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Intra-annual tracheid production of Norway spruce and Scots pine across a latitudinal gradient in Finland

Tuula Jyske[a], Harri Mäkinen[a,*], Tuomo Kalliokoski[a,b], Pekka Nöjd[a]

[a] Finnish Forest Research Institute, Southern Finland Regional Unit, PO Box 18, 01301 Vantaa, Finland
[b] Department of Forest Sciences, University of Helsinki, PO Box 62, 00014 Helsinki, Finland

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ABSTRACT

Considerable changes in tree growth are projected due to the expected climate change. The expected changes of climate call for a better insight into the growth responses of trees to varying environmental conditions over large geographical regions. The aim of this study was to analyse the intra-annual tracheid production of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) across a latitudinal gradient in Finland (60–68°N). The number of tracheids and the day of the year for the onset, fastest rate, and cessation of tracheid production were determined from microcores repeatedly collected in nine stands during growing seasons of 2001–2009. The onset of tracheid production varied from late May in southern Finland to mid-June in northern Finland. On all stands, tracheid production initiated earlier and ceased later for Scots pine than for Norway spruce. On average, the fastest tracheid production rate occurred slightly after the summer solstice, but variation between sites and years was high. In the northernmost Scots pine stand, the length of the growing season was less than two months and the onset of tracheid production required clearly lower *TS* than elsewhere. The results imply that within Finland, year-to-year weather variation has a marked impact on the timing of tracheid production. However, the results indicate that the Norway spruce and Scots pine have adapted and are able to adjust their tracheid production according to the local conditions.

1. Introduction

The timing, rate, and duration of xylem cell production and differentiation (i.e., xylogenesis) are key features in determining the quantity (radial increment) and quality (wood and fibre properties) of wood (e.g., Plomion et al., 2001). Cellular divisions in the vascular cambium produce new xylem cells, which undergo differentiation including radial enlargement, secondary cell wall formation and lignification, and cell death. Extrinsic and intrinsic factors control intra-annual xylem formation in a complex, interactive way. Previous studies at high latitudes and altitudes have emphasized the role of climatic factors, especially temperature, in triggering the onset and regulating the rate of tracheid production (Begum et al., 2007; Seo et al., 2008; Rossi et al., 2007; Gruber et al., 2010; Jyske et al., 2012; Lupi et al., 2012b). Photoperiod (Rossi et al., 2006b) and water availability also play a role in determining the intra-annual dynamics of radial increment and xylem characteristics (e.g., Jyske et al., 2010; Gruber et al., 2010).

Even though several recent studies have focused on the intra-annual radial increment of conifers at high latitudes (e.g., Mäkinen et al., 2003; Schmitt et al., 2004; Rossi et al., 2008; Seo et al., 2008; Hölttä et al., 2010; Jyske et al., 2010; Kalliokoski et al., 2013), our knowledge on the phenomenon is still not complete. Since measuring tracheid production at short intervals at the cellular level is laborious, we lack long-term data on the intra-annual tracheid production (cf., Henttonen et al., 2009). Further, tracheid production has generally not been monitored over large geographical regions (cf., Rossi et al., 2008). In Finland, earlier studies have either been based on a limited number of trees and sites (Mäkinen et al., 2003, 2008; Nöjd et al., 2008) or on cross-sectional inventory data with only a single-time radial increment measurement from each tree (Henttonen et al., 2009). Our recent results from a provenance experiment of Norway spruce (*Picea abies* (L.) Karst.) in southern Finland indicated that year-to-year and tree-to-tree variation in the timing of intra-annual radial increment were larger than the between-provenance variation (Kalliokoski et al., 2012).

Longer time series and geographically more extensive data sets are required for a deeper understanding on the variation of

* Corresponding author. Tel.: +358 29 5325265/+358 40 8015265; fax: +358 29 5322103.
E-mail address: harri.makinen@metla.fi (H. Mäkinen).

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intra-annual tracheid production and the factors controlling it. These type of data are especially valuable, since considerable changes in tree growth are projected during the next few decades due to the expected warming of climate and the rising trend of the atmospheric CO_2 (e.g., Kellomäki et al., 2008). The predicted elevation in temperature is expected to prolong the growing season (Peltola et al., 2002; Jylhä et al., 2009; Ruosteenoja et al., 2011) and cause tracheid production to start earlier. However, an earlier onset of cambial activity may increase the vulnerability of trees to frost damage (Häkkinen et al., 1995). Thus, a deeper understanding on the factors controlling the annual progress of cambial activity including provenance-climate interactions would help, e.g., to select proper genetic material and thus mitigate the possible climate induced risks in forestry practice.

The aim of this study was to assess intra-annual tracheid production in Norway spruce and Scots pine (*Pinus sylvestris* L.) across a latitudinal gradient in Finland. We studied the variation of the growth onset, peak (i.e., maximum rate of tracheid production) and cessation, and the number of tracheids produced, as well as the length of the increment period between the sites, species, and years. During the growing seasons of 2001–2009 we extracted microcores from a total of 127 dominant or co-dominant trees at nine sites. From the microcores, the timing and rate of tracheid production were determined and related to variation of temperature sum (*TS*).

