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Intra-annual height growth dynamics of Scots and lodgepole pines and its relationship with meteorological parameters in central Latvia

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Abstract. The Scots pine (*Pinus sylvestris* L.) is the second-most widely used tree species in forestry in Latvia and is the only species used for afforestation on nutrient poor soils that cover considerable forest land in Latvia. Several studies have shown that, in such conditions, the lodgepole pine (*Pinus contorta* var. *latifolia*) may be more productive in terms of biomass and yield. It is important to consider climate change studies to assess the potential for a larger-scale use of the lodgepole pine in forestry. The aim was to assess the intra-annual height growth patterns of both species, the differences between them, and the influence of meteorological parameters on their height growth. Their height growth was monitored on a weekly basis in two sampling sites in central Latvia, and the height increment curves were described by Gompertz's model. The height growth dynamics of individual trees and species differed notably, indicating the potential for the selection of the best-adapted genotypes. Our results indicate that the early onset of the active growth phase might be the most important factor determining the total height increment for both species. Temperature-related meteorological parameters were the only ones with a statistically significant influence on pines height growth and only when at least one of the variables were standardised prior to the analysis. A temperature increase had a slightly stronger positive effect on the growth of the lodgepole pine, indicating that it might be suitable for more intensive use in forestry under the climate change scenarios for Latvia.

Key words: apical growth, growth intensity, height increment, *Pinus contorta*, *Pinus sylvestris.*

INTRODUCTION

The adaptation of forestry to the foreseen climate change scenarios might be one of the greatest challenges for modern forestry (Millar et al., 2007; Lindner et al., 2010; McLane et al., 2011a). Apical or the height growth of trees is among the most important factors to assess regarding species selection for future forestry to ensure that the use of species and families is as productive as possible and is less vulnerable to the changing environment (Neimane et al., 2016). Over the last several decades, the vast majority of studies in the field of dendroclimatology have focused on assessing the influence of climate on tree radial growth (Speer, 2010; McLane et al., 2011a; Seidling, 2012;

Rimkus et al., 2018). However, studies on the relationship between climate and height growth have been scarce (McCarroll et al., 2003; Lindholm et al., 2009a), presumably due to the complexity of gathering data on height increments in comparison to collecting data on radial increments (Jansons et al., 2013). Furthermore, in most of these studies, the climate effect on the inter-annual height growth has been assessed (Pensa et al., 2005; Lindholm et al., 2009b), while the intra-annual height growth and its determinants have been less studied (Neimane et al., 2016).

The height growth of monocyclic tree species, such as the Scots pine (*Pinus sylvestris* L.) and lodgepole pine (*Pinus contorta* var. *latifolia*), is influenced by the conditions of the previous growing season, affecting bud development and inducing stem units and storage of carbohydrates, and of the current growing season, affecting the timing and speed of shoot elongation as well as assimilation (Jalkanen & Tuovinen, 2001; Salminen & Jalkanen, 2005; Lindholm et al., 2009a). Regarding pine species, most studies on height growth and the climate relationship have been conducted in areas close to the northern distribution border of particular species (Jalkanen & Tuovinen, 2001; Pensa et al., 2005). In northern regions, due to the short length of the growing season, the role of the current-year meteorological conditions in determining the annual height increment might be less important than in regions with a longer growing season.

Another obstacle to assess climate and the intra-annual height growth relationship is the sigmoidal pattern of height growth with the obvious phase of active growth and the less intense growth prior and afterwards, which does not correspond to the intra-annual trend of meteorological conditions. However, this intra-annual height growth trend can be described using nonlinear growth models, such as Gompertz's model (Fekedulegn et al., 1999). The coefficients of these models can be used to evaluate the growth dynamics between species, families of particular species, or even on the tree level, thus providing a tool for selecting genotypes with the necessary traits (e.g. higher total increment or more rapid growth) (Neimane et al., 2016).

