






Variation of growth and phenology traits in poplars planted in clonal trials in Northern Europe—implications for breeding

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Abstract

The increased demand for wood to replace oil-based products with renewable products has lifted focus to the Baltic Sea region where the environment is favorable for woody biomass growth. The aim of this study was to estimate broad-sense heritabilities and genotype-by-environment (G×E) interactions in growth and phenology traits in six climatically different regions in Sweden and the Baltics. We tested the hypothesis that both bud burst and bud set have a significant effect on the early growth of selected poplar clones in Northern Europe. Provenance hybrids of *Populus trichocarpa* adapted to the Northern European climate were compared to reference clones with adaptation to the Central European climate. The volume index of stemwood was under low to medium genetic control with heritabilities from 0.22 to 0.75. Heritabilities for phenology traits varied between 0.31 and 0.91. Locally chosen elite clones were identified. G×E interactions were analyzed using pairwise comparisons of the trials. Three different breeding zones for poplars between the latitudes of 55° N and 60° N in the Baltic Sea Region were outlined. The studied provenance hybrids with origin from North America offer a great possibility to broaden the area with commercial poplar plantations in Northern Europe and further improve the collection of commercial clones to match local climates. We conclude that phenology is an important selection criterion after growth.

Keywords Provenance hybrids · *Populus* · *trichocarpa* · Sweden · Baltic countries · Volume index · Quantitative genetics · Heritability

Introduction

Medium Rotation Forests with fast-growing *Populus* species offer a significant complementary source of renewable raw materials for various industries worldwide [1]. Woody crops

with fast-growing deciduous species create an opportunity for efficient land use while providing a number of ecosystem services [2]. In recent years, the interest in poplars and the establishment of new plantations has been steadily increasing in the whole Nordic-Baltic region [3]. This trend has been promoted by the success of Swedish poplar plantations established at the beginning of the 1990s using a *Populus maximowiczii* Henry × *P. trichocarpa* Torr. & Gray hybrid “OP42.” The mean annual biomass production in these plantations regularly reaches 10 Mg DW ha⁻¹ year⁻¹ (25 to 30 m³ ha⁻¹ year⁻¹ stemwood) within a rotation period of ca. 20 years [3–5].

However, further expansion of the area of poplar plantations in the region needs to be facilitated through an increased genetic variation of commercially deployable planting stock. This is particularly important as poplars are becoming of interest for planting at higher latitudes in Sweden or in continental climate conditions in the Baltic region. In a search for productive and climate-adapted poplar material for central Swedish conditions, Ilstedt [6] repeatedly tested more than 100 clones of intra- and interspecific hybrids of

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P. trichocarpa and *P. deltoides* W. Bartram ex Marshall × *P. trichocarpa* hybrids originating below 50°N, bred and selected in Geraardsbergen, Belgium. In spite of initially fast growth, many clones were eventually damaged by early autumn frosts and low winter temperatures owing to the late and insufficient bud set. Later on, Christersson tested the same material in southernmost Sweden at 55° 39' N [7]. He also pointed out the vulnerability of the material to early autumn frosts, particularly of the *P. deltoides* hybrids, while evaluating a number of intraspecific *P. trichocarpa* hybrids as potentially usable in southern Sweden.

In another study of 54 poplar clones imported via Holland and grown at two sites in southern Sweden at 56° N, the authors noticed a better growth of “balsam type” poplars (i.e., belonging to species and hybrids of the *Tacamahaca* section) compared to pure species and hybrids with *P. nigra* L. and *P. deltoides* [8]. Later on, this material was extended with clones from the IUFRO collection selected in Finland for winter hardiness, and also with a number of commercial clones [9, 10]. Besides a strong influence of genotype on growth in terms of high broad-sense heritability, there was also a generally stable clonal performance over different sites and a positive correlation between the late autumn foliage coloration and growth, suggesting that clones having green canopy late in the autumn generally perform better. The positive relationship between lifetime growth, measured as increase in height or weight, and late cessation of growth in autumn, i.e., the length of the growth period, is well-documented in common garden studies and clone trials of several *Populus* species [11–14]. Savage and Cavender-Bares [15] showed that northern species of *Populus* and *Salix* exhibited slower growth rates than southern species only when grown under shorter summer day lengths than expected in their native range. Rather, the apparent trade-off between growth and freezing tolerance was related to the adaptive phenology strategy. The conclusion was that *Salix* and *Populus* species should grow better under conditions more similar to those in their native environments. A similar conclusion was drawn by Evans et al. [16] from a common garden study of *P. angustifolia*, where the transfer of provenances both southwards and northwards resulted in poor growth due to either too early bud set or too late leaf senescence leading to autumn and winter frost damage. Consequently, we would expect that the adaptation of non-native poplar species in the Nordic-Baltic region would require the selection of clones with phenology that optimally match the local climate conditions in terms of timing of bud burst and bud set. In practice, this means that different clones will tend to be optimal for deployment at latitudes of 55° N, 60° N, or 64° N.

