# The early growth and fall frost damage of poplar clones in Latvia

D. Lazdiņa<sup>\*</sup>, S. Šēnhofa, M. Zeps, K. Makovskis, I. Bebre and Ā. Jansons

Latvian State Forest Research Institute 'Silava', Rigas 111, LV 2169 Salaspils, Latvia \*Correspondence: dagnija.lazdina@silava.lv

Abstract. The early growth and frost damage of *Populus* spp. was studied in two sites. The height of 23 five-year-old poplar clones was measured in the central part of Latvia; and the early-fall frost damage of 19 one-year-old and two-year-old poplar clones were assessed in the eastern part of Latvia. The relation between the height growth and frost damage of 16 clones, which were common for both sites, was assessed. The phenologically dormant stage was denoted for three clones, among which two are collected across Latvia (the origin un-known; introduced in 1960s). All the other clones had trees with damaged leaves and two clones had stem damage. The height of the clones ranged from 273.3 ± 60.2 to 711.0 ± 32.0 cm. The 3 most productive clones (LV3, LV1 and LV4) significantly (P < 0.01) exceeded others, by 34 and 65% for height and biomass, respectively. The mean height of these clones was 649.0 ± 21.5 cm and stem biomass varied from  $33.7 \pm 4.2$  to  $55.0 \pm 6.4$  tfresh ha<sup>-1</sup> (planting density 6,500 trees ha<sup>-1</sup>). The clone had significant (P < 0.01) effect on the phenological stage, leaf and stem frost damage, as well as on the height and stem biomass. No relation (P > 0.05) between the frost damage of leaves and both tree height and stem biomass was found. The results suggest that fast-growing frost-tolerant clones might be selected.

Key words: height growth, height increment, biomass, frost damage, frost tolerance, short rotation coppice.

### **INTRODUCTION**

A high productivity of the intensively grown *Populus spp.* has been reported (Heilman & Xie, 1993; DeBell et al., 1996; Scarascia-Mugnozza et al., 1997; Rae et al., 2004). It is strongly determined by genetics, and the growth and yield of the *Populus* clones substantially differs. A high number of *Populus* clones is introduced in the northern Europe (Karačić et al., 2003; Christersson, 2006; Karačić & Weih, 2006), mainly for the establishment of the plantations with the optimum (intended) rotation period of 5–10 to 20–30 years for biomass and solid wood production, respectively (Hynynen et al., 2004; Rytter & Stener, 2005; Tullus et al., 2012). For the last 15 years, substantial amount of *Populus* plantations has been established on abandoned agricultural land (Lazdiņš et al., 2010; Jansons et al., 2014) as well as in forest (Rytter et al., 2015). Nevertheless, poplars are suitable for biomass production also as the agricultural crop (Daugaviete et al., 2015; Smilga et al., 2015; Zeps et al., 2015).

High productivity of *Populus* hybrids is related to the prolonged vegetation period, in comparison to the parental species (Yu et al., 2001). Many of these hybrids can be

grown beyond the natural range of their parents (Sykes et al., 1996). The growth cessation is affected by a complex of environmental factors, among which the increased photoperiod might delay the bud set if the clone is moved northward from the region of the genotype origin (Li et al., 2002; Ingvarsson et al., 2006; Kalcsits et al., 2009). Trees which are not acclimatised to the growing site could be damaged by cold injuries (Sykes et al., 1996). In the northern Europe, the severe frost damage of the introduced poplar clones has been reported (Ferm et al., 1989; Christersson, 1996; Ilstedt, 1996; Telenius, 1999; Karačić et al., 2003; Christersson, 2006; Pliura et al., 2014), linked with the decreased vitality and mortality of trees (Xiang et al., 1991; Diamandis & Koukos, 1992; Pliura et al., 2014). Frost damage has negative effect on the stem quality, e.g. formation of multiple leaders, deformed stem straightness, stem cracks (Verwijst et al., 1996; Christersson, 2006), which is important shortage for solid wood production. However, Schreiber (2012) have suggested that the potential benefits (biomass production) of northward transferred *P. tremuloides* outweigh the potential frost-related risks in western Canada. He has observed almost twice increased biomass for ten-year-old P. tremuloides clones which were transferred even 7° latitude to the north with no decrease of the survival rate (Schreiber et al., 2013). These clones showed delay of the leaf shedding and their frost hardiness was lower than that of the local origin clones; still it was sufficient to not experience the early-fall frost damage. Similarly, some, but not severe, adaptation problems for northward transferred poplar clones has been reported in Lithuania (Pliura et al., 2014).

The aim of the study was to assess the productivity and early-frost damage of the *Populus* clones in Latvia. We hypothesed that (1) the recently introduced clones are more productive, as a result of continuous breeding; but (2) the clones introduced in the 1960s (cuttings from mature trees collected across Latvia) are more tolerant to the frost damage due to the appropriate frost-tolerance of their parent trees.