The Scots pine is the most widely used species in forestry in Latvia, covering 33% of all the forest area (Ministry of Agriculture, 2019). One of the major causes for such intense use and natural distribution of the Scots pine is its ability to occupy nutrient-poor and sandy soils (Richardson, 2000). Forests growing on nutrient-poor soils compose 16% of the total forest area in Latvia. From these forests, a notable part is located on sandy soils, occupying 282,000 ha of forest land. Currently, afforestation is ongoing to a large extent in nutrient-poor soils, and these areas are used only for establishing Scots pine stands.

However, several studies have shown that the lodgepole pine can demonstrate higher productivity (both in terms of yield and biomass) in such conditions (Elfving & Norgren, 1993; Elfving et al., 2001; McLane et al., 2011b; Jansons et al., 2013; Fries et al., 2017). Moreover, information on the cause of such differences in productivity between these two *Pinus* species is scarce. Furthermore, several recent studies have focused on solutions, such as early thinning, using small-scale forest machinery, and simplifying the assortment system to secure high growth rates in such afforested territories (Kalēja et al., 2014; Prindulis et al., 2015; Lazdiņš et al., 2016), while the potential of a wider use of the lodgepole pine has been poorly analysed. The aim of the study was to assess the formation of the intra-annual height increment of the Scots pine and lodgepole pine and the relationship between the meteorological parameters and height growth to better understand the potential for a more intense use of these species in Latvia, considering the foreseen changes in the climate.

MATERIALS AND METHODS

Study area and sampling sites

The sampling sites were located in central Latvia, 13 km apart in Zvirgzde (56°39' N, 24°27' E) and Daugmale (56°47' N, 24°35' E) for the lodgepole pine and Scots pine, respectively. Both sampling sites were situated on a flat relief, and the elevation was between 20 and 30 m a.s.l. The lodgepole pine sampling site in Zvirgzde was an experimental (provenance) trial planted in 2000 with two-year-old bare-rooted seedlings. The forest type in the lodgepole pine sampling site according to the classification system used in Latvia (Bušs, 1976) corresponded to *Vacciniosa* in nutrient-poor mineral soil. The Scots pine was represented by open pollinated families of plus-trees selected in Latvia. Each family consists of progenies of a single mother tree, all together there were 22 families. The Scots pine sampling site in Daugmale was located in nutrient-poor mineral soil and corresponded to the *Cladinoso-callunosa* forest type (Bušs, 1976). The age of the trees at the time of measurement was 6 years.

The climate in the study area is determined by dominant western winds that bring moist and warm air masses from the Baltic Sea and the Atlantic, resulting in mild and oceanic weather throughout the year. According to the data from the nearest meteorological station of the Latvian Environment, Geology, and Meteorology Centre, the mean annual temperature is about 5.5 °C, and the annual precipitation ranges from 500 to 650 mm. The monthly mean air temperature ranges from ~-5 °C to 17 °C. January is the coldest month, and July is the warmest month. The length of the vegetation period is around 185 to 190 days.

Sampling and meteorological data

The intra-annual height growth of both species was monitored on a weekly basis by measuring the increment of the apical shoot. The measurements started in year 2012 in the middle of April for the Scots pine and at the beginning of May for the lodgepole pine sampling site and ended in the middle of July (2012) for both sites. For height growth monitoring in both sampling sites, trees were selected randomly, avoiding trees with visible insect or browsing damage. In total, the height growth was monitored for 71 lodgepole pines and 468 Scots pines.

Near the Zvirgzde sampling site, the meteorological conditions were monitored on-site for the whole time of analysis by the meteorological station Wireless Vantage Pro2 (Davis Instruments) to obtain data on the air temperature, precipitation, air humidity, solar radiation, and atmospheric pressure. Daily temperature data were also obtained from the nearest meteorological station of the Latvian Environment, Geology, and Meteorology Centre – Lielpeci.

Data analysis

To describe the intra-annual height growth of the monitored trees (individually, between and within species) the nonlinear Gompertz model was fitted (1):

$$f(A) = \alpha \exp(-\beta \exp(-\kappa A)) \tag{1}$$

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where α – asymptote parameter; β – displacement parameter or biological constant; κ – growth rate parameter; A – days since the beginning of the year.

