

Intra-annual dynamics of height growth of Norway spruce in Latvia

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Abstract. Norway spruce (*Picea abies* (L.) Karst.) is a tree species with the highest economic importance in northern Europe. Therefore, it is important to improve knowledge of the potential effects of climatic changes on the growth of this tree species. An essential part of the information is the tree’s intra-annual growth cycle. There are comprehensive studies describing the formation of radial increments of coniferous trees; however, information on height growth in hemiboreal forests is scarce. The aim of our study was to characterize the intra-annual height growth of Norway spruce in Latvia. The data was collected from two Norway spruce trials located in in former arable and forest land in the central part of Latvia, including 89 and 68 open-pollinated families (respectively) of plus-trees. Weekly height increment measurements of 20 trees per family were carried out during the 9th growing season. Growth intensity culminated in 10 ± 0.2 mm day⁻¹, following similar trend, but resulting consistently in significantly different values between the trials; the higher growth intensity was observed in higher trees and families, which also showed higher frequency of lammas shoots, boosting their height superiority even further. Significant family effect on all coefficients of shoot elongation curves, described by Gompertz model, was found. Both tree height and height increment at family mean level was strongly correlated with the asymptote parameter ($r_{fam} = 0.93$, $P < 0.01$) and the growth rate parameter ($r_{fam} = -0.70$, $P < 0.01$).

Key words: *Picea abies* (L.) Karst, height growth, shoot elongation, growth intensity, open-pollinated family.

INTRODUCTION

Norway spruce (*Picea abies* (L.) Karst.) is widely planted in northern and eastern Europe for timber production. Due to its large branch biomass (Libiete-Zalite & Jansons, 2011; Libiete-Zalite et al., 2016), logging residues are often collected in spruce stands and in some regions stumps are also extracted (Lazdins & Zimelis, 2012; Zimelis et al., 2012). Biomass exploitation is expected to flourish in the future, upgrading the commercial value of spruce stands (Bardulis et al., 2012; Kaleja et al., 2013). In most of the Baltic Sea region countries, active tree breeding programs exist and hence, improved seed material is available in order to boost increment and/or improve other traits of trees (Jansson et al., 2013; Irbe et al., 2015; Jansons et al., 2015a). Furthermore, vegetative propagation and fertilization of Norway spruce is possible at a commercial scale,

providing opportunities for further increase of the stands productivity (Jansons et al., 2016). The use of improved plant material (especially clones) increases the regeneration costs, therefore it is important to assess and minimize the potential risks, i.e., ensure adaptation to climatic changes, namely, increasing length of vegetation period and increasing temperature.

Temperature has been identified as the dominant environmental signal that triggers tree phenology (Körner, 2003). However, its impact on Norway spruce growth under average conditions is not easily detected, since trees respond less strongly to climatic variation, than to extreme conditions (Mäkinen et al., 2003). Long-term trends in the temperature-height growth relationship for coniferous trees, had been analysed using annual meteorological data and information on height increments from repeated measurements or destructive sampling (Kroon et al., 2011; Jansons et al., 2013a; 2013b; 2015b). Nevertheless, such an approach does not allow the determination of the exact moments during the vegetation period bearing critical influence of meteorological conditions – for this purpose detailed information on intra-seasonal height growth intensity is required (Jansons et al., 2014). The information would also allow the evaluation of the relative importance of length of the growth period vs. the growth intensity in the total length of annual height increment and thus providing more detailed information on climate adaptation.

Numerous studies have found a great variability of climatic adaptive traits for Norway spruce, both between provenances and between families within a provenance (Krutzdch, 1974; Danusevicius, 1999; Eriksson, 2008). These differences were influencing survival and stem quality of trees, mainly due to frost damages (Persson & Persson, 1992). Also shoot growth differences between provenances (Pollard & Logan, 1974; Skrøppa & Magnussen, 1993), and more recently between families have been found (Skrøppa & Steffenrem, 2015). However, no such studies including family components had been carried out in Latvia before. The aim of our study was to characterize the intra-annual height growth of Norway spruce in Latvia. Data from this initial study could be used to design more comprehensive research work in the future for predictions of the influence of climatic changes and consideration in tree breeding.