#### **MATERIALS AND METHODS**

The study sites are located in the central and eastern part of Latvia, near Skrīveri (56°39' N, 25°7' E) and Kalsnava (56°41' N, 25°58' E), respectively. In Skrīveri, height of 23 Populus clones (Table 1; planting density c.a. 6,500 trees ha<sup>-1</sup>) was measured after the second, third and fifth growing season. The clones (at least 30 cuttings from each) are planted in mono-clonal row-plots on flat area with similar growing conditions (former agricultural land) in spring 2001. The distance between the rows 2.2 m, between the trees within the row 0.7 m. Clones AF2, AF6, AF7 and AF8 are planted in 3 replications, all the other clones in 1–2 replications, distributed evenly and randomly over the site. After the first growing season, all clones with the exception of AF2, AF6, AF7 and AF8 were browsed by cervids to the ground level. These clones have additional measurements of height after the first and fourth growing season. Planting material (cuttings) from Skrīveri was used to establish clonal collection in Kalsnava in 2014 and 2015. In Kalsnava, the frost damage of 19 one-year-old and two-year-old Populus clones was assessed. The clones were planted in narrow spacing mono-clonal rows in nursery bed with no replications within small area. The terrain was flat, no frost-shelter were provided from any side of the site (open-field).

Clone	$N_{\mathrm{H}}$	N <sub>FD-1</sub>	N <sub>FD-2</sub>	N <sub>ABG</sub>	Origin of planting material
LV1	22	_	_	8	mix of 12 commercial poplar clones from Sweden
LV3	22	10	2	10	(registration number KB-003, Swedish Forestry
LV4	22	18	37	9	Agency); Tacahamaca section
LV5	17	29	2	6	
LV7	18	22	1	12	
LV9	17	27	2	9	
LV10	21	16	2	13	
LV11	18	21	27	11	
LV12	16	12	102	7	
LV14	21	_	43	13	
LVX	19	25	1	10	
AF2	72	27	_	_	Alasia New Clones, produced by ALASIA Franco
AF6	55	28	_	_	Company, Italy;
AF7	100	27	_	_	AF2 ( <i>P. canadensis</i> ), AF6 ( <i>P. generosa</i> $\times$ <i>P. nigra</i> ),
AF8	122	29	_	_	AF7 ( <i>P. generosa</i> $\times$ <i>P. canadensis</i> ) and AF8
					(P. generosa $\times$ P. trichocarpa)
Max11		126	_	_	clone series from Germany:
Max24	_	191	_	_	hybrids of <i>P. maximowiczii</i> and <i>P. trichocarpa</i>
OP42		27			P. maximowiczii × P. trichocarpa
P0114	40	26	1	26	Populus × woobstii (R.I. Schröd. ex Regel) Dode;
					progenies (cuttings) of poplar trees collected across
					Latvia (Jansons et al., 2014)
POP1	14	_	_	2	progenies (cuttings) of poplar trees collected across
POP2	20	_	_	10	Latvia; presumably Tacahamaca and Aigeiros
POP3	14	_	_	8	sections, introduced (origin unknown) in 1960s
POP4	15	14	_	14	(Saliņš, 1971)
POP5	15	_	_	5	
POP6	13	_	_	10	
POP7	6	_	_	_	

Table 1. The number of trees and origin of clones studied in Skrīveri ( $N_H$  and  $N_{ABG}$ ) and Kalsnava ( $N_{FD-1}$  and  $N_{FD-2}$ )

 $N_{\rm H}$  – number of trees measured for height after the fifth growing season;

N<sub>FD-1</sub> - number of one-year-old trees, which have assessment of frost damage;

NFD-2-number of two-year-old trees, which have assessment of frost damage;

 $N_{ABG}$  – number of trees used to develop the above-ground biomass equation.

The relation between height and frost damage of the 16 clones (common for both study sites) was assessed. In both sites, clones might be divided into groups, according to the origin of the used planting material. The clones of Swedish, Italian, German origin, as well as the clone OP42 are introduced recently, during the last 10 years. Clones collected across Latvia are progenies (cuttings) of the poplars that survived after introduction, most likely, in 1960s. Among them, clone P0114 has been tested and is registered as the forest reproductive material (Community Plant Variety Office, 2014). All the available information of the origin of planting material (region, species) is given in Table 1.

The frost event occurred in the beginning of October, 2015 (Fig. 1). From September 7<sup>th</sup> to October 6<sup>th</sup>, the mean of diurnal minimum and maximum temperatures were +8.0 and +17.8 °C, respectively. The temperature first dropped below zero at night to October 7<sup>th</sup>. From October 7<sup>th</sup> to 15<sup>th</sup>, the mean diurnal temperature ranged from -3.3 to +10.2 °C. The minimum temperature was -5.2 °C, recorded in October 12<sup>th</sup>.



**Figure 1**. Temperature fluctuation ( $\Delta t = 15 \text{ min}$ ) for the period from the 2<sup>nd</sup> decade of September to the 3<sup>rd</sup> decade of October.



Figure 2. The schematic visualization of leaf and stem damage grades.

In October 15<sup>th</sup>, the visual frost damage was assessed (Fig. 2). The bud set was used to determine if trees were still in phenologically active stage or dormant. The damage of the leaves was evaluated at five grade scale. Grade  $1_L$  ('intact leaves') corresponds to the visually intact leaves, Grade  $2_L$  ('mild damage') to the several frost damaged leaves, Grade  $3_L$  ('moderate damage') to the damage of most leaves in the current-year leading shoot and Grade  $4_L$  ('severe damage') to the damage of most leaves of the whole tree. The Grade  $5_L$  corresponds to the trees in the phenologically dormant stage, i.e. leaves were already fallen before the freezing-event and buds were set. Similarly, the damage of stem was evaluated according to five grades. The Grade  $1_{ST}$  ('intact stem') corresponds to the visually intact stem, Grade  $2_{ST}$  ('mild damage') to the several stem injuries, Grade  $3_{ST}$  ('moderate damage') to the damage of more than  $\frac{1}{3}$  of height and Grade  $5_{ST}$  to the damage of whole stem.