Gompertz's model has been used for both intra-annual height growth (Fekedulegn et al., 1999) and intra-annual radial growth (Seo et al., 2011) curve development in biology. The coefficients of Gompertz's model parameters were used to assess the differences in height growth trends at a species level: lodgepole pine vs. Scots pine, as well as within species (between Scots pine families). The *F* test was used to compare the variances of the Gompertz model coefficient values between the two species, whereas the *t*-test was performed to compare the mean values (the normality was checked by graphical inspection). The differences in values of the Gompertz model parameters between families of Scots pine were assessed using the analysis of variance. Pearson's correlation analysis was used to assess the relationship between the total annual height increment and the coefficients of Gompertz's model.

During the first stage of analysis, the raw data of both the height growth intensity (intensity defined as height increment mm day^{-1}) and meteorological parameters were used. Prior to the next two steps of analysis, either data on the height growth intensity or data on both the height growth intensity and meteorological parameters were standardised. The standardisation was conducted by applying a cubic-smoothing spline, thus reducing the intra-annual biological and meteorological trends of the analysed variables. The cubic-smoothing spline is an empirical model that uses a flexible curve, which is allowed to adjust at a regular interval and has been considered to provide an organic fit to the data (Speer, 2010). All steps of the data analysis were carried out using the statistical software R 3.3.2. (R Core Team, 2013).

RESULTS AND DISCUSSION

Even though the height growth intensity trends of the lodgepole pine and Scots pine showed similar patterns, especially the sharp decrease in height growth intensity in the last week of May, the correlation of these variables was not statistically significant ($r = 0.59$; $P > 0.05$). Due to the too-late start of height growth monitoring in the sampling site at Zvirgzde in this study, the exact onset of the height growth was missed for the lodgepole pine. Both species reached the maximum of their height growth intensity within May 2012, but slight differences exist in the timing of the most intense growth. The lodgepole pine reached the peak of its height growth intensity of 11.02 ± 2.12 mm day^{-1} (mean ± standard deviation) earlier than the Scots pine, and after reaching the peak, the height growth intensity gradually decreased (Fig. 1, b, c). Meanwhile, the Scots pine reached a maximum height growth intensity of 10.61 ± 2.71 mm day^{-1} (mean ± standard deviation) one week later but kept relatively intense growth for a slightly longer period. Such intense height growth early in the growing season is associated with the use of stored carbohydrates along with the ability of the pine species to produce around 30% of the whole growing season in photosynthates in spring in favourable conditions (Dougherty et al., 1994; Hansen & Beck, 1994; Strand et al., 2002). Considering the small distance between both sampling sites, the different timing of the most active phase of height growth might be caused by the phenology of the two species (Dougherty et al., 1994; Chuine et al., 2006) rather than by meteorological conditions.

