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INTRA-SEASONAL DEVELOPMENT OF RADIAL INCREMENT OF *PICEA ABIES* IN LATVIA

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Abstract
Norway spruce (*Picea abies* (L.) H.Karst.) is amongst the most important tree species for forestry in Latvia. It has been suggested that due to the foreseen climate change the productivity of Norway spruce in Latvia may decrease. Continuous observations of radial increment allow to identify periods with different growth intensity and to study the effect of environmental conditions on radial increment during them. The aim of this study was to analyse stem radial variation of Norway spruce in mixed-species stand in response to meteorological conditions over one growing season. Stem radial variation of one Norway spruce tree was monitored by band dendrometer throughout the growing season of 2013. Cumulative radial increment was divided into contraction, recovery and increment phases by the stem cycle approach. Four periods with distinct apportionment of these phases were identified – winter/spring dormancy, spring/summer growth, growth termination and autumn hydration fluctuations. Radial increment began in the second part of May and the most active increment was observed during period of spring/summer growth. This period lasted for 42 days with the mean amplitude of stem radial variations reaching 0.06 mm while the length of increment phase reached up to two days. Throughout the growing season increment was facilitated by an increase in the temperature. Meanwhile, the effect of precipitation was insignificant, presumably due to sufficient water availability and low interspecies competition for it, characteristic in mixed species stands due to differences in depth and distribution of root systems between the species.
Key words: Norway spruceband dendrometer, stem cycle approach, stem radial variation, dendroclimatology.

Introduction

Adaptation of forestry to the foreseen climate change scenarios has been considered as one the greatest challenges for modern day forestry (Lindner *et al.*, 2014). In this regard, radial growth of trees and its relationship with climatic factors have been vastly studied in recent decades (Sheppard, 2010; Speer, 2010). However, majority of these studies have focused on tree rings and anatomic elements of xylem formed over a longer period of time (Zweifel *et al.*, 2006; Matisons & Brumelis, 2012; Senhofa *et al*., 2016). Meanwhile, the effect of climate on radial growth with a higher temporal resolution is less commonly studied, presumably due to a more complex data gathering, processing and analysis (Bouriaud *et al.*, 2005; Zweifel *et al.*, 2006; McMahon & Parker, 2015). Nevertheless, findings in the studies of a high temporal resolution favour to understand ecophysiological processes affecting the tree radial growth (Deslauriers, Rossi, & Anfodillo, 2007; Michelot *et al.*, 2012; Van der Maaten, Van der Maaten-Theunissen, & Spiecker, 2012; De Swaef *et al.*, 2015).

Band dendrometers are amongst the most widely used and accessible instruments to obtain continuous measurements on stem radial variation (SRV) (Deslauriers, Rossi, & Anfodillo, 2007; McMahon & Parker, 2015) that can been used to study radial growth, water status and transport, nutrition, carbon relations, phenology of trees (De Swaef *et al.*, 2015). According to Daudet *et al.* (2005), SRV is a result of several simultaneously co-acting mechanisms – reversible contraction and expansion of dead conducting tissues due to fluctuations in internal tensions, hydration induced reversible shrinkage and swelling of living tissues, irreversible radial growth and thermal expansion and contraction. Thus, the extraction of radial growth from the time series of stem radial variation is a crucial step for further analysis (Deslauriers, Rossi, & Anfodillo, 2007; De Swaef *et al.*, 2015) and has been the main reason for criticism of dendrometers (Makinen, Nojd, & Saranpaa, 2003). Nevertheless, several methods such as 'stem cycle approach' and 'daily approach' have been elaborated to extract growth signal from the time series of SRV (Downes, Beadle, & Worledge, 1999; Deslauriers, Rossi, & Anfodillo, 2007; Deslauriers *et al.*, 2011).

While traditional forestry tends to focus on single species stands, ecological modelling has shown that stands with several species coexisting in complementary niches may be more productive due to a higher use of the available resources (Loreau & Hector, 2001; Morin *et al.*, 2011). Such mixed species stands are also believed to be less vulnerable to uncharacteristic and extreme weather events caused by climate change due to spatial and temporal differences of limiting factors of coexisting species (Shanin *et al.*, 2013).