The effect of tree age on the frost damage was assessed at the individual tree level for 10 clones. Clone LV4, LV11 and LV12 had sufficient number of one-year-old and two-year-old trees, thus the distribution of number of trees among the grades of leaf and stem damage were assessed for only these clones.

The fresh above-ground biomass in the leafless stage was calculated by Equation 1. This equation is developed based on the biomass measurement of randomly selected ramets (number by clone is shown in Table 1) in Skrīveri after the fourth growing season (height range from 159 to 546 cm).

$$ABG_{fresh} = 10^{-6} \cdot H^{2.7759},\tag{1}$$

where:  $ABG_{\text{fresh}}$  – fresh above-ground biomass in leafless state, kg; H – tree height, cm.

To model potential productivity of different clones at the stand level (6,500 trees ha<sup>-1</sup>), three assumptions of the tree recovery were made: (1) the undamaged trees (Grade  $1_L$  and  $1_{ST}$ ) and trees with the several frost damaged leaves (Grade  $2_L$ ) have no biomass reduction; (2) trees with the damage of most leaves in the last-year leading shoot (Grade  $3_L$ ) or with the several stem injuries (Grade  $2_{ST}$ ) have biomass reduction by 20%; (3) trees with the more severe damage (Grade  $4_L$  and  $5_L$  of leaf damage and/or Grade  $3_{ST}$ – $5_{ST}$  of stem damage) experience mortality. These assumptions are not tested, therefore the results are used only to illustrate the potential effect of the frost injuries.

The Shapiro-Wilk test was used to assess the normality of the data. The one-way analysis of variance was used to assess the differences of the height among the clones. The Kruskal-Wallis test was used to assess the differences of the biomass among the clones. The generalized linear model multivariate was used to assess (1) the effect of the clone and age on the phenological stage and level of leaf and stem damage and (2) the effect of the mean grade of leaf and stem damage on the tree height and biomass. The Chi-squared test was used to assess the distribution of the number of damaged trees of clones LV4, LV11 and LV12 among the grades of leaf damage and within the one-year-old and two-year-old trees. All tests were performed at  $\alpha = 0.05$ . All calculations were done in R 3.0.2. (R Core Team 2013).

### **RESULTS AND DISCUSSION**

In total, 65.4% of trees were in the active phenological stage. All trees in the phenologically dormant stage were found for clones P0114, POP4 and LV10 (Table 2). All trees still growing were denoted for 10 clones, while 6 clones had trees in both phenological stages. The significant (P < 0.01) differences of phenological stage that were found between clones are in accordance with the moderate to strong genetic control of the bud set of *Populus spp.* (Hall et al., 2007; Rohde et al., 2011), and the variation of bud set timing may show high (up to ca. 100 days) differences between clones of different origin (Howe et al., 2000; Christersson, 2006; Friedman et al., 2008). The perennial plants in temperate and boreal zone are adapted to the seasonal cycle of the growth and winter dormancy (Howe et al., 2003; Rohde & Bhalerao, 2007). In our study, surviving clones from the earlier introduction (locally collected) demonstrated better fit to environment. The timing of the bud set is an important adaptive trait (Hänninen et al., 1990). At first, growth cessation is induced by decrease of day-length and temperature, than cold acclimation, endodormancy occurs and, finally, plants reach the maximal cold hardiness. Genotypes transferred northward delay the bud set mainly due to the longer daylight, while the genotypes transferred from the northern areas (or high elevations) tend to set bud earlier in the fall, than trees from the local populations (Weber & Stettler, 1985; Skrøppa & Magnussen, 1993).

Clone	Phenologic	Leaf damage Grades					Stem damage Grades					T - 4 - 1	
	Dormant	Active	$1_{\rm L}$	$2_{\rm L}$	3 <sub>L</sub>	$4_{\rm L}$	$5_{\rm L}$	$1_{ST}$	$2_{ST}$	3 <sub>ST</sub>	$4_{ST}$	$5_{ST}$	– I otal
AF2	_	27	_	10	17	_	_	27	_	_	_	_	27
AF6	_	28	3	12	13	_	_	28	_	_	_	_	28
AF7	_	27	_	3	24	_	_	27	_	_	_	_	27
AF8	_	29	_	10	19	_	_	29	_	_	_	_	29
P0114	27	_	_	_	_	_	27	27	_	_	_	_	27
POP4	14	_	_	_	_	_	14	14	_	_	_	_	14
LV10	18	_	_	_	_	_	18	18	_	_	_	_	18
LV11	_	48	21	13	14	_	_	48	_	_	_	_	48
LV12	13	101	33	34	4	30	13	114	_	_	_	_	114
LV14	_	43	_	_	43	_	_	23	20	_	_	_	43
LV3	1	11	_	1	_	10	1	10	1	_	1	_	12
LV4	_	55	42	11	1	1	_	55	_	_	_	_	55
LV5	30	1	_	_	1	_	30	31	_	_	_	_	31
LV7	_	23	_	_	_	23	_	23	_	_	_	_	23
LV9	_	29	11	17	_	1	_	29	_	_	_	_	29
LVx	5	21	_	_	_	21	5	26	_	_	_	_	26
Max11	59	67	_	_	_	67	59	126	_	_	_	_	126
Max24	143	48	_	_	5	43	143	142	49	_	_	_	191
OP42	_	27	_	_	1	26	_	27	_	_	_	_	27