MATERIALS AND METHODS

The study was carried out in two Norway spruce progeny trials in central Latvia, Rembate (56°46'N, 24°48'E) and Auce (56°29'N, 22°52'E), including 89 and 68 open-pollinated families (22 families common in both sites) of plus-trees selected from different regions of the country. The trials were planted in 2005, using 3 year-old bare-rooted plants, on fertile abandoned agricultural land, corresponding to *Oxalidos* forest type according to classification used in Latvia (Bušs, 1976), cambisol according to FAO WRB soil classification (Nikodemus et al., 2008) with 2 x 2.5 m spacing in Rembate and on forest land with fertile drained mineral soil (*Myrtillosa mel.* forest type, arenosol) with 2 x 3 m spacing in Auce. Inter-annual height increment differences in those trials had been analyzed (Neimane et al., 2015), therefore this study focuses on intra-annual height growth. Measurements were carried out during 9th growing season of trees, bud-burst date assessed (visiting the site every 2 days until approximately half of the trees had bud-burst) and weekly height increment measurements carried out for 20 randomly selected trees per family, avoiding trees with browsing damage, insect damage or broken

top. Additional assessment was carried out at the end of September, marking the trees with lammass shoots. Daily temperature and precipitation data were obtained from the closest stations of Latvian Environment, Geology, and Meteorology Centre.

The non-linear Gompertz model was fitted per tree individually and per family (1)

$$f(A) = \alpha \exp(-\beta \exp(-kA)) \quad (1)$$

where: α – asymptote parameter; β – displacement parameter; k – growth rate parameter and A – day since beginning of the year. This model has been advised as being sufficient for the height growth curve development, in this case, using tree age as dependent parameter A (Fekedulegn et al., 1999).

The t -test was used to assess differences between groups of trees stopping the height growth at different time periods, as well as to evaluate differences in tree height, length of height increment and height growth intensity between the trees forming and not forming lammass shoots at the end of vegetation period. It was also used to assess differences in height increment between groups of trees with different times of growth cessation. The Pearson correlation test was used to assess the relationship of growth intensity between the trials, links between height and height increment, relationship between proportion of trees that had stopped the growth at certain period during the season and total length of height increment, as well as link between estimated Gompertz model parameters and family mean height and individual tree height. Analyses were carried out using the statistical package R 3.0.2. (R Core Team, 2013).

RESULTS AND DISCUSSION

The trend of Norway spruce height growth intensity was similar in both sites (Fig. 1), as indicated by the strong correlation of mean values of this trait between the trials ($r = 0.91$, $P < 0.01$). Peak of height growth intensity was reached in the first two weeks of June, when it was 10 ± 0.2 mm day⁻¹ (mean, \pm 95% confidence interval) in Rembate and 8 ± 0.4 mm day⁻¹ in Auce. Differences in growth intensity could partly be explained by temperature: in 73% of days in the assessed period it was higher in Rembate than in Auce, differences in diurnal mean was on average was 0.7°C, in minimum 0.4 °C and maximum 0.8°C (Fig. 1); similar temperature differences in the year prior to measurement were observed. In the analysis of formation of radial increment (secondary growth) of 75-year-old Norway spruce, Giagli et al. (2016) found, that the monthly minimum temperature in January-April, as well as the monthly maximum temperature during the growing period was a major factor affecting the average rate of cambial cell production and amount of precipitation, the main factor positively influencing the duration of it. Primary (apical) growth is also reported to be influenced by precipitation; however, in our study, no differences in precipitation sum between the meteorological stations closes to sites were found and the on-site measurements were not available. Hence it was not possible to evaluate the impact of inter-annual variation in precipitation in relation to the height increment.

The observed differences in growth may be caused not only by meteorological conditions, but presumably can be linked to other factors, e.g., soil conditions that have an effect on growth of trees. At the beginning of the season trees were significantly ($P < 0.01$) higher in Rembate than in Auce (117 ± 1.6 cm and 72 ± 2.1 cm, respectively). These differences, in turn, affected total length of height increment (it was strongly correlated with initial tree height ($r = 0.78$, $P < 0.05$ and $r = 0.54$, $P < 0.05$ in Rembate and Auce, respectively), and therefore also the growth intensity.