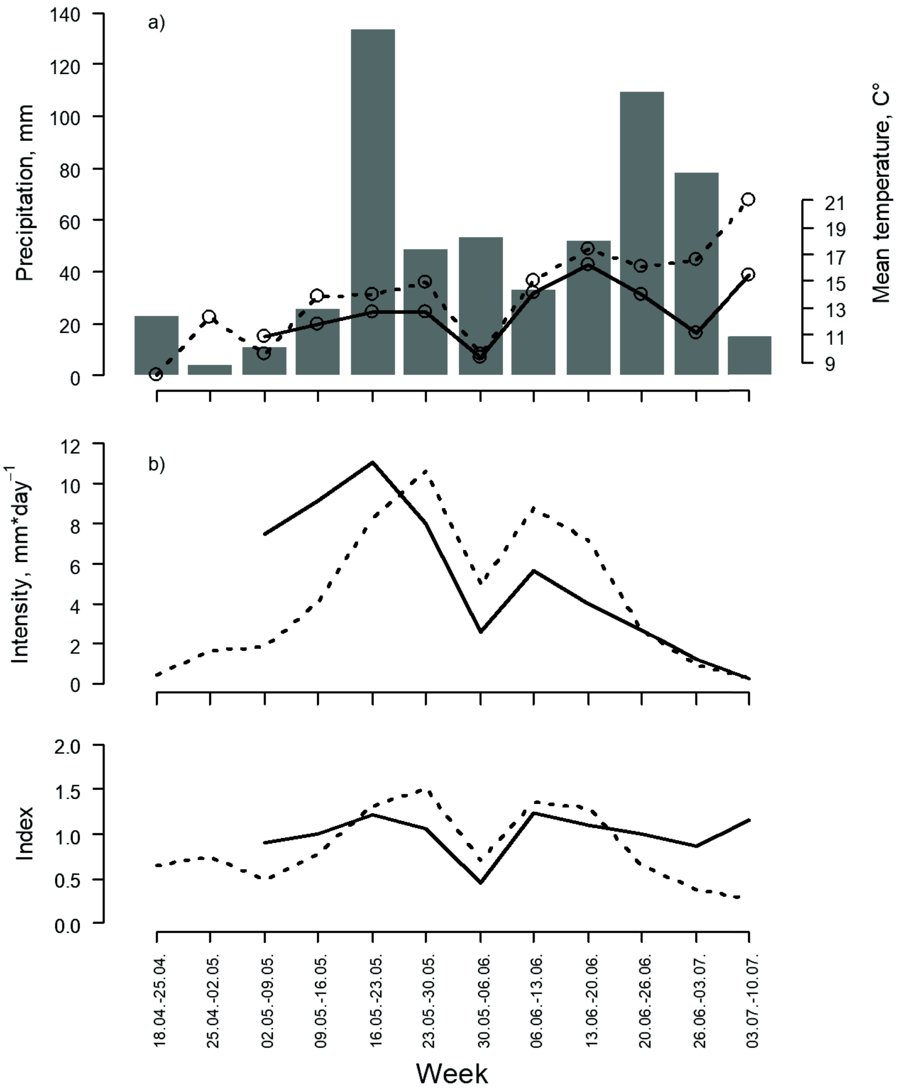

Figure 1. a) Meteorological parameters (weekly mean temperature recorded near the sampling site (points joined by a solid line) and at the nearest meteorological station (points joined by a dashed line) and precipitation sums (bars) recorded near sampling sites) during height growth monitoring; b) Raw and c) standardised data on the height growth intensity of lodgepole pine (solid line) and Scots pine (dashed line).

The Gompertz model was successfully fitted to the height-increment curves of all trees that continued height growth at least until the middle of the monitoring period and to the mean height-increment curves per species (Fig. 2). Similarly, on the intra-annual height growth of the Norway spruce (*Picea abies* (L.) Karst.), Neimane et al. (2016) reported that the variance of the Gompertz model coefficients showed that the intra-annual growth curves of the studied trees differed notably (Fig. 3). However, no statistically significant differences were found in the mean value and variance of the asymptote parameter values of the Gompertz model between both species (Fig. 3). Although the homogenous variance and mean value of the asymptote parameter indicated that the total annual height increment of the studied trees did not differ significantly between the species, from the forestry point of view, these differences were notable because the mean annual height increment of the lodgepole pine in the analysed year was 19.85% higher. Similar slightly higher but insignificant results for certain provenance of lodgepole pine in comparison to Scots pine were reported in study by Jansons et al., 2013. The mean values of the growth rate parameter of the two species were not statistically different, whereas the variances of this parameter differed (*P* < *0.001*). The homogenous mean values of the growth rate show that the average rate at which the total height increment was reached during the active growth phase did not differ between both species. The mean value of the biological constant or displacement parameter in the Gompertz model was higher for the Scots pine in comparison to the lodgepole pine, and this difference was statistically significant (*P* < *0.001*) even though there were no statistically significant differences in variances of this constant between the species. The lower value of the biological constant means that the lodgepole pine started the active growth phase sooner after the onset of height growth than the Scots pine. The height growth trends of both species and the above-mentioned differences in the timing of the peak of the height growth intensity corresponded to this finding. Nevertheless, differences in the mean value of the biological constant might also be affected by the missed height growth onset for the lodgepole pine. All Gompertz model coefficients differed significantly (*P* < *0.001*) between the Scots pine families (group of progenies of a single plus-tree), thus indicating the potential for the selection of genotypes with the necessary height growth patterns. Similar results were reported by Neimane et al. (2016) on the height growth of the Norway spruce.