Norway spruce is the third most widely used tree species in forestry in Latvia covering 18% of all forest area (State Forest Service of Latvia, 2017) and is commonly used in single species stands. The aim of the study was to assess the intra-annual SRV and the effect of meteorological parameters on SRV of Norway spruce growing in mixed species stand over one growing season.

Materials and Methods

Throughout the growing season of 2013, SRV was monitored for one 60 years old Norway spruce tree located in a mixed-stand with black alder (*Alnus glutinosa* (L.) Gaertn.), Scots pine (*Pinus sylvestris* L.) and common aspen (*Populus tremula* L.) on wet and nutrient rich peat soil in north-west Latvia (57°40' N lat., 22°19' E long.). The forest type corresponded to *Filipendulosa* (Bušs, 1976). In the study area, climatic conditions are affected by dominant oceanic air masses, providing this area with relatively mild weather throughout the whole year where 30-year mean air temperatures in July and February range from +15.2 to -3.6 °C, respectively (Draveniece, 2007). Meteorological parameters were monitored on-site by the meteorological station Wireless Vantage Pro2 (Davis Instruments). In order to calculate the vapour pressure deficit (VPD), saturation vapour pressure (e_s) was found:

$$e_s = 6.11 \times \exp\ LRv\left(1273 - 1T\right), \qquad (1)$$

where L is the latent heat of vaporization (2.5× 106 J kg^{-1}), Rv is the gas constant for water vapour (461 J K^{-1} kg^{-1}). Afterwards, calculation of VPD was done as:

$$VPD = e_s \frac{100 - RH}{100}, \qquad (2)$$

where RH is relative humidity.

Monitoring of SRV started on the 113th day of the year (DOY 113) (23 April) and continued for 195 days (Fig. 1, (C)). Stem radial variation was measured hourly by automatic band dendrometer DRL26C (EMS Brno, Czech Republic) which was placed 130 cm above the ground. To reduce the impact of hygroscopic swelling and shrinkage, a partly loosened outermost layer of bark was removed before installing of dendrometer. Time series of cumulative SRV was divided into contraction (C), recovery (R) and increment (I) phases by the stem cycle approach (Downes, Beadle, & Worledge, 1999; Deslauriers *et al.*, 2003). This method defines: C as a period between the first maximum of stem radius and consecutive minimum; R as a period from minimum until the point where previous maximum has been reached or until the beginning of the next contraction phase; I as a period until the next maximum resulting in either positive or negative value, depending on whether or not the previous maximum has been exceeded (Deslauriers *et al.*, 2003; Vieira *et al.*, 2013). Cycle consisted of