In an attempt to select commercially deployable material, the Swedish clone testing program was eventually broadened to include a wider range of latitudes, from 56° N to 65° N, using additional material from northern provenances of

P. trichocarpa in Canada and Italian *P. deltoides* × *P. nigra* hybrids [17]. The most important lessons from an early evaluation of these trials, which included pairs of forest and set-aside agricultural sites, as well as a population of hybrid aspen (*P. tremuloides* Michx. × *P. tremula* L.), was that poplars had low survival and growth on the northern sites and were underperforming on forest sites compared to hybrid aspen. Despite poor genotypic correlations between growth and phenology for poplars in the above-mentioned study, the results indicated a tendency for positive correlation between growth and a combination of an early flushing and late leaf coloring, which can be interpreted as a positive effect of a longer green canopy duration on growth. Pliura et al. [18] also found the *P. maximowiczii* × *P. trichocarpa* hybrids to be most suitable for the climate conditions in Lithuania when they compared growth and adaptive traits of 105 clones at two sites. The authors found that most adaptive traits were under strong genetic control with significant genotype-by-environment (G×E) interactions for many growth traits. Furthermore, negative correlations between tree condition and autumn leaf shed phenology in their study indicated that trees with late growth cessation appear to suffer from adaptation problems. Consequently, the strong genetic control of growth and phenology traits allows for significant improvement of clonal performance through selection for adaptation to varying environmental conditions. Such a selection among hybrids and native individuals is oriented towards optimization of the transition between dormancy and growth at both ends of the growing season, prolonging it as much as possible while keeping the risk of frost damage at a reasonably low level [6, 19, 20].

In the 1990s, in an attempt to adapt *P. trichocarpa* to the climate in central Sweden, Ilstedt [21] made a large number of crossings between 13 female and 11 male *P. trichocarpa* parents of different geographic origins in North America resulting in approximately 7000 progenies. Since 2003, around 100 clones were selected for testing in a number of clonal trials in Sweden, Latvia, and Lithuania. This material is a subject of the present study in which we explore phenotypic variation, broad-sense heritability, and genotype-by-environment (G×E) interaction for a number of phenology and growth traits as well as survival. Our main hypothesis is that both bud burst and bud set have significant effects on early growth of poplars in the Baltic Sea Region. The specific aims are to (i) estimate the genotypic components of clonal variance of growth and phenology traits within each trial, (ii) to investigate if the observed early growth performance of poplar clones is correlated with their phenology within each trial, and (iii) to evaluate trait correlations between pairs of trials to identify G×E interaction. Finally, we aimed to (iv) outline major breeding zones for poplar in the Baltic Sea Region. This study will improve our knowledge about the genetic background in variation of growth and phenology traits in Northern Europe and advance our understanding of

the possibilities to select commercially deployable clones after short-term testing by including phenology as an additional selection criterion after growth.

Materials and methods

Field trials and poplar material

We studied six clonal trials with poplars located in regions with variable climatic conditions around the Baltic Sea (Fig. 1). Two of the northernmost trials were located in central Sweden at 60° 37' N and 59° 83' N degrees of latitude (Tierp, Bodarna; Table 1). These two trials belong to different climatic zones according to Redalen [22]. Two clonal trials were located in Arlösa, southwestern Sweden, at 56° 42' N; 12° 56' E and in Ludza, eastern Latvia, at 56° 43' N; 27° 41' E representing one maritime and one more continental site at this latitude. Similarly, with two Lithuanian trials, Anykščiai and Šašaičiai at 55° 22' N; 25° 04' E and 56° 01' N; 22° 20' E, the first was located easterly in a more continental climate and the second westerly in a somewhat more maritime climate. A complete randomized block design with four blocks and five trees per clone and block was applied in Tierp and Ludza. A randomized block design with four blocks and one line plot of five trees per clone and block was applied in Bodarna and Arlösa, while single-tree plots in 16 replications were planted at Šašaičiai and Anykščiai (Table 1).