**Table 2.** The number of trees according to phenological stage and leaf and stem damage grades

Out of the assessed 585 trees, 81% had damaged leaves at various grades (Table 2). Among the actively growing trees, four clones (LV3, LV7, LVX and OP42) had a high proportion (> 80%) of trees with the severely damaged (Grade  $4_L$ ) leaves. Clone LV4

showed the highest frost resistance – 76% of trees had intact leaves (Grade  $1_L$ ). Similarly, Howe et al. (2000) have reported significant differences and a wide range of the frost damage among clones: in the scale of 10, the least-square means were from –0.8 to 9.5. The frost damage of stem was less common (Table 2). Among the dormant trees, clone LV3 had one tree with the mild stem damage (Grade  $2_{ST}$ ). The high susceptibility of stem frost damage was denoted for clones Max24 and LV14, which had 87% and 100% of still growing trees mildly (Grade  $2_{ST}$ ) damaged, respectively. The severe (Grade  $4_{ST}$ ) stem damage was denoted for one tree (clone LV3). These results confirm that trees that set buds later in the fall are more susceptible to the frost damage (Junttila & Kaurin, 1990; Howe et al., 2000).

The tree age had significant (P < 0.01) effect on the level of damaged leaves, but not on the stem damage (P > 0.05) at individual tree level. Significant (P < 0.01)differences were found also among the clones of the same age. All trees from clones LV4 and LV11 were in the active phenological stage, regardless of the age (Table 2). Also all two-year-old trees and most (87%) of the one-year-old trees from clone LV12 were active. For these three clones, no stem damage was denoted but the damage of leaves differed significantly (P < 0.01) between trees of different age. Within clones LV4 and LV11, all two-year-old trees were intact (Grade  $1_L$ ) while one-year-old trees were damaged (Grade  $2_L$  and  $3_L$ ). In contrast, within clone LV12, most of the two-year-old trees were damaged severely (Grade  $4_L$ ) but one-year-old trees had milder damage (Grades  $3_L$  and  $4_L$ ). Younger and, consequently, shorter trees might be more damaged by frost. First, a number of physiological changes, including these which are regulating bud activity, are related with maturation (Brunner et al., 2003; Rozi et al., 2010). For instance, the spring phenology of five temperate tree species was found to be ontogenetically determined rather than result from microclimate (Vitasse, 2013). The ontogenetic effect has also been indicated by increased susceptibility to frost damage of one-year-old *Populus* × rasumowskyana shoots that were emerged after the coppicing in the south-western Finland (Ferm et al., 1989). Younger trees tend to emerge leaves earlier than adults (Vitasse et al., 2014), therefore have higher probability to suffer from early spring frosts. However, similar freezing resistance has been observed for leaves at the same developmental stage for seedlings and saplings (< 0.3 m and 2–4 m height, respectively) in comparison to adult trees (25–30 m height) for several temperate broadleaved species during the leaf-flushing (Vitasse et al., 2014). Also the cold hardiness was found to increase with age, and show significant differences between the adult individuals and trees in the juvenile stage for a number of deciduous species (Lim et al., 2014; Hofmann et al., 2014). Second, smaller trees are more exposed to frost. Relatively larger part of smaller trees is located near the ground, where, in open sites, the air temperature is the lowest (Snyder & Melo.Abreu, 2005). For instance, in the southern Sweden in clear-cut area during three growing seasons the observed mean difference between the minimum temperatures in 0.4 and 1.7 m height was 1.6 °C, reaching maximum difference of 3.8 °C (Langvall & Ottosson-Löfvenius, 2002). Consequently, shorter stands have higher probability of frost damage than taller stands. Moreover, the commercial plantations are commonly established on agricultural lands, often situated in open fields. This could lead to uneven distribution of damaged trees within the plantation – heavier damage nears the edge of plantation and less damaged trees in the centre of it or in the border with mature forest where mutual shield is provided (Verwijst et al., 1996).

After the bud set, i.e. phenologically dormant trees, are more tolerant to the frost damage (Junttila & Kaurin, 1990; Frewen et al., 2000; Howe et al., 2000), but too early bud set interferes with the growth and these trees tend to be shorter (Li et al., 1993; Howe et al., 2000). Thus, the trade-off between utilizing the full growing season and the proper frost-tolerance might occur. However, the frost injury depends on the frost event occurrence and severity. For instance, no frost damage of the clones AF2, AF6, AF7 and AF8 were observed during the first three years in Skrīveri (Lazdiņa et al., 2014). But in the study year, 97% of these trees had mild and moderate (Grade  $2_L$  and  $3_L$ , respectively) damage of leaves (Table 2).

