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Influence of lammas shoots on height of young Scots pines in Latvia

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Abstract. Scots pine is a commercially important tree species in northern Europe. Climate changes in combination with genetics cause differences in the tree growth rhythm, including the formation of lammas shoots. The aim of the study was to assess the relation between the occurrence of lammas shoots and the height of young Scots pines and its implications in tree breeding. Tree height was repeatedly measured, and the presence of lammas shoots was assessed at the end of the 4^{th} through 8^{th} growing seasons in two open-pollinated progeny trials (Daugmale and Norupe, both including the same 61 families) in the central part of Latvia. The proportion of trees with lammas shoots (max. 23%) decreased over the observation years. In both trials, at the age of 7 years, trees that had formed lammas shoot during at least one of the observed years were significantly ($P < 0.001$) higher than trees with no lammas shoots: 226 ± 3.5 cm vs 213 ± 3.3 cm in Norupe and 146 ± 3.9 cm vs 121 ± 1.9 cm in Daugmale, respectively. When only dominant trees (1,000 ha^{-1}) were considered, the height superiority of trees with lammas shoots remained in Daugmale (trial with highest proportion of trees with lammas shoots), but not in Norupe. The earliest formed lammas shoots (assessed in the 4^{th} growing season) had the strongest effect on the tree height. A correlation between the mean height and the proportion of trees with lammas shoots in the particular family was not found ($P > 0.05$).

Key words: second flushing, dominant trees, height superiority, open-pollinated family.

INTRODUCTION

Scots pine is a commercially important tree species in northern European countries that occupies > 30 million ha of forest land, with a total growing stock of ca. 3,300 million m^3 (41% of the wood resources in the region) (Rytter et al., 2013). It is also a dominant tree species in forest land in Latvia (Lazdins et al., 2010; Kaleja et al., 2013).

Due to the economic importance of the species, substantial amount of dendrochronological analysis and modelling has been conducted to understand the possible effects of climatic changes on growth. These studies have shown a significant effect of meteorological conditions on radial and height increments, and shifts in the periods of year with significant influence of particular meteorological parameters on growth, as the climate is changing (Jansons et al., 2013a; Jansons et al., 2013b; Henttonen et al., 2014; Jansons et al., 2015). Moreover, climatic changes are expected to affect the ratio of radial and height growth due to increased inter-annual variation and time-lag of correlations between these two increments (Salminen et al., 2009). This ratio, presumably, might also be affected by the occurrence of lammas growth – the second flushing in the end of the vegetation period.

Increasing occurrence of lammas shoots has been reported over the last years in Norway and has been attributed to a possible effect of changing climatic conditions (Søgaard et al., 2011). Links between meteorological conditions and occurrence of lammas shoots has also been suggested by other studies of Norway spruce (Neimane at al., 2015), Scots pine (Ehrenberg, 1963), and other pine species (Kushida, 2005) as well as fir species (Hallgren & Helms, 1988).

Modelling efforts (using both dendrochronology data and physiological parameters, i.e., process-based models) have been made to predict the effect of climatic changes on the yield of forest stands in different conditions (Sabaté et al., 2002). In boreal forests, increased productivity of the most common tree species, including Scots pine, is expected (Briceño-Elizondo et al., 2006).

Tree growth as well as its predicted changes is affected by genetics (Jansons, 2005; Jansons et al., 2006; Rieksts-Riekstins et al., 2014). Genetics are also the cause of differences in tree growth rhythm, formation of the increments (Rone, 1975; Ununger et al., 1988; Søgaard et al., 2011) and, in combination with favourable meteorological conditions, also of the formation of lammas shoots. Genetic differences in formation of lammas shoots have been well studied for spruce at the provenance level (Danusevičius & Persson, 1998) as well as the family level (Skrøppa & Steffenrem, 2015); however, fewer studies have addressed it for the Scots pine. The aim of our study was to assess the relation between the occurrence of lammas shoots and the height of young Scots pines in Latvia and its implications in tree breeding.