All six trials were established on productive former agricultural fields with diverse climatic [23–25] and edaphic conditions (Table 1; S1). Before planting, all the trials were fenced, ground vegetation was treated with the herbicide Round-up and the soil was plowed and harrowed. The two Lithuanian trials were planted with 30-cm-long cuttings whereas the other four trials were established using containerized plants with shoot lengths of 40 to 100 cm. The plants were pre-grown from 5- to 10-cm-long cuttings 1 year before planting except for clone “OP42” in Ludza which was planted as 20 cm rooted cuttings pre-grown in a greenhouse 2 months before the trial was established. The green shoots of “OP42” were ca. 20 cm long at planting.

The tested poplar material belonged to four different groups: (1) provenance hybrids of *P. trichocarpa* bred at the Swedish University of Agricultural Sciences; (2) clones derived from selected individuals from natural populations of *P. trichocarpa*; (3) *P. balsamifera* in British Columbia, Canada, and (4) 24 reference clones, which are hybrids between different *Populus* species from diverse breeding programs (Table 2).

Measurements and observations

Measurements of tree diameter at breast height (*dbh*) and tree height (*h*), as well as survival inventories (*s*), were conducted after 4 growing seasons between 2010 and 2017, in Arlösa, Tierp, Ludza, Šašaičiai, and Anykščiai, and after 7 growing seasons at Bodarna. The clonal performance was assessed on the basis of volume index $v_i = d^2h$. In addition, an assessment of spring phenology in all trials and an assessment of autumn phenology in the Baltic trials were conducted according to the scale described in Table 3. Spring and autumn phenology were examined, to determine if growth of poplar clones in different climatic regions was correlated with their phenology.

We made the following assumptions prior to the analyses of our data to facilitate the comparability of our trials. (1) At Anykščiai, we used growth data after the 3rd growing season to avoid the effect of fertilization applied in this particular trial at the beginning of the 4th growing season. However, we still used the phenology screened at age 4 assuming the positive correlation of the same phenology variables between different years [26, 27]. (2) At Tierp, the measurements and observations from the blocks 3 and 4 were used for statistical analyses of growth and phenology. The trees in blocks 1 and 2 were heavily damaged by extensive vole populations (*Microtus agrestis* and *Arvicola terrestris*), which significantly affected growth of the trees in these two blocks and were therefore excluded from the statistical analyses. (3) At Bodarna, we used 7th year growth for statistical analysis, as the mean size of the trees on this clayey site was comparable to the 4th year growth at the other five sites on sandy loam, indicating that competition between the trees in all trials was similar (Table 4). (4) At Bodarna, bud burst was scored in the beginning of the 10th growing season, assuming it to be positively correlated with the bud burst in earlier years [26, 27].

Statistical analyses

We used a quantitative genetic analysis to describe the variation in heritable traits. The analyses of the trials at Tierp, Ludza, Šašaičiai, and Anykščiai were based on single-tree plots, while at Bodarna and Arlösa, we analyzed the means of line plots. Means of the line plots were calculated to obtain a single value per block and genotype, which enabled us to compare Arlösa and Bodarna trials with single-tree plots in the other trials in this investigation. Variance components were derived using a restricted maximum likelihood procedure (REML) in a linear mixed model in SYSTAT Version 13. The analyses were undertaken separately for each trait and trial assuming that the genotypes were unrelated, with CLONE as random effect and BLOCK as the fixed categorical effect. The spatial variation in microenvironment was accounted for by the random effects of ROW and within

Table 1 Description of the trials. Growing degree days (GDD) at $T_{base}=5^{\circ}\text{C}$ per calendar year, were calculated as the sum of GDDs for each day $(T_{max}+T_{min})/2-T_{base}$. GDDs with negative value were not included. Start of a growing season was defined as the first day with mean daily temperature of at least 5°C after which the mean daily temperatures of following days were above 5°C . End of the growing season was defined as the last day with mean daily temperature of 5°C . The data on precipitation and GDD refer to the actual years of growth in each trial location