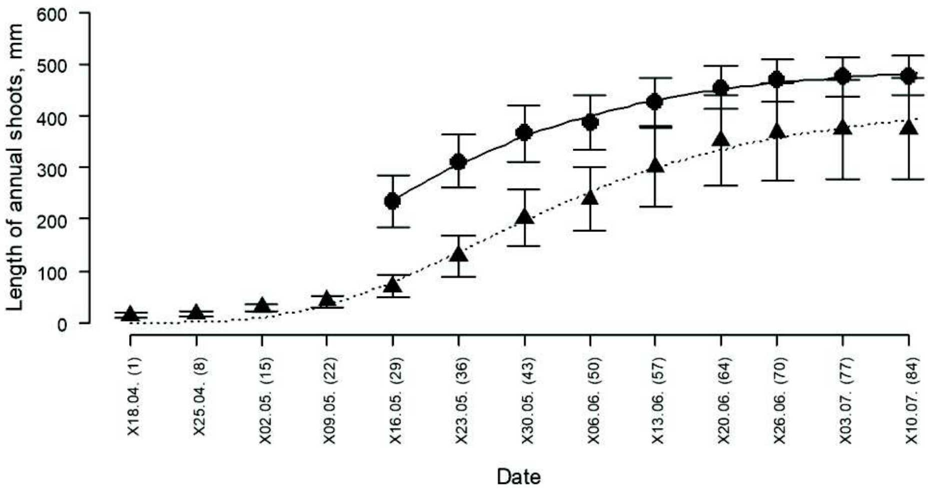

Figure 2. Mean total height increment of lodgepole pine (dots) and Scots pine (triangles) and fitted curves of the Gompertz model (solid and dashed lines for the lodgepole and Scots pine, respectively) during height growth monitoring. Whiskers show the standard deviation and number in brackets represent day of growth.

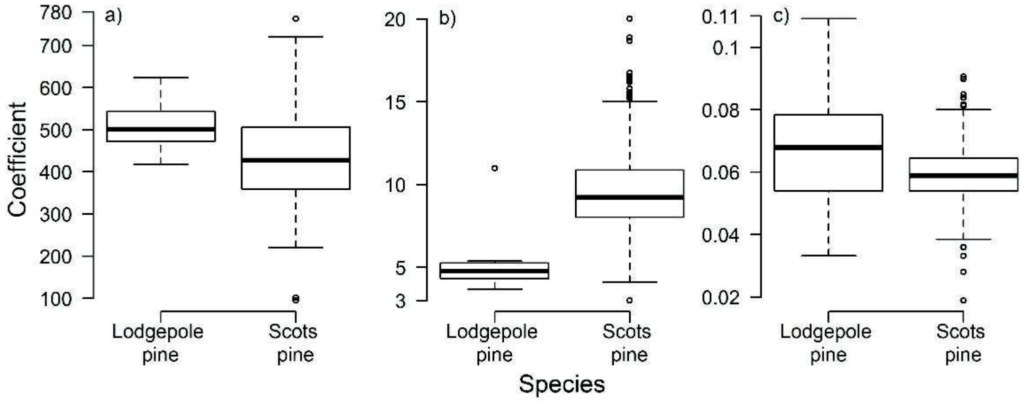

Figure 3. Variation of a) α – asymptote parameter; b) β – biological constant, and c) κ – growth rate coefficient values of the nonlinear Gompertz model fitted to the intra-annual height increment of individual trees of the lodgepole pine and Scots pine. Bold lines represent the median. Boxes correspond to the lower and upper quartiles. Whiskers show the minimum and maximum values (within 150% of the interquartile range from the median), and outliers are shown by circles.