MATERIALS AND METHODS

The study was carried out in two open-pollinated progeny trials, both including the same 61 families of Scots pine plus trees selected across Latvia. The trials are located in the central part of Latvia (56º50´N, 24º38´E – Norupe and 56º47´N, 24º30´E – Daugmale), both established using one-year-old containerised seedlings at the spacing of 1.5 × 2 m in the *Vacciniosa* forest type (Bušs, 1976), site index $H_{100} = 26$ and $H_{100} = 24$, respectively. Inventoried trees were planted in block plots (seven trees in four rows in Norupe and five trees in two rows in Daugmale) randomly distributed in three (Norupe) or four (Daugmale) replications. According to the data of the Latvian Environment, Geology, and Meteorology Centre, the mean annual temperature in the region is +7.7 °C, and the mean annual precipitation is 690 mm. Both sites had similar meteorological conditions, as suggested by their location in the same climatic research unit data point (Jones et al., 1999) as well as measurements of temperature carried out directly in both sites for short periods of time during May-September, including in years of lammas shoot inventories.

Tree height was measured for 3,295 trees at the end of the 4th through 7th growing seasons. For all these trees, the presence of lammas shoots was assessed at the end of the 4th through 8th growing seasons, excluding the 7th season in Norupe. The lammas shoot was defined as the second flushing of the apical or lateral bud (at the base of the terminal bud) of the top shoot, reaching the length of at least 1 cm and producing a terminal cluster. After the 10th growing season, the presence of the additional whorls formed as a result of lammas shoots at the particular season was assessed. No frost damage of the shoots was observed in any of the seasons. The relationship between the tree height and the presence of lammas shoots was assessed for dominant trees (corresponding to 1,000 trees ha^{-1}) of each block plot.

The *t*-test was used to assess the differences of the tree height in both trials (in particular age) and between the height of trees with and without lammas shoots in each trial. The chi-squared (χ^2) test was used to assess the differences in the distribution of the proportion of trees with lammas shoots among the tree height classes and to assess whether trees with lammas shoots in the current season form lammas shoots in the next season more frequently than trees without lammas shoots in the current season. The Pearson correlation test was used to assess the relation of the proportion of trees with lammas shoots in the families between the years and between the trials and to assess the relation between mean tree height of family and the proportion of trees with lammas shoots.

RESULTS AND DISCUSSION

In both trials, the proportion of trees with lammas shoots was decreasing during the observation period. From the age of 4 to 8 years, it decreased from 11% to 4% in Daugmale and from 23% to 1% in Norupe (Fig. 1). These results are consistent with previous studies that have found a decreasing tendency to form lammas shoots for pine and spruce with increasing tree age (Ehrenberg, 1963; Rone, 1985). For example, Ehrenberg (1963) noted that the average percentage of proleptic pines decreased from the age of 7 to the age of 11 years. Aldén (1971) explained this tendency by the fact that small trees (plants) have limited storage capacity of nutrients; therefore, the surplus of carbohydrates is directly used to form lammas shoots, in contrast to larger trees, which can store the excess nutrients.

The trend of a decreasing proportion of trees with lammas shoots with an increase in tree age was broken in the last observation period in the Daugmale trial, where they were in higher frequency than in the two previous seasons. Presumably, it might be due to meteorological conditions. There were no notable differences in monthly mean air temperature from April till September during the observation period; however, a sharp temperature increase at the end of July in the 8th growing season in comparison to a slight decrease or no changes at the same period in previous years was observed. In this season, minor changes in precipitation in the first week of August in comparison to the last week of July were also observed (in the closest meteorological station).

It suggests that the relative changes, not necessarily the mean values of any of the meteorological parameters (temperature or precipitation) at the right period of the annual cycle of tree growth could trigger the formation of lammas shoots. It is in line with findings by Carvell (1956) in a 6-year-old *Pinus resinosa* plantation, noting that lammas shoots were much more abundant after a late rainy period in the dry summer than in 'normal' summers (three previous observation years). The trend of decreasing frequency of trees with lammas shoots with increasing age was not disrupted in Norupe, presumably due to higher capacity to store excess nutrients (larger trees) or some unfavourable factors (i.e., more intense competition between the trees due to their size or low precipitation, which is impossible to determine exactly due to lack of measuring devices inside the trials).

West & Ledig (1964) have shown a significant effect of both the year of assessment and the local conditions on the proportion of trees with lammas shoots. The latter is supported also by other studies of pine (Ehrenberg, 1963; Aldén, 1971) and spruce (Rone, 1985; Søgaard et al., 2011; Neimane et al., 2016) that emphasise the increased formation of lammas shoots on nutrient rich soils. Rikala (1992) found positive correlation between the occurrence of lammas shoots and the nitrogen concentrations of both soil and needles. Consequently, in two seasons when the highest proportion of trees with lammas shoots was noted (i.e., the 4th and 5th seasons), it was twice as high in Norupe (with a slightly higher soil fertility) than in Daugmale.