Site	Tierp	Bodarna	Arlösa	Ludza	Šašaičiai	Anykščiai
Region	Uppland (Central Sweden)	Uppland (Central Sweden)	Halland (Southern Sweden)	Latgale (Eastern Latvia)	Klaipeda (Western Lithuania)	Vilnius (Eastern Lithuania)
Latitude, Longitude	60° 37' N, 17° 45' E	59° 83' N, 17° 83' E	56° 42' N, 12° 56' E	56° 43' N, 27° 41' E	56° 01' N, 22° 20' E	55° 22' N, 25° 04' E
Management history	Former grassland	Former arable land	Former arable land	Former arable land	Former arable land	Former arable land
Year of planting	2008 Oct	2007 May	2007 May	2013 June	2014 April	2014 April
Number of clones, N	28	32	32	108	25	25
Experimental design	Randomized block design with 4 blocks	Block design with 4 blocks, line plots	Block design with 4 blocks, line plots and block	Randomized block design with 4 blocks	Randomized single-tree plots with 16 plots	Randomized single-tree plots with 16 plots
Replications	5 trees per clone and block	5 trees per clone and block	5 trees per clone and block	5 trees per clone and block	1 tree per clone and block	1 tree per clone and block
Planting density	3 × 3 m	3 × 3 m	3 × 3 m	3 × 3 m	3 × 2 m	3 × 2 m
Total number of trees, n	560	640	640	2120	400	400
Soil textural class	Sandy loam below the layer of organic soil	Silty clay	Sandy loam	Sandy loam	Sandy loam	Sandy loam
Precipitation during actual growing seasons, mm	386	379	762	350	441	450
GDD	1471	1720	1787	1562	1755	1820
Start of the actual growing seasons, DOY	106	90	88	100	104	96
End of the actual growing seasons, DOY	283	303	298	275	300	300