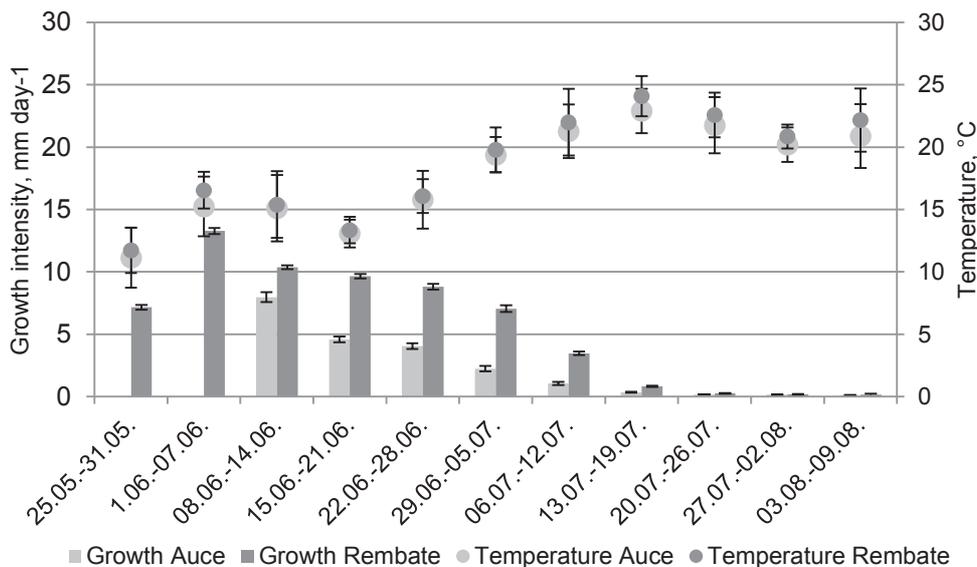


Figure 1. Growth intensity and diurnal mean temperature in Rembate and Auce.

Lammas shoots were observed for a relatively high proportion of trees in both sites: 14.0% in Rembate and 22.3% in Auce (Neimane et al, 2015). Trees with lammas shoots had similar trend in changes of growth intensity during the growth period than trees without them (Fig. 2). However, they were growing notably (on average by 23%) and, in most observation periods, also significantly ($P < 0.05$) faster. Consequently, trees with lammas shoots also had longer height increment, both in absolute and relative (as proportion of tree height) terms. As a result, height superiority of trees with lammas shoots, in comparison to those without, increased from 14% at the beginning of the season to 18% at the end of it in Rembate. Similarly, in Auce trees forming lammas shoots at the end of growing period had a 11% higher increment in comparison to trees that didn't and their relative length of height increment was significantly larger, 23% and 19%, respectively. A significant relationship between tree height and presence of lammas shoots was also previously reported in Latvia from an analysis of more than 100 stands (Neimane et al., 2016). Significant cumulative influence of lammas shoots on tree height had been found at the end of the 13th growing season trees with the lammas shoots in Norway spruce progeny trials were 14–20% taller than trees without it (Neimane et al, 2015). We can conclude, that a self-reinforcing loop is formed: larger, stronger trees have higher growth intensity and more frequently form lammas shoots, even further

increasing their height superiority. Genetic link between these traits was similar: proportion of trees with lammas shoots in the family correlated moderately and significantly both with tree height and height increment: $r_{fam} = 0.50$ (Neimane et al., 2015). Overall significant family effect on the proportion of trees showing lammas shoots was found; this was in accordance with the results of previous studies, reporting moderate (Hannerz, 1999) or high (Skrøppa & Steffenrem, 2015) heritability of this trait.