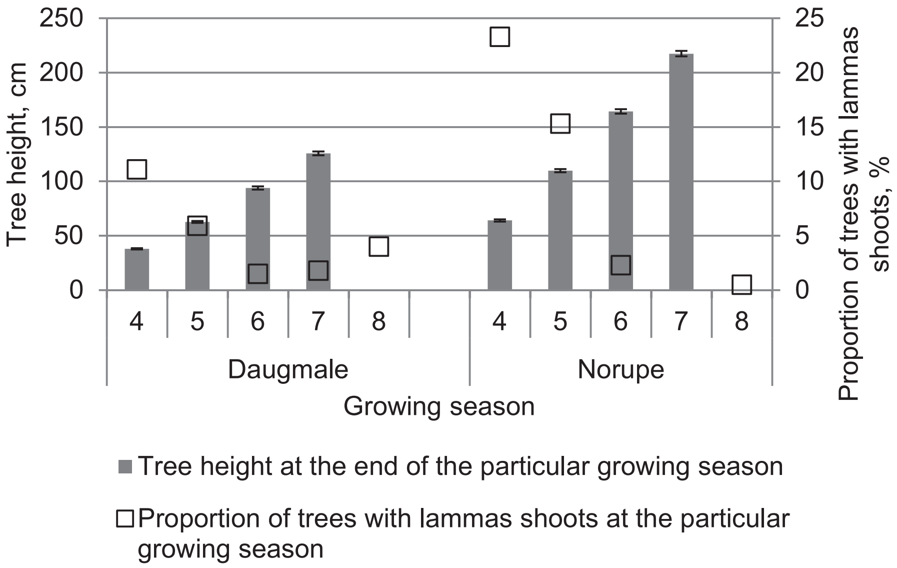

Figure 1. Tree height and proportion of trees with lammas shoots in Daugmale and Norupe.

The appearance of the lammas shoots was significantly affected by genetics (family). The highest proportion of trees per family with current year lammas shoots reached 41% and 48% in Daugmale and Norupe, respectively. The highest proportion of trees per family with lammas shoots at least in one growing season reached 65% in Daugmale and 68% in Norupe. There were only two families with no trees with lammas shoots in any of the years during the observation period in Daugmale and none in Norupe.

These results are consistent with a number of studies that acknowledged the genetic control of the tree growth rhythm and the formation of lammas shoots for pine and spruce, including the differences of frequency of the lammas shoot formation between provenances and between families (Ehrenberg, 1963; West & Ledig, 1964; Hoffmann, 1965; Rone, 1975; Danusevičius & Persson, 1998; Søgaard et al., 2011; Skrøppa & Steffenrem, 2015). Rudolph (1964) noted that the occurrence of lammas shoots between seed sources showed a clinal or continuous pattern and suggested that the trait could be controlled by multiple genes. Similar clinal trends in proportion of trees with lammas shoots ranging from 5% (northernmost origins) to more than 40% (southernmost origins) were found also in the analysis of 8-year-old *Picea sitchensis* trials in Norway (Magnesen, 1986).

Interaction between the genetics (provenance) and environment (site) on the formation of lammas shoots had been found in studies of *Abies* species at the age of 3 years (Hansen et al., 2004). In our study the proportion of trees with lammas shoots in the family between trials (Table 1) correlated at a similar level as tree height: at the end of the 4th growing season $r = 0.28$ ($P < 0.05$), 5th growing season $r = 0.46$ ($P < 0.001$), 6th growing season $r = 0.15$ ($P > 0.05$), and 8th growing season $r = 0.27$ ($P < 0.05$). The strongest relationship ($r = 0.56$; $P < 0.001$) between trials was observed between the proportion of trees in the family with lammas shoots in at least one growing season.

Between observation years, the proportion of trees with lammas shoots in the families correlated significantly, reaching up to $r = 0.54$ and $r = 0.43$ (both $P < 0.001$) in Daugmale and Norupe, respectively, between the 4th and 5th seasons. Similarly, strong correlation between the proportion of trees with lammas shoots in the family has been observed in the spruce progeny trial at the age of 5 years in Norway and 21 years in Finland (Søgaard et al., 2011). Also, the family mean height correlated significantly between the years and was $r > 0.89$ and $r > 0.78$ (both $P < 0.001$) in Daugmale and Norupe, respectively.