The height growth showed temporal differences among the clones (Fig. 3). After the second growing season, the best results were demonstrated by clones AF6, LV3 and LV12:  $159.5 \pm 10.5$ ,  $154.3 \pm 14.2$  and  $143.9 \pm 8.5$  cm, respectively. The significant  $(P \le 0.01)$  differences between the clones were found, mostly caused by the superiority of clone AF6 and slow growth of clones POP1, POP2 and POP6. It should be noted that most of the other clones had similar or higher height as clones AF2, AF8 and AF7, regardless of the browsing at the end of the previous growing season. This indicates sprouting ability and vigorous growth due to the established root system (Christersson, 1986), and this advantage foster the yield of the second rotation to exceed yield of the first rotation (Dillen et al., 2013). The height differences between clones increased with age. After the second growing season 80 significantly different pairs between clones were found, after the third season 124, while after the fifth growing season this number increased to 169. After the fifth growing season, the height of clones ranged from  $273.3 \pm 60.2$  to  $711.0 \pm 32.0$  cm, and most of the clones LV exceeded those collected in Latvia, as well as AF2, AF7 and AF8. Each of the three highest clones (LV3, LV1 and LV4) was significantly higher than most of the other clones (Fig. 3). The height of these clones was  $649.0 \pm 21.5$ , exceeding ( $P \le 0.01$ ) others by 34%. The same three clones had the highest biomass and exceeded others by 65%. The fresh above-ground biomass of clones LV3, LV1 and LV4 was  $8.47 \pm 0.99$ ,  $6.40 \pm 0.88$  and  $5.19 \pm 0.64$  kg (Fig. 4). The corresponding biomass (planting density 6,500 trees ha<sup>-1</sup>) of these clones was  $55.0 \pm 6.4$ ,  $41.6 \pm 5.7$  and  $33.7 \pm 4.2$  t<sub>fresh</sub> ha<sup>-1</sup>, respectively. In comparison, the mean above-ground biomass of the other clones was  $14.8 \pm 0.7$  t<sub>fresh</sub> ha<sup>-1</sup>. The mean biomass increment of the three most productive clones was  $8.7 \pm 0.7$  t<sub>fresh</sub> ha<sup>-1</sup> year<sup>-1</sup>.

The relatively high genetic control of bud set indicates the relatively low microenvironmental effect (Howe et al., 2000). Hence, the relation of growth and frost-tolerance of the same clones in different sites was analysed. Similar (both P > 0.05) height and above-ground biomass of clones was found, regardless of the mean grade of leaf damage. In contrast, significant (P = 0.049 and P = 0.026, respectively) positive relation between both height and biomass with grade of the stem damage was found. This was caused by clones LV14 and LV3 – relatively high and productive clones that had 46.5 and 16.6% of trees with stem damage (Table 2), respectively. The trade-off between growth and bud set is reported by some authors that have noted the tendency of the clones that set bud early to be shorter than others (Li & Adams 1993) and the other way around – trees that set buds later to be higher and have larger diameter (Pliura et al., 2014). Our results are consistent with this belief, regarding the negative effect of stem damage on tree height and biomass. In contrast, no support to the trade-off was showed by similar level of leaf damage. It should be kept in mind, that the relations between

clonal means are demonstrated and further studies should be done to assess these relations at the individual tree level.



**Figure 3.** Height of clones after the first to fifth growing season and the confidence interval of height after the fifth growing season. The significant differences of the height after the fifth growing season between the three best (LV3, LV1 and LV4) and the other clones are denoted by symbols.



**Figure 4.** Fresh above-ground biomass of clones in the leafless stage. The significant differences of biomass between the three best (LV3, LV1 and LV4) and the other clones are denoted by symbols. Line shows median, box represents 1<sup>st</sup> and 3<sup>rd</sup> quartile, whiskers mark range (not exceeding 150% of interquartile distance) and circles denote outliers of the datasets.

The cold-resistance up to  $-70^{\circ}$  C of the *Populus* species have been reported (Friedman et al., 2008). However, the mortality caused by the cold-injuries is possible if trees are not completely hardened and the sudden drop of temperature occurs (Friedman et al., 2008). Strong negative correlation between the fall frost damage and winter survival has been noted for poplars (Howe et al., 2000), as well as the changes of allometry (lower shoot weight) after the spring frost damage for one of two assessed

Salix hybrids during the first year after the coppicing (Verwijst et al., 1996). The heaviest damaged stand parts had biomass reduction in comparison to undamaged parts for both assessed clones by 47 and 60% (Verwijst et al., 1996). Similarly, Ilstedt (1996) has reported the dieback of ca. 20-60 cm of leading shoots after the fall frost at the age of 2–4 years for most of the poplar hybrid clones that where transferred as far as 10° latitude from the origin of the parental species. The dieback of up to one meter long leading shoot of some 2–3 years old poplar hybrid clones during the winter has mainly resulted with tree death, while other clones had experienced 10-20 cm long shoot dieback and successfully recovered (Christersson, 2006). Dieback of up to three meters long leading shoots of 11-year-old trees (height more than 20 m) were recorded due to the severe winter in 2001–2002 (Christersson, 2006). At the age of 13 years, 15% of the clones were dead due to the frost damage (Christersson, 2006). Nevertheless, frost damage may have indirect negative effect - decreased tree vitality, increased susceptibility to diseases and reduced wood quality. Therefore, we assumed that damaged trees might have biomass reduction, depending on the grade of damage. According to our assumptions (see Materials and Methods), the highest above-ground biomass reduction due to the frost damage caused mortality was expected for clones LVX, LV3 and LV7 (Fig. 5). The potential mortality of these clones resulted in biomass reduction by 80.8, 93.3 and 100%, respectively. Moreover, the clone LV3 would have the absolutely highest above-ground biomass if no frost damage would occur. The loss of biomass of the other clones varied from 0.6 to 29.3%. No biomass reduction was expected for clone P0114, POP4 and LV10. Yet, appropriate frost-tolerance of locally collected clones does not result in higher yield, in comparison to less frost-tolerant but more productive recently introduced clones at the particular frost-event. Further tests in different conditions and age need to be carried out for more comprehensive conclusions.