Rossi et al. (2008) have shown that the onset of diameter increment occurs after surpassing a temperature threshold and in late summer diameter increment correspondingly cease when temperature drops below a critical value. Thus, we hypothesized that the trees at the northern sites initiate their tracheid production later and cease it earlier and at a lower *TS* than the trees at the southern sites.

2. Materials and methods

2.1. Study sites

The material consisted of Norway spruce and Scots pine trees growing in nine stands across a latitudinal gradient in Finland (60–68°N) (Fig. 1, Table 1). The stands were 32–79 years old, located on the medium infertile, medium fertile, and fertile sites typical for Scots pine and Norway spruce, classified as *Vaccinium*, *Myrtillus* (in northern Finland, the sites of the corresponding fertility levels are called as *Uliginosum–Empetrum–Myrtillus* type and *Vaccinium–Myrtillus* type, respectively) and *Oxalis–Myrtillus* site types, respectively (Cajander, 1949). The southernmost sites (Solböle and Ruotsinkylä) were located at low altitude (30–45 m a.s.l.) but the altitude of the sites increased northward, being 390 m a.s.l. in Värriö (Table 1).

The stands had been managed following the recommendations for practical forestry (Finnish Forestry, 2011), but for all sites at least 10 years had elapsed since the last thinning. The southernmost stand (Solböle in Tammisaari) belongs to a provenance trial including 19 provenances originating from Finland and central Europe (Kalliokoski et al., 2012). For this study, only the southern Finnish provenance representing local seed material was selected. All the other stands were naturally regenerated and represent the local origin. The stands in eastern Finland (Koli and Jaamankangas) belonged to artificial soil frost experiments (Repo et al., 2007; Jyske et al., 2012). In this study, only the untreated control trees were used.

2.2. Meteorological data

For each site, weather data of the nearest meteorological station of the Finnish Meteorological Institute was used (Table 1), except

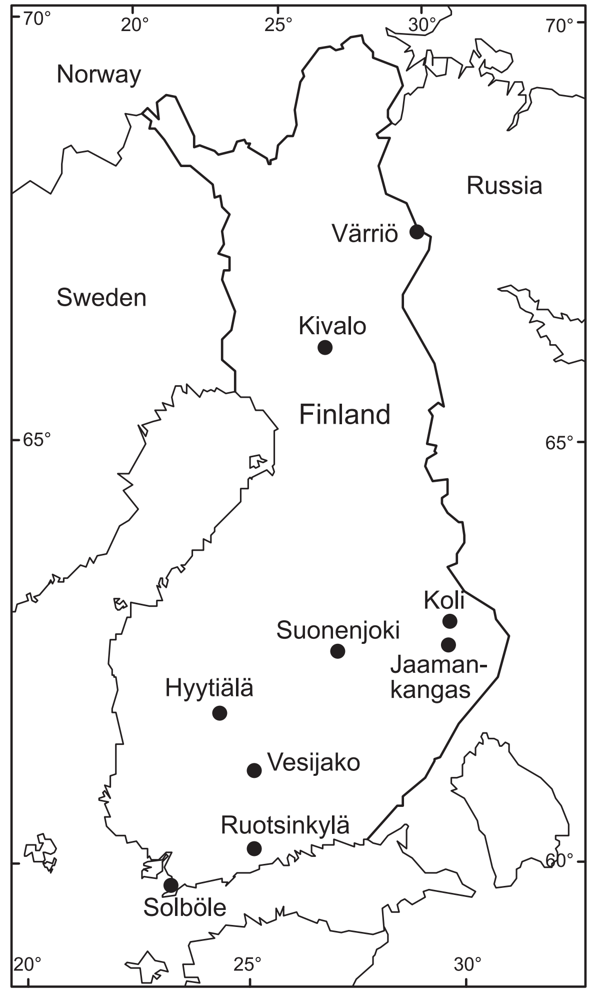

Fig. 1. Location of the study sites.

for Jaamankangas, where air temperature was measured at the height of 2 m above the ground at the site (105T thermocouple, Campbell Scientific, Shepshed, U.K.). Air temperature and precipitation sum were monitored every three hours. TS_i (degree days, d.d.) at day n was calculated as a sum of positive differences between the daily mean air temperature (T_i) and the threshold value +5 °C:

$$TS_i = \sum_{i=n_{start}}^{n} (T_i - 5), \quad \text{if} \quad T_i > 5 \tag{1}$$

Various threshold temperatures from 0 °C to +10 °C have been used for mid-latitude and tropical species for measuring vegetative development (Arnold, 1959; Holdridge, 1967). In Fennoscandia, due to snow cover and frozen soil, the freezing point (0 °C) has been found too low for describing the development stages of various plants (Sarvas, 1972; Diekmann, 1996; Heikinheimo and Lappalainen, 1997). In spring, calculation of *TS* was started when five consecutive days had $T \geq +5$ °C (n_{start}). Threshold +5 °C (or +6 °C) is a commonly used standard in calculating the effective temperature sum in forestry and agriculture (so-called thermal growing season) (Nuttonson, 1955; Monteith, 1981). Below that threshold, the temperature is not considered effective by convention.

2.3. Field sampling

Within each site, three to nine dominant or co-dominant sample trees were selected for monitoring tracheid production during