Table 1. Pearson's correlation coefficients between the proportion of trees with lammas shoots at the age of 4 to 6 years, based on the family means

Trial and Season of Lammas Shoots Assessment	Daugmale-4	Daugmale-5	Daugmale-6	Norupe-4	Norupe-5
Daugmale-5	0.54^{***}				
Daugmale-6	0.29^{*}	0.34^{**}			
Norupe-4	0.28^{*}	0.29^{*}	0.14		
Norupe-5	0.40^{***}	0.46^{***}	0.32^{**}	0.43^{***}	
Norupe-6	0.39^{**}	0.15	0.15	0.08	0.34^{**}

* $P < 0.05$; ** $P < 0.01$; ** $P < 0.001$.

During the study years, trees in Norupe were significantly ($P < 0.001$) higher than in Daugmale, exceeding the latter by 75% (Fig. 1). In both trials, at the end of the 7th growing season, trees that had formed lammas shoots during at least one of the assessment seasons were significantly ($P < 0.001$) higher than trees with no lammas shoots: 226 ± 3.5 cm vs 213 ± 3.3 in Norupe and 146 ± 3.9 cm vs 121 ± 1.9 cm in Daugmale, respectively (Fig. 2). Similar trends – more frequent lammas shoots for the highest trees within the provenance – had also been observed in studies of Scots pines in Sweden (Ehrenberg, 1963) and in analyses of spruce (Rone, 1985; Neimane et al., 2015).

For example, Neimane et al. (2015) found that trees with lammas shoots (at least in one of the three assessment seasons) were 14% to 20% higher than trees without them at the age of 13 years. Hoffmann (1965) reported even higher differences in spruce trials at the same age, at 33%; moreover, he found a tendency of the differences to increase with tree age. Analysis of other tree species (e.g., *Pinus banksiana* and *Pinus resinosa*) also linked the presence of lammas shoots with tree vigour and superior height as well and found that lammas shoots in the current year do not have a negative effect on the length of height increment in the next year (Carvell, 1956; Rudolph, 1964).

When only dominant trees (corresponding to a density of 1,000 trees ha^{-1}) were considered, the height superiority of trees with lammas shoots over the trees without them remained (166 ± 4.6 cm vs 149 ± 2.8 cm, respectively) in Daugmale; however, it was less pronounced. The superiority of all trees with lammas shoots was 20%, while the superiority of such dominant trees was 11%. In Norupe, the height superiority of all trees was 6%, but the dominant trees showed the opposite (non-significant, $P > 0.05$) trend; the height of the dominant trees with and without lammas shoots was 248 ± 3.6 cm and 251 ± 3.0 cm, respectively.

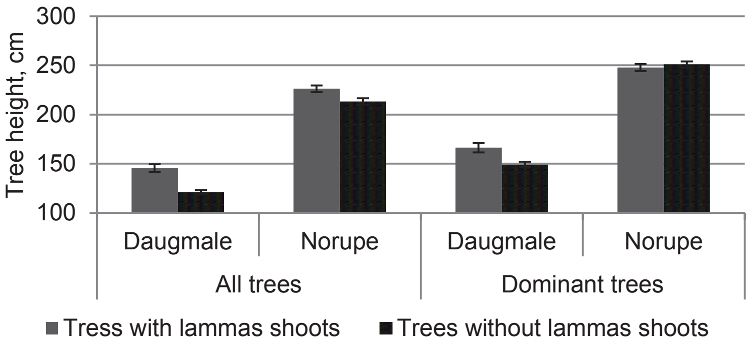

Figure 2. Height of the 7-year-old trees with and without lammas shoots at the end of at least one assessment season.

Other types of analysis showed similar results. In Daugmale, the proportion of trees with lammas shoots from all trees ($P < 0.001$) and dominant trees ($P < 0.001$; Fig. 3) differed significantly among the height classes, but in Norupe, the proportion of trees with lammas shoots was largest among the highest trees only when all trees were included in the analysis ($P < 0.001$), but not when dominant trees were evaluated.

