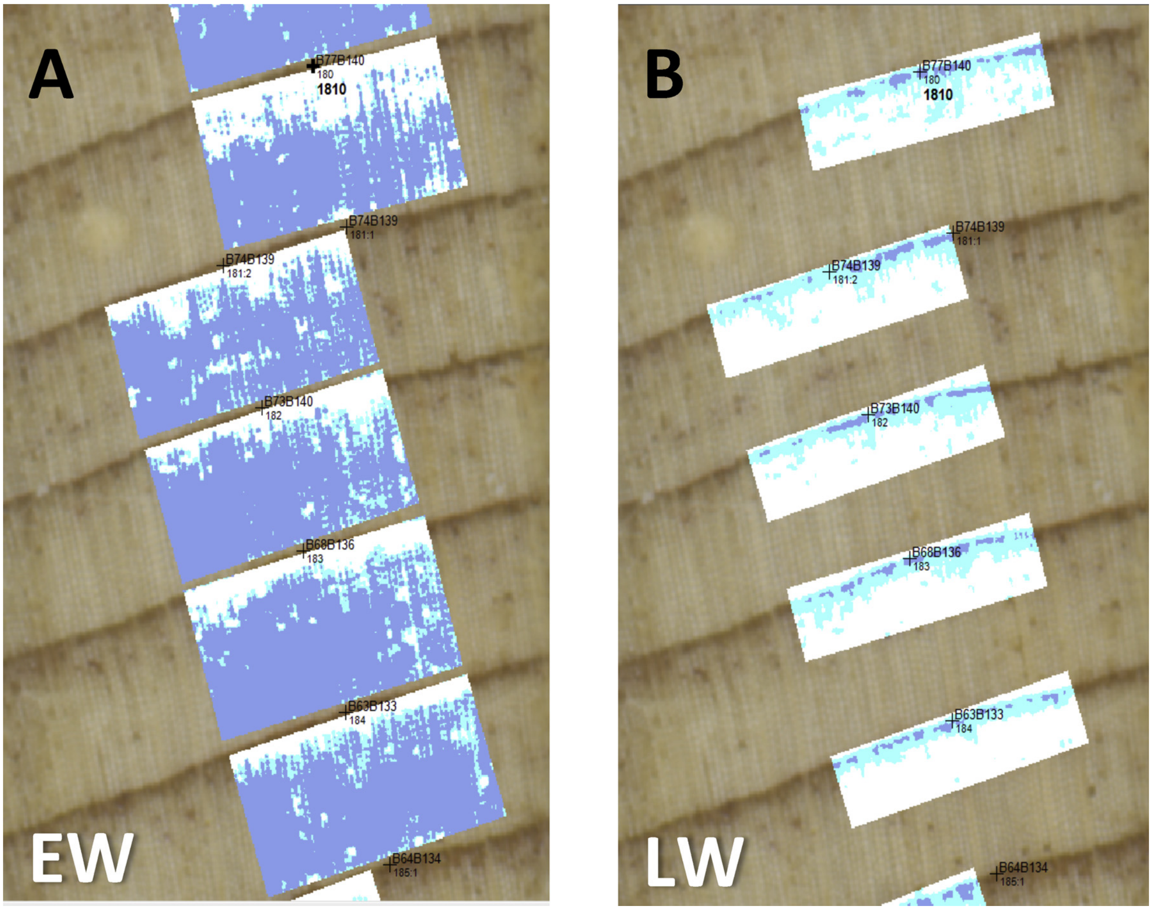

Fig. 1. CooRecorder image analysis software collects BI and RW measurements for each annual ring. For EW (A) all pixels in the highlighted box are sorted by dark and light wood (white and blue, respectively), and the whitest 85% of pixels are measured (dark blue). For LW (B) measurements are taken from the 15% of the darkest pixels (dark blue). To measure ΔBI the LW measurements are subtracted directly from the EW measurement, using an average of 100% of the pixels (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Campbell et al., 2007). The procedure is theoretically based upon the compound lignin's propensity to absorb ultraviolet light more readily than other wood structural components (Fukazawa, 1992). It is likely, however, that BI also reflects cellulose and hemi-cellulose, both of which are companion constituents of lignin in tracheid cell walls (Vincent, 1999; Yan et al., 2004). The higher the degree of reflected blue light, the less dense (i.e., less lignified) the wood and vice versa (Fig. 1). The understanding of this property dates back to Lange (1954) who utilized UV photomicrographs to measure the lignin content in the latewood of spruce. However it was only recently that Gindl et al. (2000) more formally made the connection between lignin content (density), as measured through UV photomicrographs, and temperature. BI from the growth rings of high-latitude/altitude trees has been shown to serve as an indirect proxy of wood density and therefore temperature of the late growing season. Consequently BI has been mostly used for high latitude/altitude conifer species where temperature has been shown to exert the greatest control on growth relative to other climate parameters (Björklund et al., 2014; 2015; Campbell et al., 2007; Dolgova, 2016; Rydval et al., 2014; 2017a; 2017b; Wilson et al., 2014; 2017a).

Both the new method of BI and the preceding work on MXD are predicated on the relationship between temperature and lignin content of the tracheid cells of conifers, and are most commonly applied to the latewood. Within a given species' optimal range, cooler temperatures inhibit and warmer temperatures enhance photosynthesis and, consequently, lignification. At high-latitude/altitude sites, cooler than average growing season temperature is correlated with less lignin allocated to tracheid cell walls, resulting in low-density rings for anomalously cool years known as "light rings" (e.g., Filion et al., 1986; Gindl, 1999; Szeicz, 1996; Waito et al., 2013). Similarly, hemispheric cooling caused by years of large volcanic eruptions may result in extreme reduction in the density of growth rings across a broad region (e.g., D'Arrigo et al., 2013; Esper et al., 2013, 2015; Gindl et al., 2000; Jacoby et al., 1999; Szeicz, 1996). Since lignification is a process secondary to the formation of the cells (i.e., cells are formed first and then lignified – *sensu* Mork, 1960) an abrupt reduction in growing season temperature below optimum levels can result not only in light rings, but often in "frost rings" where tracheid cells deficient in lignin rupture in response to freezing of their internal water (Fig. 2). Conversely, a warmer than average end to the growth season allows for a greater degree of lignification and an increase in the density of the latewood.

Given the discussion above, it stands to reason that BI would afford the same advantages over RW as does MXD, and for a fraction of the cost in time and money. Wilson et al. (2014) show that BI typically requires a larger sample size than MXD to improve signal strength, but due to the comparatively low cost of generating BI this is usually not a concern. Potential limitations remain, however, such as the effect of color changes at the heartwood-sapwood boundary for many species that can impart trend to data that may have nothing to do with a systematic climate related change in density (Björklund et al., 2014). Discoloration may also occur as the result of physiological response to a variety of non-climatic factors such as infusion of resin (and other compounds) near the site of an injury. Hence, trees with a particularly high contrast of wood color due to high resin content may exhibit either an abrupt or slow change in reflectance values that is not climatic in origin, and which distorts the BI time series (Fig. 3). It is currently