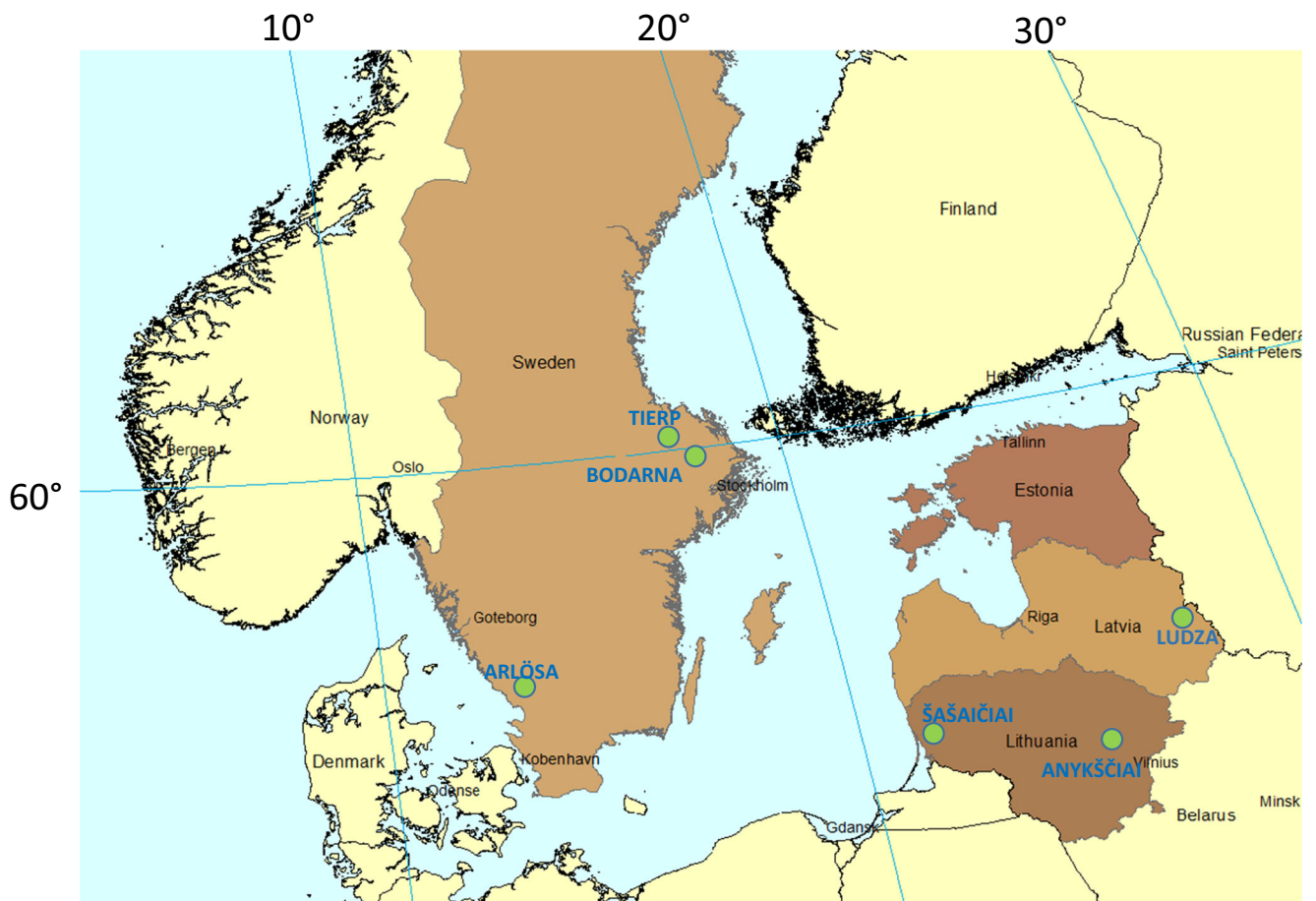


Fig. 1 Location of clonal trials with poplars in the Baltic Sea Region in Northern Europe between 55° and 61° of northern latitude and 12° and 25° of eastern longitude

row POSITION of a tree or line plot both nested within BLOCK. The values for volume index (v_i) were logarithmically transformed prior to analysis. The clonal values for specific traits were calculated as the sum of mean trait value and the random effect predictions for individual clones (BLUPs (best linear unbiased predictions)) from the linear mixed model.

The broad-sense heritabilities of clonal values (H_c^2) were calculated as a proportion of genotypic (clonal) variance component of total random variance:

$$H_c^2 = (\sigma_G^2) / (\sigma_G^2 + \sigma_{en}^2) \quad (1)$$

where σ_G^2 is the variance component for the random effect CLONE and σ_{en}^2 is the environment-related variance component calculated as the sum of spatial variance and residual variance as

$$\sigma_{en}^2 = \sigma_{spatial}^2 + \sigma_c^2 \quad (2)$$

The repeatability of predicted clonal mean values (R_G^2) was calculated as

$$R_G^2 = (\sigma_G^2) / (\sigma_G^2 + \sigma_{en}^2 / k) \quad (3)$$

where σ_G^2 and σ_{en}^2 denote the genotypic and environmental component of variance as in equation 1 and k is the harmonic mean number of replications per clone. The standard errors for repeatability estimates were calculated based on the formula for unequal number of observations [28]:

$$SE(R_G^2) = \sqrt{\frac{2(n-1)(1-R_G^2)^2 [1 + (k-1)R_G^2]^2}{k^2(n-N)(N-1)}} \quad (4)$$

where N is the number of clones tested and n is the total number of individual values. The coefficients of genotypic, environmental, and phenotypic variances were calculated as

$$CV_G = \sigma_G \times 100 / \mu \quad (5)$$

$$CV_{en} = \sigma_{en} \times 100 / \mu \quad (6)$$

$$CV_{ph} = \sigma_{ph} \times 100 / \mu \quad (7)$$

where σ_G , σ_{en} , and σ_{ph} denote genotypic, environmental, and phenotypic standard deviation and μ is the phenotypic mean of the trait.

Table 2 Number of tested *Populus* clones per trial and species/hybrid in current study. The provenance hybrids of *P. trichocarpa* bred at Swedish University of Agricultural Sciences are denoted as T×T_{SLU}. Clones derived from selected individuals from natural populations of *P. trichocarpa* and *P. balsamifera* in British Columbia, are indicated as T and B, respectively. Among reference clones from Central Europe are several commercial hybrids of *P. maximowiczii* × *P. trichocarpa* (M×T),

P. nigra × *P. maximowiczii* (N×M), *P. nigra* × *P. deltoides* (N×D). The *P. trichocarpa* × *P. deltoides* (T×D) and *P. trichocarpa* × *P. trichocarpa* (T×T_{REF}) hybrids are originally from a poplar breeding program at INBO in Belgium. The reference clones of *P. trichocarpa* are of unknown origin (T_{REF}). The *P. tremula* × *P. tremuloides* hybrids are from a breeding program at Latvian Forest Research Institute SILAVA

Species groups	Trials					
	Tierp	Bodama	Arlösa	Ludza	Šašaičiai	Anykščiai
1. <i>P. trichocarpa</i> × <i>P. trichocarpa</i> clones bred for northern latitudes, T×T _{SLU}	8	8	6	74	11	11
2. <i>P. trichocarpa</i> , T	16	20	17	22		
3. <i>P. balsamifera</i> , B	1	2	2			
4. Reference clones						
M×T (OP42, Hybrid 275, OP41, Matrix24; Matrix49)	2	2	2	2	4	4
N×M (Max1; Max3; Max4)					3	3
N×D (AF3; AF6; AF7; AF13; AF34)					5	5
T×D (70.045/1; 69.037/2; 78.026/12)			2	2	1	1
T×T _{REF} (S.192–5*V24/12; 70.038/20; 70.038/67; 240)	1		3	4	1	1
T _{REF} (1559; Spirit)				2		
<i>P. tremula</i> × <i>P. tremuloides</i>				2		

Genotypic correlations between the different traits within the same trials were estimated using Spearman rank correlation analysis.