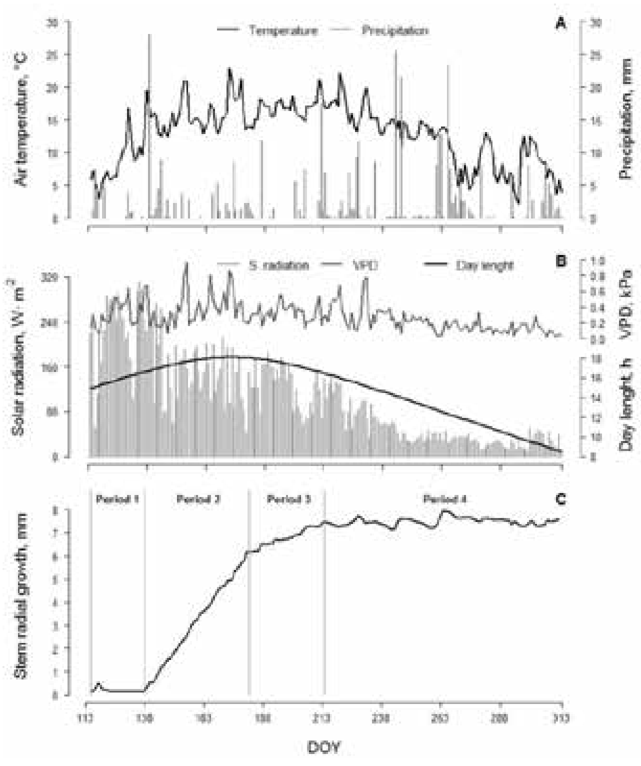

Figure 1. **(A)** Mean diurnal air temperature (black line) and precipitation sum (bars), **(B)** solar radiation (bars), VPD (grey line) and daytime length (black line), **(C)** stem radial variation per day of year (DOY). Vertical lines in **(C)** separate distinct periods of increment: Period 1 – winter/spring dormancy; Period 2 – spring/summer growth; Period 3 – growth termination; Period 4 – autumn hydration fluctuations.

phase C followed by phase R and of phase I, in case the increment occurred before the next contraction. For each cycle duration and amplitude of variation was calculated. The amplitude of SRV and phase I were used as criteria to divide the series of cumulative SRV in four periods - winter/spring dormancy (P1), spring/summer growth (P2), growth termination (P3) and autumn hydration fluctuations (P4). These periods were determined as follows: P1 – as a period before the beginning of continuous positive increment; P2 – a period from the beginning of continuous positive increment until spring/summer maximum (the point after which increment continued notably slower); P3 from the end of P2 until SRV started to fluctuate greatly but with a relatively insignificant increment; P4 as a period of the greatest fluctuations in SRV but almost no increment. Besides the aforementioned criteria, in the stem cycle approach the exact division between periods depends also on expert opinion (Vieira *et al.*, 2013), thus complicating a precise replication of the study. Nevertheless, the impact of expert opinion cannot significantly alter the results.

Pearson`s correlation analysis was performed to assess the effect of meteorological conditions on SRV at different phases and separately for each period. For the correlation analysis, hourly maximum and minimum air temperature, sum of precipitation, VPD and solar radiation were used. To avoid the misleading effect of missing data and different lengths of periods of SRV on results of statistical tests, correlation analysis was validated using bootstrap procedure with 10'000 iterations (Vieira *et al.*, 2013). All steps of data analysis were carried out using statistical package R 3.3.2. (R Core Team, 2013). Its package 'dendrometeR' was used (Van der Maaten *et al.*, 2016) to apply the stem cycle approach.

Results and Discussion

Seasonal and diurnal SRV

SRV followed clear seasonal pattern showing notable differences in amplitude and duration of phases within each period (Fig. 1 C). During the P1, only slight fluctuations in SVR were present, except for the abrupt swelling and shrinkage observed at the very beginning of SVR monitoring. This extrinsic pattern might be caused by the sudden increase followed by decrease in temperature (Fig. 1 A), which may have led to the release of water from the living tissues as part of physiological mechanism to avoid intracellular freezing (Ameglio, Cochard, & Ewers, 2001; Charrier, Cochard, & Ameglio, 2013). A positive radial increment started at DOY 138, marking the start of P2. Within P2, cumulative curve of SRV followed a relatively sharp and steady increment with just minor (in terms of duration and amplitude) phases C and R (Fig. 1 A; Fig. 3). P2 lasted for 58 days and the mean amplitude of stem radial variation during it reached 0.06 mm while the length of phase I reached up to two days. Transition between P2 and P3 occurred in the second part of June, but was not as obvious as transition between the first two periods. During P3, the increment trend of cumulative curve of SRV started flattening due to decrease in duration and amplitude of phase I (Fig. 3 C & F) and increase of duration of phases R and C (Fig. 3 A, B, D & F). P4 started in the beginning of August, and during it, the greatest amplitude of all three phases and almost even apportionment of duration of these phases was observed, resulting in the most notable fluctuations in cumulative curve of SRV. The maximum stem diameter was observed at the end of September and can be attributed to rehydration of stem in response to replenishment of soil water content rather than radial growth (Deslauriers, Rossi, & Anfodillo, 2007).