**Figure 5.** Potential (modelled) loss of the fresh above-ground biomass in the leafless stage (planting density 6,500 trees ha<sup>-1</sup>).

Authors are aware that the assumptions placed in the model might not hold. Poplars have good regeneration ability after damage, as demonstrated by results (height growth) after the first-year browsing damage (Fig. 3), and also concluded by other studies (Mulak

et al., 2006; Hamberg et al., 2011; Myking et al., 2011). For instance, 'soon recovery' after fall frost damage has been reported for northward transferred cuttings at the age of 2–4 years in the southern central Sweden (Ilstedt, 1996). Moreover, the frost damage could occur only in the frost years; while, in the absence of fall frost, trees might gain due to the prolonged growing season.

## CONCLUSIONS

Frost injuries might result in noticeable biomass reduction and mortality of the most productive clones. Hence, the assessment of productivity, frost-tolerance and their interaction ensures valuable information for further clone tests. Clone had significant (all P < 0.01) effect on the phenological stage, leaf and stem frost damage, height and biomass. Our hypothesis was confirmed. Clones (cuttings) which are introduced in the 1969s were less frost-damaged than these which are introduced recently. However, the latter were superior in height and the above-ground biomass production (in the leafless stage). The significant (P < 0.05) trend of more stem damage for more productive clones was found. In contrast, the frost damage of leaves had no effect on both tree height and biomass (both P > 0.05). Therefore, the results suggest that fast-growing and frost-tolerant clones at the particular age could be selected.

ACKNOWLEDGEMENTS. Experimental plots were established by implementation of European Regional Development Fund projects

No 2010/0268/2DP/2.1.1.1.0/10/APIA/VIAA/118 and

No 2013/0049/2DP/2.1.1.1.0/13/APIA/VIAA/031 (data analysis done during Latvian Council of Science project 'Adaptive capacity of forest trees and possibilities to improve it' (No 454/2012).

#### REFERENCES

- Brunner, A.M., Goldfarb, B., Busov, V. & Strauss, S.H. 2003. Controlling maturation and flowering for forest tree domestication. In Stewart, C.N. (ed.): *Transgenic Plants: Current Innovations and Future Trends*. Wymondham: Horizon Press, pp. 9–44.
- Christersson, L. 1986. High technology biomass production by *Salix* clones on a sandy soil in southern Sweden. *Tree Physiol.*, **2**(1-2-3), 261-272.
- Christersson, L. 1996. Future research on hybrid aspen and hybrid poplar cultivation in Sweden. *Biomass Bioenerg.* **11**, 109–113.
- Christersson, L. 2006. Biomass production of intensively grown poplars in the southernmost part of Sweden: Observations of characters, traits and growth potential. *Biomass Bioenerg*. **30**(6), 497–508.
- Community Plant Variety Office. 2014. Official Gazette of the Community Plant Variety Office, 6, 195 pp.
- Daugaviete, M., Lazdina, D., Bambe, B., Bardule, A., Bardulis, A. & Daugavietis, U. 2015. Productivity of different tree species in plantations on agricultural soils and related environmental impacts. *Baltic Forestry* 21(2), 349–358.
- DeBell, D.S., Clendenen, G.W., Harrington, C.A. & Zasada, J.C. 1996. Tree growth and stand development in short-rotation Populus plantings: 7-year results for two clones at three spacings. *Biomass Bioenerg* 11, 253–269.
- Diamandis, S. & Koukos, P. 1992. Effect of bacteria on the mechanical and chemical properties of wood in poplars damaged by frost cracks. *Eur. J. For. Pathol.* **22**(6–7), 362–370.