The genotype × environment (G×E) interactions were analyzed through type B genotypic correlations [29, 30] of the same trait between pairs of trials. New genotypic values (BLUPs) were calculated for each pair of trials including only common clones in these pairs. The type B genotypic correlations were estimated as [31]:

$$r_{Gxy} = r_{xy} / (r_{TPx} \times r_{TPy}) \tag{8}$$

where r_{xy} is the product-moment correlation between best linear

unbiased predictor (BLUP) values for a specific trait in a pair of trials x and y . The estimated relation between true and predicted genotypic values for a trait, r_{TPx} and r_{TPy} , respectively, were calculated as $(H^2k)/(1+H^2(k-1))$, where H^2 is the broad-sense heritability of a trait in an individual trial and k is the harmonic mean number of replications per clone. Thus, the term $r_{TPx} \times r_{TPy}$ takes into account different heritabilities of traits and different harmonic means of replications per clone in pairs of trials. Several pairs of trials were not compared as they had only five common clones (Arlösa-Anykščiai, Arlösa- Šašaičiai, Bodama-Anykščiai, Bodama-Šašaičiai, Tierp-Anykščiai, Tierp-Šašaičiai).

Table 3 Description of the measurements and observed characteristics of the poplar trees. y_r , the age of the trees at the time of inventory. The stem characteristics were described for the main stem over bark up to the current year increment

Measurements/characteristics	Abbreviation	Description
Survival	s_{yr}	Survival of the trees. proportion. scale 0–1
Tree diameter at breast height	dbh_{yr}	Diameter at breast height (mm)
Tree height	h_{yr}	Total height (dm)
Stage of bud break	BBR_{yr}	6 classes: 0—dormant buds; 1—bud swollen, no leaf initials visible; 2—breakage of the buds, tips of the leaves visible (1–2 mm); 3—leaves partially unfolded; 4—leaves completely unfolded; 5—leaves completely unfolded, shoot increment ≥ 1 cm
Stage of bud set	$BSet_{yr}$	5 classes: 0—bud set; 0.5—closed apical bud; 1—apical bud visible but still open; 2—internode elongation ceased, no bud visible; 3—apical shoot fully growing

Table 4 The phenotypic mean of tree growth traits of all *Populus* clones at six trials in Northern Europe (μ), range of variation and coefficient of phenotypic variance (CV_{ph} ; %) of the measured and observed characteristics. *s*, survival; *dbh*, diameter at breast height (mm); *h*, tree height (dm); *BBR*, bud burst; v_i volume index; *BSet*, bud set; *n*, number of observations (trees). The number after the abbreviations denotes age of the trees at the time of inventory

