Identifying the main drivers for the production and maturation of Scots pine tracheids along a temperature gradient

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ARTICLE INFO

ABSTRACT

Even though studies monitoring the phenology and seasonal dynamics of the wood formation have accumulated for several conifer species across the Northern Hemisphere, the environmental control of tracheid production and differentiation is still fragmentary. With microcore and environmental data from six stands in Finland and France, we built auto-calibrated data-driven black box models for analyzing the most important factors controlling the tracheid production and maturation in Scots pine stem. In the best models, estimation was accurate to within a fraction of a tracheid per week. We compared the relative results of models built using different predictors, and found that the rate of tracheid production was partly regular but current and previous air temperature had influence on the sites in the middle of the temperature range and photosynthetic production in the coldest ones. The rate of mature cell production was more difficult to relate to the predictors but recent photosynthetic production was included in all successful models.

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1. Introduction

In extra-tropical areas, trees seasonally produce new wood (i.e., xylem), which serves as mechanical support, water and nutrients conduction, and storage of carbohydrates, water and defensive compounds. In conifers, the xylem mainly consists of one type of cells called tracheids. New tracheids are produced by cell division in the cambium, after which they follow a differentiation program involving enlargement, secondary wall formation, lignification, and programmed cell death. The regulation of tracheid formation is dependent on both endogenous factors, such as genotype and hormonal signalling, and exogenous factors such as the environment (Fritts, 1976; Plomion et al., 2001; Rossi et al., 2006; Vaganov et al., 2006). The phenology and intra-annual dynamics of the xylem production and maturation has already been accurately quantified for several species (Rossi et al., 2013; Cuny et al., 2014), but our

knowledge of the influence of environmental factors on these processes is fragmentary (Vaganov et al., 2006; Delpierre et al., 2016b).

The importance of air temperature, especially in the onset of xylem growth, has been widely reported. Rossi et al. (2008) observed that the onset of xylogenesis occurred with daily average temperature of 8–9 °C. An earlier onset and later ending of cell division cause a longer duration of xylem formation at higher temperatures (Rossi et al., 2011). Also a temperature sum approach has been used for modelling the onset of xylem formation (Seo et al., 2008; Swidrak et al., 2011; Jyske et al., 2014; de Lis et al., 2015).

In addition to air temperature, photoperiod has been reported to affect growth in many species (Partanen et al., 2001; Seo et al., 2011; Cuny et al., 2015), and the cell division rate has been found to decline after summer solstice (Rossi et al., 2006; Cuny et al., 2015). Zhai et al. (2012) found positive correlations between the minimum and mean air and soil temperature and tracheid formation in Jack pine (*Pinus banksiana* L.) stem. Oberhuber et al. (2014) found a negative relationship between vapour pressure deficit (VPD) and tree ring increment indicating that high VPD and the resulting high evaporative demand reduces turgor pressure in cells, as well as cell division and enlargement. Also in drought-prone areas, water

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deficits in late spring and summer play a critical role in the onset of xylogenesis and xylem cell production (Kalliokoski et al., 2012; Ren et al., 2015; Oberhuber et al., 2014; Lempereur et al., 2015). The role of different environmental factors controlling intra-annual growth dynamics most likely vary depending on growing environment but this is still not clearly understood.

Photosynthesis provides material for the growth and wood formation. A positive connection between annual ring width and net ecosystem productivity (NEP) or gross primary production (GPP) has been reported (Ohtsuka et al., 2009; Babst et al., 2014; Gea-Izquierdo et al., 2014; Schiestl-Aalto et al., 2015). On the other hand, Delpierre et al. (2016a) demonstrated that soil water and VPD are more important variables than carbon fluxes in determining weekly rates of wood formation in a temperate Oak. Zweifel et al. (2010) found a close relationship between stem radius changes and monthly and half-hourly NEP and monthly GPP but their study was based on stem radius measurements, which also include the swelling and shrinking of stems due to changes in water balance as well as the growth and regeneration of the phloem.

A detailed view on the importance of different environmental factors and photosynthetic production may help us perceive the effects of changing climate on secondary growth and the acclimation capacity of trees. The aim of this study is to examine which climatic and ecophysiological factors explain best the intra-annual dynamics of cell production and maturation in Scots pines (*Pinus sylvestris* L.) in different environments. Thus, we selected six Scots pine stands (three in Finland along a latitudinal gradient and three in France along an altitudinal gradient) from which we have three to four years (depending on the stand) of wood formation monitoring and environmental data, including measured daily average of temperature, radiation, and precipitation, air humidity as VPD, and modelled soil moisture and GPP. The total number of tracheids at different stages of cell differentiation and the number of mature tracheids (i.e., tracheids that had completed differentiation) were obtained from weekly microcore samplings.