- Dillen, S.Y., Djomo, S.N., Al Afas, N., Vanbeveren, S., & Ceulemans, R. 2013. Biomass yield and energy balance of a short-rotation poplar coppice with multiple clones on degraded land during 16 years. *Biomass Bioenerg* 56, 157–165.
- Ferm, A., Hytönen, J. & Vuori, J. 1989. Effect of spacing and nitrogen fertilization on the establishment and biomass production of short rotation poplar in Finland. *Biomass* 18(2), 95–108.
- Frewen, B.E., Chen, T.H.H., Howe, G.T., Davis, J., Rohde, A., Boerjan, W. & Bradshaw, H.D. 2000. Quantitative trait loci and candidate gene mapping of bud set and bud flush in Populus. *Genetics* 154(2), 837–845.
- Friedman, J.M., Roelle, J.E., Gaskin, J.F., Pepper, A.E. & Manhart, J.R. 2008. Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evol. Appl.* 1(4), 598– 607.
- Hall, D., Luquez, V., Garcia, V.M., St Onge, K.R., Jansson, S. & Ingvarsson, P.K. 2007. Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula*, L.): a comparison of neutral markers, candidate genes and phenotypic traits. *Evolution* 61(12), 2849–2860.
- Hamberg, L., Malmivaara-Lämsä, M., Löfström, I., Vartiamäki, H., Valkonen, S. & Hantula, J. 2011. Sprouting of *Populus tremula* L. in spruce regeneration areas following alternative treatments. *Eur. J. For. Res.* **130**(1), 99–106.
- Hänninen, H., Häkkinen, R., Hari, P. & Koski, V. 1990. Timing of growth cessation in relation to climatic adaptation of northern woody plants. *Tree Physiol.*, **6**(1), 29–39.
- Heilman, P.E. & Xie, F.G. 1993. Influence of nitrogen on growth and productivity of shortrotation *Populus trichocarpa x Populus deltoides* hybrids. *Can. J. For. Res.* 23, 1863–1869.
- Hofmann, M., Jager, M. & Bruelheide, H. 2014. Relationship between frost hardiness of adults and seedlings of different tree species. *iForest* 7(5), 282–288.
- Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H. 2003. From genotype to phenotype: unravelling the complexities of cold adaptation in forest trees. *Can. J. Bot.* **81**(12), 1247–1266.
- Howe, G.T., Saruul, P., Davis, J. & Chen, T.H.H. 2000. Quantitative genetics of bud phenology, frost damage, and winter survival in an F2 family of hybrid poplars. *Theor. Appl. Genet.* **101**, 632–642.
- Hynynen, J., Ahtikoski, A. & Eskelinen, T. 2004. Yield and profitability of aspen plantation. *Metsä tieteen aikakauskirja* 1, 113–116. (In Finnish.)
- Ilstedt, B. 1996. Genetics and performance of Belgian poplar clones tested in Sweden. For. Genet., 3(4), 183–195.
- Ingvarsson, P.K., García, M.V., Hall, D., Luquez, V. & Jansson, S. 2006. Clinal variation in phyB2, a candidate gene for day-length-induced growth cessation and bud set, across a latitudinal gradient in European aspen (*Populus tremula*). *Genetics* **172**(3), 1845–1853.
- Jansons, Ä., Zurkova, S., Lazdiņa, D. & Zeps, M. 2014. Productivity of poplar hybrid (*Populus balsamifera* × *P. laurifolia*) in Latvia. *Agronomy Research* **12**(2), 469–478.
- Jansons, Ä., Zeps, M., Rieksts-Riekstiņš, J., Matisons, R. & Krišāns, O. 2014. Height increment of hybrid aspen Populus tremuloides × P. tremula as a function of weather conditions in south-western part of Latvia. *Silva Fenn.* **48**(5), pp. 13.
- Junttila, O. & Kaurin, Å. 1990. Environmental control of cold acclimation in *Salix pentandra*. *Scand. J. For. Res.*, **5**:(1–4), 195–204.
- Kalcsits, L.A., Silim, S. & Tanino, K. 2009. Warm temperature accelerates short photoperiodinduced growth cessation and dormancy induction in hybrid poplar (*Populus* × spp.). Trees 23(5), 971–979.
- Karačić, A. & Weih, M. 2006. Variation in growth and resource utilisation among eight poplar clones grown under different irrigation and fertilisation regimes in Sweden. *Biomass Bioenerg* 30(2), 115–124.