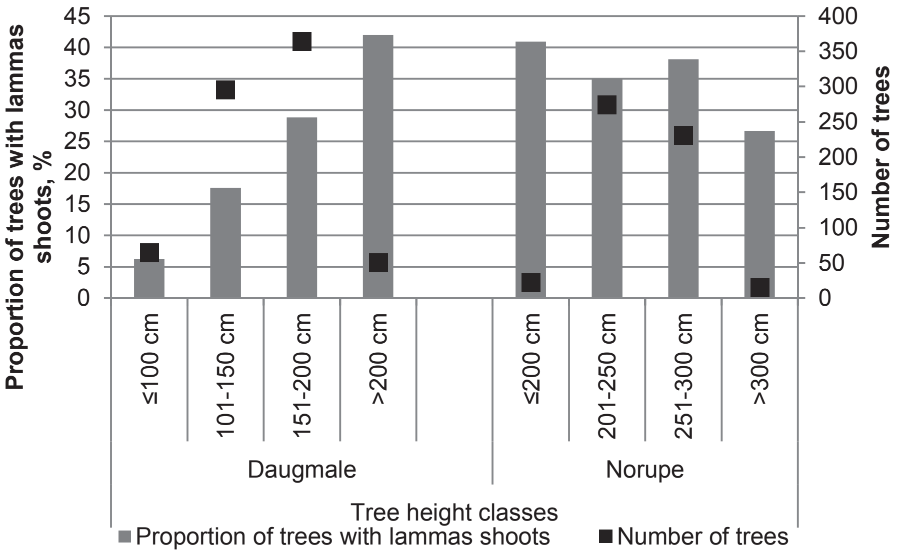

Figure 3. Proportion of dominant trees with lammas shoots at the end of at least one assessment season among the tree height classes.

The link between tree height and the presence of lammas shoots is rather straightforward for spruce since, for this tree species, lammas shoots are most often formed by the apical bud, directly increasing the height increment (Neimane et al., 2015). However, for Scots pine, for 22% of trees, lammas shoots were formed both at the terminal and lateral buds and only 5% were solely by terminal buds (Rikala, 1992), indicating that some indirect link between growth and presence of lammas shoots might exist, and presumably, better growth is cause for formation of lammas shoots not *vice versa*. Better-growing trees produce excess nutrients at an early age, which are used to form lammas shoots (Aldén, 1971) and since no damage of the lammas shoots occurs (according to our field observations), this further boosts the growth superiority of those trees, forming a self-reinforcing loop.

This hypothesis is supported by the fact that, in both trials, the earliest formed, i.e., assessed in the 4th growing season, lammas shoots had the strongest effect on the tree height. In Daugmale, at the end of the 4th growing season, the height of trees with lammas shoots significantly ($P < 0.001$) exceeded that of trees without lammas shoots by 31% (Fig. 4). After the 5th growing season, trees that had formed lammas shoots in the previous but not in the current year (4+5-) exceeded the height of trees without lammas shoots by 33% ($P < 0.001$), and trees that had lammas shoots in the both current and previous year (4+5+) exceeded by 24% ($P < 0.001$). However, trees that had lammas shoots only in the current year (4-5+) had similar (difference 8%, $P = 0.053$) height to trees without lammas shoots. In Norupe, at the age of 4 years, the height of trees with lammas shoots exceeded ($P < 0.001$) the height of trees without lammas shoots by 10%, and the trend indicated by other values (4+5- = 7%, $P < 0.001$, 4+5+ =6%, $P < 0.05$ and 4-5+ =3%, $P > 0.05$) was similar to that observed in Daugmale, even so the differences were smaller (Fig. 4). The effect of the early (formed in the 4th growing season) presence of lammas shoots on the tree height remained significant during the study years. For trees with lammas shoots during this season, height at the age of 7 years exceeded that of trees without lammas shoots by 30.0% and 8.4% in Daugmale and Norupe, respectively.

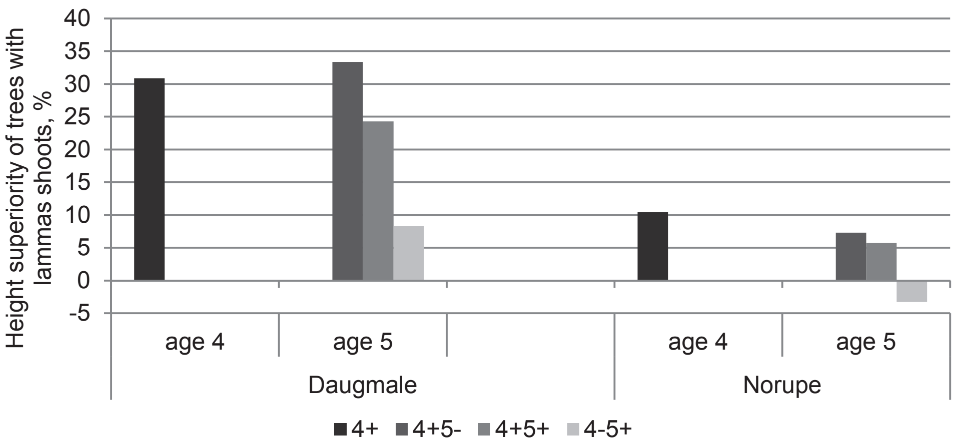

Figure 4. Height superiority at the age of 4 and 5 years for trees with lammas shoots: at the end of the 4th season (4+); only at the end of 4th, but not at the 5th season; in both at the end of the 4th and 5th seasons (4+5+); only at the end of the 5th, but not in the 4th season. Height of trees without lammas shoots is represented as 0.