Contrary to the results of studies on intra-annual SRV of trees growing in drought prone environment (Vieira *et al.*, 2013), in our study the increment continued to increase since the start of P2, while notable shrinkage of stem at late summer was not observed. An increase of temperature in late summer and its cumulative effect leads to decline in soil water content, while the transpiration demand increases with temperature and daytime length (Herzog, Hasler, & Thum, 1995). Thus, to minimize the risk of hydraulic failure the transpiration demand is reduced by stomatal closure, resulting in lower metabolic activity and, consequently, decline of radial growth (Zweifel *et al.*, 2006; King *et al.*, 2013). Apparently, in our study site water availability was sufficient throughout the whole growing season not imposing tree to enter quiescence. Low values of VPD and an increase in precipitation during P3 and P4 correspond to this assumption (Fig. 1 A & B).

Similarly as in the study of Vieira *et al.* (2013), diurnal fluctuations in SRV followed a rather similar trend during all four periods (Fig. 2). The highest value of stem diameter was observed from 4 till 9 AM, with the peak value earlier in the morning in P2 and P3 which were characterized with a higher daytime length. While, due to internal transport of water from storage to conductive tissues to meet the transpiration demand (Herzog, Hasler, & Thum, 1995; King *et al.*, 2013), stem diameter was the lowest during the middle of the day and started to replenish in the evening. Maximum mean diurnal amplitude of SRV (0.06 mm) was observed in P2.

Response of SRV to meteorological parameters

Response of amplitude and duration of SRV to meteorological parameters differed between phases and periods (Fig. 4). Contrary to the findings of Vieira *et al.* (2013), climatic signal in duration was

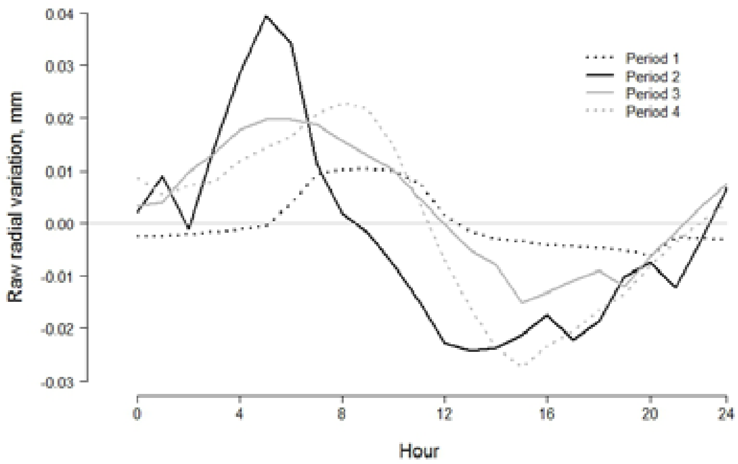

Figure 2. Diurnal cycle of stem radial variation in each period.