- Karačić, A., Verwijst, T. & Weih, M. 2003. Above-ground woody biomass production of shortrotation *Populus* plantations on agricultural land in Sweden. *Scand. J. For. Res.* 18(5), 427–437.
- Langvall, O. & Ottosson-Löfvenius, M. 2002. Effect of shelterwood density on nocturnal nearground temperature, frost injury risk and budburst date of Norway spruce. *For. Ecol. Manage.* **168**(1), 149–161.
- Lazdiņa, D., Bārdulis, A., Bārdule, A. Lazdiņš, A., Zeps, M. & Jansons, Ā. 2014 The first threeyear development of ALASIA poplar clones AF2, AF6, AF7, AF8 in biomass short rotation coppice experimental cultures in Latvia. *Agronomy Research* 12(2), 543–552.
- Lazdiņš, A., Lazdiņa, D. & Liepa, I. 2010. Characterization of naturally afforested farmlands in Latvia. In *Annual 16<sup>th</sup> International Scientific Conference Proceedings*. Jelgava, LLU, 176–182.
- Li, C., Puhakainen, T., Welling, A., Viherä-Aarnio, A., Ernstsen, A., Junttila, O., Heino, P. & Palva, E.T. 2002. Cold acclimation in silver birch (*Betula pendula*). Development of freezing tolerance in different tissues and climatic ecotypes. *Physiol. Plant.*, **116**, 478–488.
- Li, P. & Adams, W.T. 1993. Genetic control of bud phenology in pole-size trees and seedlings of coastal Douglas-fir. Can. J. For. Res. 23(6), 1043–1051.
- Li, P., Beaulieu, J., Corriveau, A. & Bosquet, J. 1993. Genetic variation in juvenile growth and phenology in a white spruce provenance-progeny test. *Silvae Genet.* **42**(1), 52–60.
- Lim, C.C., Arora, R. & Krebs, S.L. 2014. Cold hardiness increases with age in juvenile Rhododendron populations. *Front Plant Sci.*, **5**, Article 542, pp. 8.
- Mulak, T., Landhäusser, S.M., & Lieffers, V.J. 2006. Effects of timing of cleaning and residual density on regeneration of juvenile aspen stands. *Forest Ecol. Manag.* 232(1), 198–204.
- Myking, T., Bøhler, F., Austrheim, G. & Solberg, E.J. 2011. Life history strategies of aspen (*Populus tremula* L.) and browsing effects: a literature review. *Forestry* 84(1), 61–71.
- Pliura, A., Suchockas, V., Sarsekova, D. & Gudynaitė, V. 2014. Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. *Biomass Bioenerg.* 70, 513–529.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.
- Rae, A.M., Robinson, K.M., Street, N.R. & Taylor, G. 2004. Morphological and physiological traits influencing biomass productivity in short-rotation coppice poplar. *Can. J. For. Res.* 34(7), 1488–1498.
- Rohde, A. & Bhalerao, R.P. 2007. Plant dormancy in the perennial context. *Trends Plant Sci.* **12**(5), 217–223.
- Rohde, A., Bastien, C. & Boerjan, W. 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiol.* 31(5), 472–482.
- Rozi, M., Wang, C.T., Ma, C., Shevchenko, O., Dye, S.J., Puzey, J.R., Etherington, E., Sheng, X., Meilan, R., Strauss, S.H. & Brunner, A.M. 2010. Populus CEN/TFL1 regulates first onset of flowering, axillary meristem identity and dormancy release in *Populus*. *Plant J.* 62(4), 674–688.
- Rytter, L. & Stener, L.G. 2005. Productivity and thinning effects in hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) stands in southern Sweden. *Forestry* **78**(3), 285–295.
- Rytter, L., Andreassen, K., Bergh, J., Ekö, P.M., Grinhölm, T., Kilpeläinen, A., Lazdiņa, D., Muiste, P. & Nord-Larsen, T. 2015. Availability of Biomass for Energy Purposes in Nordic and Baltic Countries: Land Areas and Biomass Amounts. *Baltic Forestry* 21(2), 375–390.
- Saliņš, S. Special types of forest plantations. In Bušs, M. & Mangalis, I. (eds.): *Forest plantations*. Zvaigzne, Rīga, pp. 379–409 (in Latvian).
- Scarascia-Mugnozza, G.E., Ceulemans, R., Heilman, P.E., Isebrands, J.G., Stettler, R.F. & Hinckley, T.M. 1997. Production physiology and morphology of *Populus* species and their

hybrids grown under short rotation. II. Biomass components and harvest index of hybrid and parental species clones. *Can. J. For. Res.* **27**(3), 285–294.

- Schreiber, S.G. 2012. Adaptation of trembling aspen and hybrid poplars to frost and drought: *implications for selection and movement of planting stock in western Canada*. University of Alberta, Edmonton, Alberta, 134 pp.
- Schreiber, S.G., Ding, C., Hamann, A., Hacke, U.G., Thomas, B.R. & Brouard, J.S. 2013. Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. J. Appl. Ecol. 50(4), 939–949.
- Skrøppa, T. & Magnussen, S. 1993. Provenance variation in shoot growth components of Norway spruce. *Silvae Genet.*, **42**, 111–120.
- Smilga, J., Zeps, M., Sisenis, L., Kalnins, J., Adamovics, A. & Donis, J. 2015 Profitability of hybrid aspen breeding in Latvia. Agronomy Research 13(2), 430–435.
- Snyder, R.L. & Melo-Abreu, J.P. 2005. *Frost protection: fundamentals, practice and economics. Frost protection: fundamentals, practice and economics*. Food and Agriculture Organization of the United Nations, Rome, 240 pp.
- Sykes, M.T., Prentice, I.C. & Cramer, W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. J. Biogeogr. 23, 203–233.
- Telenius, B.F. 1999. Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. *Biomass Bioenerg* **16**(1), 13–23.
- Tullus, A., Rytter, L., Tullus, T., Weih, M. & Tullus, H. 2012. Short-rotation forestry with hybrid aspen (*Populus tremula* L.× *P. tremuloides* Michx.) in Northern Europe. *Scand. J. For. Res.* **27**(1), 10–29.
- Verwijst, T., Elowson, S., Li, X. & Leng, G. 1996. Production losses due to a summer frost in a *Salix viminalis* short-rotation forest in southern Sweden. *Scand. J. For. Res.* 11(1–4), 104–110.
- Vitasse, Y. 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytol* **198**(1), 149–155.
- Vitasse, Y., Lenz, A., Hoch, G. & Körner, C. 2014. Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. J. Ecol. 102(4), 981–988.
- Weber, J.C. & Stettler, R.F. 1985. Genetic variation and production of *Populus trichocarpa* and its hybrids. I. Morphology and phenology of 50 native clones. *Can. J. For. Res.* **15**(2), 376–383.
- Xiang, C., Sun, H. & Li, G. 1991. Bacterial swollen stem canker on poplar: the disease and its causes. J. Northeast For. Univ. 2(1), 48–55.
- Yu, Q., Tigerstedt, P.M.A. & Haapanen, M. 2001. Growth and Phenology of Hybrid Aspen Clones (*Populus tremula* L. × *Populus tremuloides* Michx.). *Silva Fenn.* **35**(1), 15–25.
- Zeps, M., Sisenis, L., Luguza, S., Purins, M., Dzerina, B. & Kalnins, J. 2015. Formation of height increment of hybrid aspen in Latvia. Agronomy Research 13(2) 436–441.