We used machine-learning as a tool for modelling the intra-annual tracheid production and maturation dynamics from environmental data. As opposed to traditional statistical analysis, advanced machine learning methods learn quickly and automatically, potentially with very large numbers of variables and samples. Similar to traditional statistical analysis, results can help understanding biological mechanisms. In practice, we employed black box models, a tool that offers great flexibility with regard to modelling. Although black box models cannot always be interpreted at the coefficient level – there may in fact be no coefficients, e.g., decision tree and nearest-neighbour methods (Hastie et al., 2001) – the results obtained can be interpreted by way of relative performance evaluation: comparing the performance of the models using different input data. For example, if soil moisture as an input predictor leads to excellent prediction of growth at one site, but poor prediction at another site, it suggests that this particular environmental measurement is more relevant to the trees under the conditions of the first site.

2. Materials and methods

2.1. Study sites

The studied Scots pines grew on six sites in Finland and France (Fig. 1) where mean annual air temperature ranged from 0.8 °C to 10.0 °C (Table 1). Finnish sites lay in the boreal zone and French sites in the temperate zone. Sites 1 and 2 are Scots pine monocultures, site 3 a mixture of Scots pine and Norway spruce (*Picea abies* (L.) Karst.) and the French sites (4–6) are mixtures of Scots pine, Norway spruce and silver fir (*Abies alba* Mill.). The studied pines in boreal
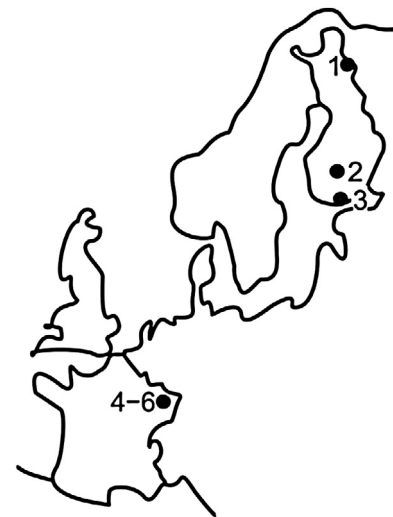

Fig. 1. Site map.

sites were middle-aged whereas the ones in the temperate sites were clearly more aged (Table 1). The sites 1 and 2 are introduced in detail by Hari et al. (1994), Hari and Kulmala (2005), respectively, and sites 4–6 in Cuny et al. (2015).

The air temperature (T), precipitation (P) and air relative humidity (RH) were measured at each site except for Ruotsinkylä (site 3). Solar radiation (I) were measured at SMEARI and SMEARII whereas the solar radiation at the French sites was measured at a nearby meteorological station and used for all the sites. For Ruotsinkylä, T, RH, P and I were attained from the nearby (5 km) weather station maintained by the Finnish Meteorological Institute. Special weather events such as drought, heavy winds etc. were not recorded in the study sites during the measured years.

Vapour Pressure Deficit (VPD, *V*, Pa) was computed as

$$V = v - RH\frac{v}{100},\tag{1}$$

where *RH* (%) is relative humidity, and *v* (Pa) the saturated water pressure,

$$v = e^{77.345 - 7235.42/T - 8.2\log(T) + 5.7113T/1000}\tag{2}$$

where temperature (*T*) is in Kelvins.

2.2. GPP estimates

We predicted daily gross primary production (GPP) and soil water content (S) using an empirical model PRELES (Peltoniemi et al., 2015). The GPP section of the model has been validated using measurements from seven pine and spruce stands located between latitudes 44°27′ and 67°22′ (Mäkelä et al., 2008). In the model, soil water content (S) is calculated using a bucket model using precipitation as an inflow and evapotranspiration and runoff as outflows. We simplified the calculation of evapotranspiration (E) as follows:

$$E = \beta_E G\frac{V}{V^{\kappa_E}} + \alpha_E(1 - f_{APAR})PARf_{W,E},\tag{3}$$

where *G* is GPP, *V* is VPD, *PAR* is the daily sum of photosynthetic photon flux density, β_E, κ_E, α_E, and f_{APAR} parameters and $f_{W,E}$ a soil water modifier as in Peltoniemi et al. (2015). The chosen soil water model is parameterized at site 2 leading there to similar results with the original model but with less complexity.

Briefly, PRELES predicts the GPP as a product of (1) potential daily light use efficiency (LUE), (2) fraction of absorbed photosynthetically active radiation (f_{APAR}) describing the photosynthesising leaf area, (3) photosynthetically active radiation (PAR), and (4)