All Gompertz model coefficients of the Scots pine showed statistically significant relationships with the total height increment, whereas this relationship for the lodgepole pine was insignificant in all cases, presumably due to the insufficient sample size. The strong correlation of the asymptote parameter with the total height increment ($r = 0.97$; $P < 0.001$) of the Scots pine trees can be explained using the total height increment as one of the starting values for fitting the Gompertz model. Scots pine trees with a longer period between the onset of growth and the start of the active growth phase tended to have a shorter total height increment, as indicated by the negative correlation ($r = -0.23$; $P < 0.001$) between the biological constant and the total height increment. The negative correlation between the total height increment and growth rate parameter ($r = -0.29$; $P < 0.001$) showed that Scots pine trees that grow faster during the active growth phase tend to have a shorter total height increment. These results might be explained by the strong correlation between the biological constant and the growth rate observed for both the Scots pine ($r = 0.78$; $P < 0.001$) and the lodgepole pine ($r = 0.88$; $P < 0.05$), indicating that the studied trees unsuccessfully tried to compensate for the late start of the active growth phase by growing faster during it.

None of the meteorological parameters showed a significant relationship with the height growth intensity when neither the height growth intensity data nor the data on the meteorological parameters were standardised (Fig. 4, a) prior to the analysis. The standardisation of the growth data time series has been a commonly applied practice in dendroclimatology and increases the signal of interest by removing the biological growth trends and variability that can be considered noise when the climate-growth relationship is studied (Speer, 2010). The height growth of trees is among such traits with an expressed biological trend, for example, growth intensity is the highest during the middle of the growing season, whereas at the beginning and end of the growing season, height growth is significantly slower (Fekedulegn et al., 1999; Seo et al., 2010). This growth trend is mainly determined by physiological processes of trees, for example, towards the end of the growing season, the secondary growth exceeds the primary growth and excess assimilates are stored for the next growing season (Pallardy, 2008; Speer, 2010). Both species reached the peak of their height growth intensity in the middle of May (Fig. 1, b), while the temperature continued to increase until July and August (Fig. 1, a), which are usually the months with the highest amount of precipitation (Kļaviņš et al., 2008). Therefore, the analysis of un-standardised data might provide erroneous results.

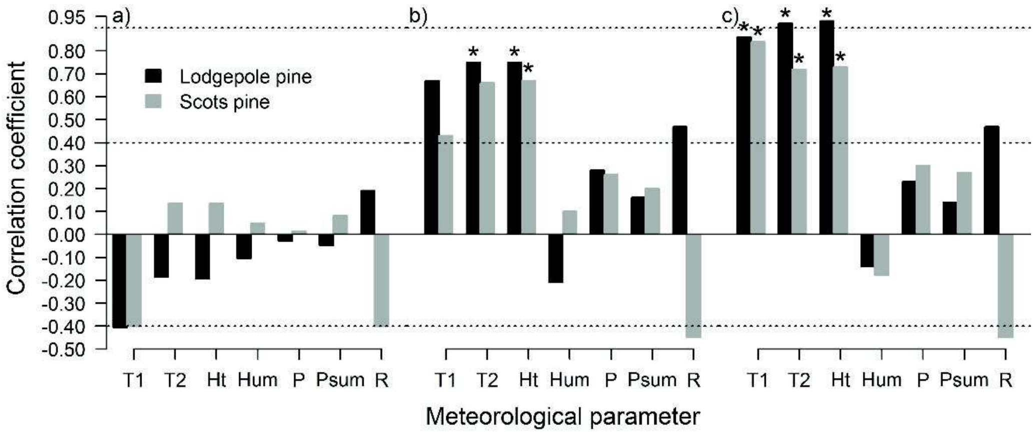

Figure 4. Coefficient values of the Pearson correlation between the meteorological parameters and height growth intensity of the lodgepole pine and Scots pine when a) raw data on both variables are used; b) raw data on meteorological parameters and standardised data on the height growth intensity are used and c) both variables are standardised prior to the analysis. Asterisks indicate statistically significant coefficient values (*$P < 0.05$*). T1 – mean growing season temperature at the nearest meteorological station; T2 – mean growing season temperature recorded near sampling sites; Ht – heat index; Hum – air humidity; P – mean precipitation; Psum – sum of precipitation; R – solar radiation.