The influence of lammas shoots is reinforced by their repeated appearance; statistically, trees with lammas shoots more frequently formed lammas shoots also in the following growing season. For instance, in Norupe, 31% of trees that had lammas shoots in the 4th growing season also formed them in the 5th growing season, but from trees without lammas shoots in the 4th growing season only 11% formed them. In Daugmale, the corresponding values were 23% and 4%. Such a trend has been noted by Ehrenberg (1963), who observed lammas shoots on pines in a progeny trial at the age of 8 to 10 years; the proportion of trees with lammas shoots varied between 0.5 to 43.7%, and within the provenance with the most abundant lammas shoots, 4.3% of trees had a second flushing in the four following years. Likewise, West & Ledig (1964) and Rikala (1992) have noted this trend for young (1- to 3-year-old) pines.

The mean height of trees with lammas shoots at any of the assessment seasons from a particular family exceeded the mean height of trees without them from the same family on average by 26 ± 5.9 cm (for the dominant trees 19 ± 6.6 cm) in Daugmale and 12 ± 6.2 cm (for the dominant trees 0.8 ± 5.4 cm) in Norupe. At the family mean level, correlation between height and the proportion of trees with lammas shoots was not found ($P > 0.05$) in any of the trials, contrary to expectations from the positive relation between the tree height and the presence of lammas shoots at the individual tree level discussed above (Figs 2, 3). This is in disagreement with studies of spruce (Hoffmann, 1965; Rone, 1985; Danusevičius & Persson, 1998; Neimane et al., 2015), where a positive relation between the tree height and the presence of lammas shoots has been found at the provenance and family mean levels. However, this is in agreement with the earlier studies of pine, where no significant relationship between the presence of lammas shoots and height growth at the provenance mean level was found (Ehrenberg, 1963).

Association between onset and cessation of pre-determined growth and formation of lammas shoots has been well established for spruce (Danusevičius & Persson, 1998; Neimane et al., 2015; Skrøppa & Steffenrem, 2015). For example, Skrøppa & Steffenrem (2015) found that families with an early growth start had the highest frequency of trees with lammas shoots (r = -0.69...-0.78; $P < 0.01$), and a similar but weaker link with growth cessation was also noted (r = -0.33...-0.55; $P > 0.01$).

In contrast to this, for Scots pines, mostly indirect evidence links early cessation with an increasing chance of lammas growth (Lanner, 1976). Also, in our study, bud-set was not assessed; therefore, the link between those traits and formation of lammas shoots could not be analysed. Notable differences in growth rhythm or too long growth of lammas shoots in the autumn would link the presence of lammas shoots to the increased frequency of frost damage and consequently stem defects. However, no frost damage was observed in our study. Stem defects observed in our trials included additional branch whorls of the main stem caused by lammas growth of apical bud, but its frequency was low. At the age of 10 years, it was noted only for 4.2% (in Norupe) and 5.0% (in Daugmale) of trees with lammas shoots in the particular year.

It corresponds well to a study by Rikala (1992) noting that only 5% of pines had lammas shoots solely from the terminal bud (leading to formation of additional branch whorls). Lammas shoots might result in formation of spike knots (Carvell, 1956; Rudolph, 1964; West & Rogers, 1965; Ehrenberg, 1970; Søgaard et al., 2011), notably deteriorating the stem quality (Ståhl et al., 1990). However, a longer time-lag is important to evaluate which shoot will develop as a spike knot and which will level out and become indistinguishable from an ordinary branch; therefore, this matter needs to be addressed in further, separate studies.

CONCLUSIONS

A strong and positive link between the occurrence of lammas shoots and tree height was observed. Moreover, the earliest formed lammas shoots have the strongest effect. The results suggest that the selection of trees with lammas shoots might result in selection of the highest trees within the family. However, it is not possible to improve the juvenile height growth by the selection of families with a high proportion of trees with lammas shoots.

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