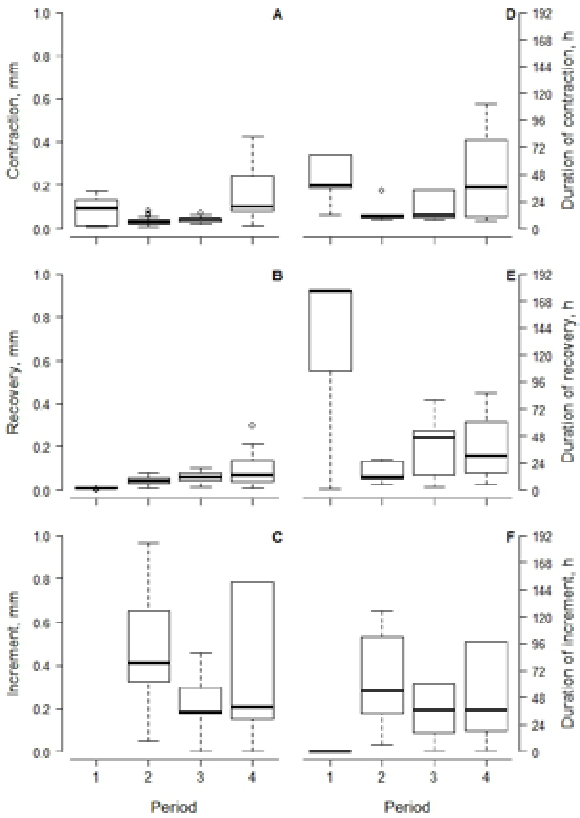

Figure 3. Amplitude (A, B, C) and duration (D, E, F) of stem radial variation per phase (contraction – A and D; recovery – B and E; increment – C and F). Bold line represents the median, box corresponds to lower and upper quartile, whiskers show minimum and maximum values (within 150% of interquartile range from median and outliers are shown by circles).

more clearly expressed than in amplitude of SRV phases.

During P1, a strong negative correlation was observed between the amplitude and duration of C and both maximum and minimum temperatures, while the temperature had a positive influence on duration of R. Such results might be explained by rehydration of stem before the beginning of growth that can be observed for trees in cold environment (Deslauriers *et al.*, 2003). In P1, this phenomena was clearly expressed during the abrupt swelling and shrinkage at the very beginning of SRV monitoring when the temperature fluctuated around the average minimum threshold (4 – 5 °C) for xylogenesis reported by Rossi *et al.* (2008). However, after this abrupt swelling and shrinkage notable rehydration was not observed until the P2.

Duration of C showed a negative correlation with temperature also in P2, P3 and P4, while the amplitude of C had a negative correlation with temperature in P3 and P4. These results can be explained by above-mentioned diurnal cycle of internal water transport between the tissues to meet the transpiration demand during the warmest part of the day (Herzog, Hasler, & Thum, 1995; King *et al.*, 2013). The negative correlation between solar radiation and both amplitude and duration of C in P4 might be explained similarly, considering the strong relationship between solar radiation and temperature, especially in autumn when the daytime length is the shortest (Fig. 1 B).

Except for the amplitude in P3, the increment in terms of duration and amplitude was facilitated by both temperature parameters and solar radiation in all periods in which increment was observed (P2, P3 and P4), and this relationship was the strongest in P4. The positive effect of temperature on increment can be explained by the direct influence of temperature on assimilation and meristematic activity, e.g., cell division, differentiation and elongation, while solar radiation directly facilitates photosynthetic activity (Pallardy, 2008).

Moisture requirements of Norway spruce are relatively high, and a positive influence of increase in summer precipitation on radial growth of this species has been shown in numerous studies (Makinen *et al.*, 2002; Andreassen *et al.*, 2006; Koprowski & Zielski, 2006). However, in our study the influence of precipitation on amplitude and duration of I was negative in periods of the most active growth, e.g., P2 and P3. Furthermore, VPD positively influenced the amplitude and duration of I in both of these periods. Presumably, these results can be explained by sufficient soil moisture level in the sampling site throughout the season and possible negative effect of rise in moisture