When the height growth intensity data prior to the analysis was standardised using the cubic-smoothing spline heat index, the mean temperature recorded near the sampling sites showed the strongest correlation with the height growth intensity of both species (Fig. 4, b). Almost identical correlation values for these two factors can be explained by the high correlation between them ($r = 0.99$, $P < 0.001$). The relationship between temperature and height growth was even further emphasised when the data on both height growth intensity and meteorological parameter were standardised before the analysis (Fig. 4, c). The mean temperature recorded at the nearest meteorological station showed a relatively high positive correlation with the standardised data on the height growth intensity, but this relationship was statistically significant only when both variables were standardised. The positive effect of temperature on the height growth of both species can be explained by the direct influence of the temperature on the assimilation and meristematic activity (e.g. cell division, differentiation, and elongation) (Pallardy, 2008). The temperature during the months of the growing season showed a significant positive relationship with the inter-annual height increment of the lodgepole pine in previous studies conducted in the same study area in Latvia, but the strength of this relationship differed between families (Jansons et al., 2013). Similarly, as in this study, Jansons et al. (2013) found no significant relationship between the temperature during the growing season and the inter-annual height increment of the Scots pine. In another study, Salminen & Jalkanen (2007) suggested that the cessation of the annual height growth occurs when a location's specific temperature sum threshold is attained. Such a threshold-related cessation of height growth would lead to a positive relationship between the height growth and temperature during the first part of the growing season and to no relationship at the last part of the season, thus possibly resulting in an insignificant relationship when the whole growing season is analysed together. The lack of relationship between the unstandardised data on the height growth and meteorological parameters is furthermore explained by the allocation of carbon for height growth from the reserves of the previous year, resulting in a lower influence on the meteorological conditions during the growth season (Jalkanen & Tuovinen, 2001; Salminen & Jalkanen, 2004). However, our results indicate that, in areas with a longer growing season, the meteorological parameters during the season might have a more important role in determining the total annual height increment than in areas further north where the previously mentioned studies have been conducted.

None of the precipitation-related meteorological parameters (e.g. the sum of precipitation, mean precipitation, and humidity) showed a statistically significant correlation with the height growth of both species. These results indicate that water availability is not the limiting factor for the height growth of both pine species in the study area. Water availability has often been reported as the main limiting factor for the growth of trees closer to the southern border of their distribution area (Lindner et al., 2010; Speer, 2010). In regions like Latvia, where the precipitation exceeds evapotranspiration (Kļaviņš et al., 2008), the lack of a relationship between the height growth and precipitation is not surprising, especially considering the high drought resistance of the pine species (Richardson, 2000). Similarly, the precipitation-related meteorological parameters of growing season have not shown a significant relationship with the inter-annual height growth of the Scots pine (Jansons et al., 2013, 2015) and the intra-annual height growth of the hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) (Jansons et al., 2014) and the lodgepole pine (Jansons et al., 2013) in other studies conducted in Latvia. The exceptions are for the height growth of the Scots pine, which was affected by the precipitation in October of the year preceding the growth, and for the height growth of the lodgepole pine, which was affected by the precipitation in February of the growth year (Jansons et al., 2013, 2015).

CONCLUSIONS

The intra-annual height growth dynamics of both the lodgepole pine and Scots pine were successfully described by the Gompertz model, but notable differences exist at the individual tree level. The relationship between the Gompertz model coefficients and total annual height increment indicate that trees starting the active growth phase earlier after the onset of height growth had a higher total annual increment, but the faster growth during the active growth phase did not compensate for the too-late start of the active growth phase. Thus, the reduced time between the onset of the height growth and the start of the active growth phase might be a more important parameter for the selection of faster-growing trees than the maximal height growth intensity.

The height growth of the lodgepole pine showed a slightly stronger relationship with the meteorological parameters than the height growth of the Scots pine, indicating that it is more sensitive to variations in meteorological parameters. Our results indicate that the increased use of the lodgepole pine in forestry might be beneficial in the long term considering the increase in temperature and the more frequent occurrence of extreme temperatures during the growing season that are foreseen in the climate change scenarios for Latvia (Kļaviņš et al., 2008; Avotniece et al., 2010).

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