Trait	Site	<i>n</i>	Mean (μ) \pm SE	Range (min–max)	CV_{ph} (%)
Survival, <i>s</i>	Tierp, <i>s</i> ₄	405	0.75 \pm 0.02	0.0–1.0	55.5
	Bodarna, <i>s</i> ₅	128	0.73 \pm 0.03	0.0–1.0	41.8
	Arlösa, <i>s</i> ₃	128	0.94 \pm 0.01	0.2–1.0	15.8
	Ludza, <i>s</i> ₄	2088	0.99 \pm 0.003	0.0–1.0	12.0
	Šašaičiai, <i>s</i> ₄	374	0.84 \pm 0.02	0.0–1.0	43.5
	Anykščiai, <i>s</i> ₄	373	0.88 \pm 0.02	0.0–1.0	34.0
Diameter, <i>dbh</i> (mm)	Tierp, <i>dbh</i> ₄	136	29.51 \pm 0.86	7.5–56.0	33.2
	Bodarna, <i>dbh</i> ₇	126	24.63 \pm 1.29	3.0–80.0	54.1
	Arlösa, <i>dbh</i> ₄	124	36.43 \pm 1.23	7.9–73.5	37.8
	Ludza, <i>dbh</i> ₄	2038	28.63 \pm 0.24	3.0–68.0	38.0
	Šašaičiai, <i>dbh</i> ₄	311	23.09 \pm 0.53	3.0–61.0	40.9
	Anykščiai, <i>dbh</i> ₃	263	24.73 \pm 0.63	5.0–55.0	35.1
Height, <i>h</i> (dm)	Tierp, <i>h</i> ₄	135	32.47 \pm 0.85	7.0–61.0	29.9
	Bodarna, <i>h</i> ₇	126	34.30 \pm 1.16	13.5–88.2	35.0
	Arlösa, <i>h</i> ₄	124	43.77 \pm 1.04	17.6–69.0	26.0
	Ludza, <i>h</i> ₄	2037	42.93 \pm 0.22	9.2–72.8	22.7
	Šašaičiai, <i>h</i> ₄	315	31.10 \pm 0.47	10.0–55.4	25.4
	Anykščiai, <i>h</i> ₃	263	29.78 \pm 0.48	14.0–53.0	22.2
Volume index, v_i (dm ³)	Tierp, v_{i4}	135	3.72 \pm 0.30	0.04–19.13	92.3
	Bodarna, v_{i7}	126	4.07 \pm 0.71	0.01–48.90	69.7
	Arlösa, v_{i4}	124	7.78 \pm 0.67	0.11–35.52	98.7
	Ludza, v_{i4}	2037	4.63 \pm 0.10	0.01–29.41	61.1
	Šašaičiai, v_{i4}	311	2.25 \pm 0.13	0.01–20.61	97.5
	Anykščiai, v_{i3}	263	2.53 \pm 0.17	0.04–14.82	91.5
Bud burst (score)	Tierp (<i>BBR</i> ₂ —date 10/04/15)	129	1.52 \pm 0.04	1.0–2.0	33.6
	Bodarna (<i>BBR</i> ₁₀ —date 19/04/26)	120	4.10 \pm 0.08	2.0–5.0	22.6
	Arlösa (<i>BBR</i> ₄ —date 10/04/16)	124	3.73 \pm 0.06	2.0–5.0	17.4
	Arlösa (<i>BBR</i> ₄ —date 10/04/27)	124	4.88 \pm 0.03	3.3–5.0	6.6
	Ludza (<i>BBR</i> ₃ —date 15/04/22)	2038	2.41 \pm 0.01	0.0–5.0	25.1
	Šašaičiai (<i>BBR</i> ₄ —date 17/04/27)	312	2.51 \pm 0.04	1.0–3.5	30.2
	Anykščiai (<i>BBR</i> ₄ —date 17/04/28)	263	3.04 \pm 0.05	1.5–4.0	30.3
	Anykščiai (<i>BBR</i> ₄ —date 17/04/14)	263	2.28 \pm 0.04	1.0–3.0	29.7
Bud set (score)	Ludza (<i>BSet</i> ₄ —date 16/09/15)	1003	0.16 \pm 0.01	0.0–4.0	192.5
	Šašaičiai (<i>BSet</i> ₄ —date 17/09/16)	315	0.59 \pm 0.04	0.0–2.0	113.7
	Anykščiai (<i>BSet</i> ₄ —date 17/09/15)	247	0.74 \pm 0.05	0.0–3.0	102.4

Results

Mean height *h* of the trees varied between 3 and 4.4 m, mean *dbh* had values between 23 and 36 mm, and mean v_i was 2.3 to 7.8 dm³. Bud burst had mean values between 1.52 in Tierp

and 4.88 in Arlösa. Mean score for bud set was between 0.16 and 0.74 in the three Baltic trials (Table 4). It is important to note here that all clonal trials in this study, except the two Lithuanian trials, had different compositions of poplar clones (Table 2), which is the reason why we test our main

hypothesis within each trial separately. Using only common clones for pairwise comparison of trials allowed identification of genotype-by-environment interactions (G×E).

Substantial clonal variation and significant correlations between phenology and growth at early ages

Plant survival varied from 73% at Bodarna to 99% at Ludza, and there were no clonal differences in survival in the four northernmost trials (S2–S5). In contrast, significantly lower survival was recorded for several *P. nigra* × *P. deltoides* (N×D) hybrids compared to the mean survival in the Lithuanian trials, which was 84–88% (S6–S7). These N×D hybrids were included among the tested clones only in the Lithuanian trials.

The broad-sense heritability estimates (H_c^2) for growth variables (*dbh*, *h*, v_i), which were expressed as the ratio of genotypic to total variance, varied from 0.22 to 0.79 (Table 5). The highest H_c^2 estimates were at Arlösa (between 0.75 and 0.79), while in the rest of the trials H_c^2 varied between 0.22 and 0.43. In all other trials, the heritabilities, i.e., variance related to clone, explained between 22.2 and 42.9% of the total variance in volume index v_i , with corresponding heritabilities from 0.22 to 0.43 (Table 5).