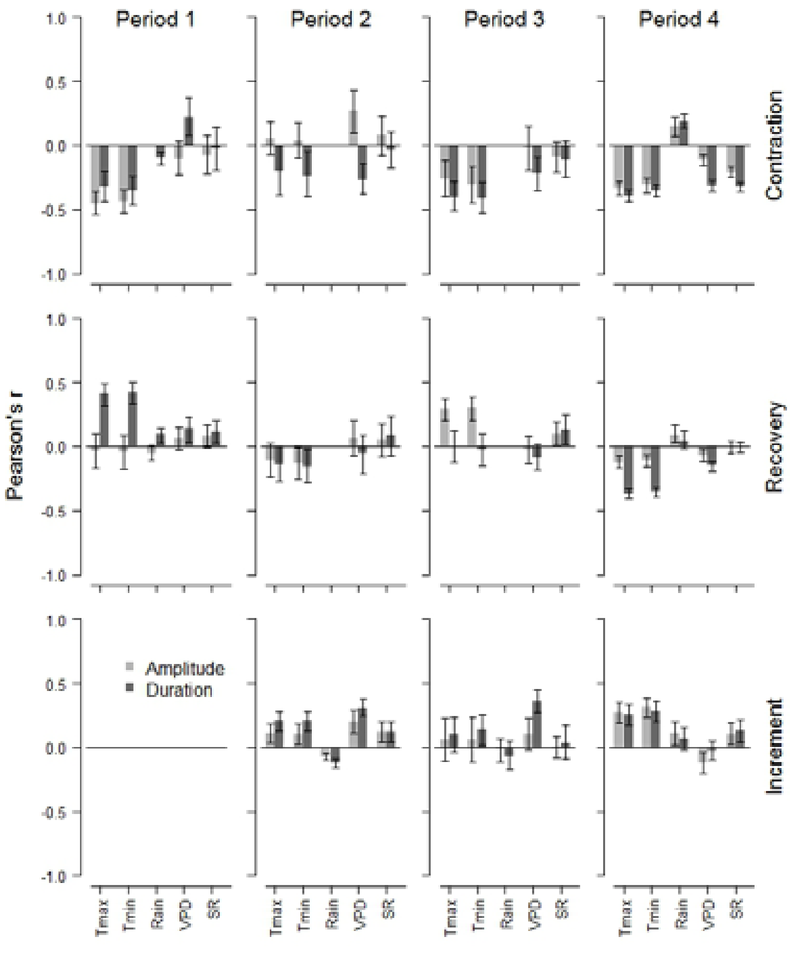

Figure 4. Bootstrapped correlations between both amplitude and duration of each phase of stem radial variation and meteorological parameters (Tmax, Tmin – maximum and minimum air temperature; Rain – sum of precipitation; VPD – vapour pressure deficit; SR – solar radiation). Correlations are significant ($p < 0.05$) if the confidence interval represented as vertical error bars does not include zero.

level caused by an increase in precipitation. In such conditions, water molecules may fill the capillary pores of soil, thus decreasing root respiration and water absorption that consequently lead to stomatal closure and reduced photosynthetic activity (Kozlowski, 1997; Parent *et al.*, 2008). VPD values during both of these periods, with a few exemptions, did not exceed 0.6 kPa (Fig. 1 B), meaning that the air was relatively saturated and did not cause notable transpiration (Oren *et al.*, 1999; Zweifel & Hasler, 2000). Furthermore, a lower competition between neighbouring trees for soil water due to differences in depth and distribution of root systems between species, may have facilitated the independence of increment from precipitation of the studied tree. Nevertheless, more comprehensive studies involving several coexisting species, the monitoring of sap flow and soil moisture level over several years are needed to properly address this question.

Climatic signal in R during P2 and P3 was less pronounced than in I and C. Sufficient soil moisture level throughout the monitoring of SRV, meaning that water resources did not limit the recovery, could be the reason for such results. While similar climatic signal in R and C during P4 might be related to interdependency between them, e.g., better rehydration leading to a higher possible contraction and *vice versa* (Vieira *et al*., 2013).

Conclusions

1. SRV monitoring revealed four distinct periods of fluctuations in and increment of stem radius of Norway spruce over one growing season. Presumably, a sufficient soil moisture level accompanied with a low competition for it between neighbouring trees of different species allowed for the studied tree to maintain the radial increment throughout most of the SRV monitoring.
2. The factors mentioned above might have decreased the dependency of the radial increment of the studied tree on precipitation during the growing season, which has been previously reported for Norway spruce.
3. The increment was facilitated by an increase in the temperature, indicating that in case of sufficient soil moisture the increment of Norway spruce could benefit from rising temperatures throughout the growing season. While artificial raising of soil moisture level might not be cost-efficient, our results indicate a potential for wider use of Norway spruce in mixed-species stands where due to contemporary niches of different species the negative affect of decrease in precipitation on productivity of this species might be lower.

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