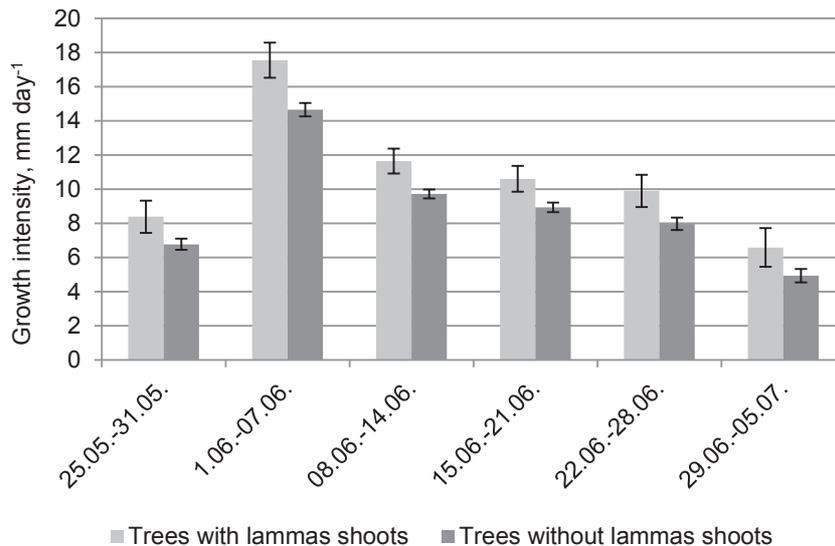


Figure 2. Growth intensity for trees with and without lammas shoots in Rembate.

Occurrence of lammas shoots at family level was linked not only to length of height increment, but also to timing of growth. Families that have early growth start and growth cessation were more likely to develop lammas shoots (Skrøppa & Steffenrem, 2015). Similar effect with regards to growth cessation was found also in our analysis.

Time of growth cessation had significant influence on the length of height increment (Fig. 3). Trees that stopped growth later had a 22% longer increment than the ones which stopped at the peak of growth cessation (13th – 26th of July). The largest trees tended to stop growing later in the season, presumably, indicating a cumulative positive impact of such a trait over time. Significant family effect on growth cessation was observed: family mean correlation between proportion of trees that had stopped their growth during last week of July or first week of August (mean $27 \pm 2.7\%$, ranging from 0 to 62%) and the total length of height increment was positive, moderate and significant ($r_{fam} = 0.38$, $P < 0.01$). Also, Skråppa & Steffenrem (2015) found, that families having later growth cessation at the age of 5 years were tallest at the age of 17 years. In this study as well as in studies in Sweden (Ekber et al., 1994) strong correlation between growth initiation and cessation was found. Both of these traits were clearly linked with frost damage, presumably explaining the observed differences in height growth between the families. In contrast, in our trials no frost damages were observed. Therefore, it is more likely, that the correlation observed in Latvia's climatic conditions is a result of better (longer) use of the vegetation period.

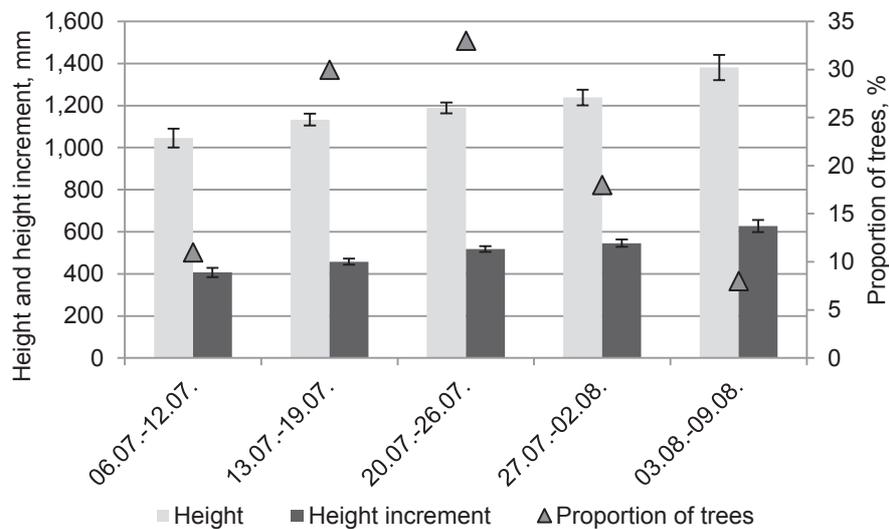


Figure 3. Height and height increment (without lammas shoot length) and proportion of trees that stopped growth at the particular period in Rembate.

Not only occurrence of lammas shoots and timing of growth cessation, but also growth intensity was an important factor affecting the length of height increment. Trees with longer height increment also showed higher growth intensity during the period of fastest growth, as well as a longer period of relative fast growth, as demonstrated by results from Auce trial (Fig. 4). This is in agreement with earlier findings by Skrøppa & Magnussen (1993) in the analysis of trials planted in Norway, noting that for spruce provenance from Baltic countries length of growth period and growth intensity were equally important in determining the total length of the annual shoot.

Differences in shoot elongation patterns had been found by numerous studies starting as early as that by Odin (1972) in the analysis of a few coniferous trees in Northern Sweden. To characterize these differences in Rembate (longer period of observations), a non-linear Gompertz model was fitted to height growth intensity data for each tree and family (median).

The models showed that intra-annual growth curves of studied trees and families differed notably. Family effect was significant on all model coefficients, indicating, that not only the intensity of height growth, but also the timing of its end was influenced by genetics even in the trial containing Norway spruce families from such a relatively small geographic area as Latvia. Both tree height and height increment at family mean level correlated strongly with the asymptote parameter ($r_{fam} = 0.93$, $P < 0.01$) and growth rate parameter ($r_{fam} = -0.70$, $P < 0.01$). Growth rate (i.e. rate of cell production) was also noted as a dominant factor in secondary growth, affecting xylem width of Norway spruce (Giagli et al., 2016). Shoot elongation curves in our trials were similar to those observed for other coniferous trees; however, the timing of end of active growth phase differed (Odin, 1972; Skrøppa & Magnussen, 1993; Rossi et al., 2006), presumably due to species differences.

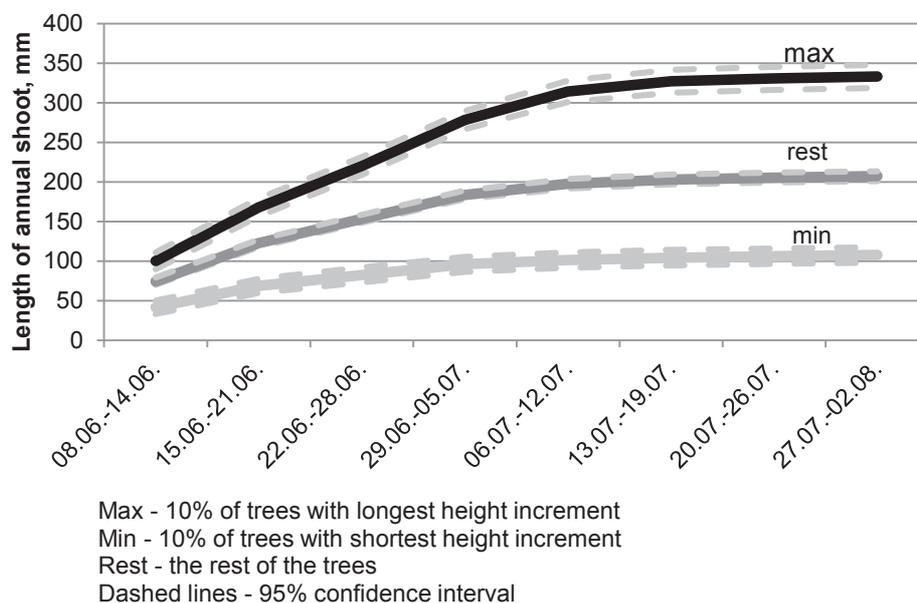


Figure 4. Dynamics of shoot elongation for trees with different annual height increment in Auce.

Results indicate, that selection of faster-growing families will most likely results in choice of genotypes with longer growth period (later cessation), higher growth intensity and higher probability to form lammas shoots. Since the length of vegetation period is expected to increase notably in the future, it is very likely that such genotypes will be capable of better utilization of the improved growing conditions. However, additional tests in growth chambers are needed to evaluate the probability that it might lead to increased frost damages, not observed in the trials currently. Even so it has been suggested that a single trial and year is sufficient for the estimation of breeding values of growth rhythm traits (Ekberg et al., 1991; Skrøppa & Steffenrem, 2015) additional information from trials in frost-prone sites would be important to draw wider conclusions.

CONCLUSIONS

The trend of Norway spruce height growth intensity was similar at both sites. The length of height increment was significantly affected by both time of growth cessation and lammas shoots; trees with lammas shoots had a similar trend in changes of growth intensity during the growth period to trees lacking lammas, whereas they grew notably and, in most observation periods, significantly faster. Family effect was significant in tree height, height increment, as well as presence of lammas shoots. Significantly different shoot elongation patterns were found between families, indicating a potential for selection of the best-adapted genotypes.

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