The broad-sense heritability (H_c^2) of bud burst had high values in all the trials (from 0.88 to 0.90), except at Tierp (0.42, Table 5). Bud set, which was scored only in Baltic trials, occurred earlier at Ludza (Latvia, $H_c^2 = 0.31$) than at both Lithuanian trials ($H_c^2 = 0.76$ – 0.83 , Table 5; S5–S7).

The coefficient of genotypic variance (CV_G) was moderate for bud burst and growth, ranging from 6.2 to 31.0 for bud burst, 12.5 to 23.0 for *h*, 16.8 to 33.7 for *dbh*, and 4.6 to 8.7 for v_i (Table 5). The CV_G of bud set ranged from 89.4 to 107.6, indicating a large genetic variance among the tested clones (Table 5). Bud burst was positively correlated with growth in both Lithuanian trials, where clones with earlier bud burst had better growth in terms of volume index or height, respectively ($r = 0.46$ at $p < 0.05$ at Šašaičiai; $r = 0.42$ – 0.51 at $p < 0.05$ at Anykščiai and Šašaičiai; Table 6; Fig. 2). In contrast, clones with late spring phenology in relation to the trial mean, had better growth in diameter, *dbh*, at Bodarna (Table 6; Fig. 2). A positive correlation between late bud set and growth was found at Ludza for all the observed growth variables and at Anykščiai for height ($r = 0.42$ – 0.50 at $p < 0.05$; Table 6; Fig. 3). Bud burst and bud set within the trials where both spring and autumn phenology were inventoried, were not correlated (Table 6).

Genotype-by-environment interaction as a base for delineation of breeding zones

Pairwise comparison of common clones revealed that their ranking according to volume index v_i did not change

significantly between the Swedish trials, Arlösa and Bodarna ($r_{Gxy} = 0.80$ at $p < 0.0001$; Table 7) and between Arlösa and Tierp ($r_{Gxy} = 0.66$ at $p < 0.005$; Table 7). Note that significant positive correlations between ranks indicate no G×E interaction in terms of early growth. In contrast, rankings of clones according to their bud burst were different at Tierp compared to Arlösa ($r_{Gxy} = 0.36$, $p = \text{ns}$) and Bodarna ($r_{Gxy} = 0.50$, $p = \text{ns}$), which indicates a G×E interaction (Table 7). Moreover, the ranking shifts occurred both in volume index v_i and bud burst in the Bodarna-Tierp pair indicating a G×E interaction (Table 7). These interactions reveal that top-performing clones at Tierp are different from those at Bodarna and Arlösa. The relative rankings of clones according to v_i and spring phenology in the pairs Bodarna-Ludza and Arlösa-Ludza did not change, indicating a common breeding zone for central and southern Sweden as well as for Latvia.

The relative ranking of clones according to their phenology did not change at Šašaičiai-Ludza and Anykščiai-Šašaičiai (significant correlations $r_{Gxy} = 0.82$ at $p < 0.05$ and $r_{Gxy} = 0.98$ at $p < 0.0001$ for *BBR* and $r_{Gxy} = 0.87$ at $p < 0.05$ and $r_{Gxy} = 0.92$ at $p < 0.0001$ for *BSet*, respectively), while ranking of clones according to their volume index v_i was not correlated (Table 7). As the rankings of common clones in the pair Anykščiai-Ludza changed in terms of both growth and phenology (Table 7), the Anykščiai region (eastern Lithuania) outlines as a separate breeding zone for poplars in the studied region. Moreover, the correlation coefficient for volume index v_i in this pair of trials was negative, meaning that top clones at Ludza, eastern Latvia, had modest growth performance at Anykščiai in eastern Lithuania (Table 7).

Early selection of poplar clones for commercial deployment in Northern Europe

We used volume index v_i after 3–4 years' growth of poplars on sandy loam soils for ranking of examined clones, while the clones at the Bodarna trial on silty clay were ranked after 7 years' growth (Figs. 4 and 5). The provenance hybrids of *P. trichocarpa* had significantly higher clonal values for v_i compared to the trial mean (i.e., were top-ranked) in the northernmost trial, at Tierp, where the sum of growing degree days was lowest, 1471, in the current study (Table 1, Figs. 4 and 5, S2). The top-ranked clones had late or intermediate bud burst (S2) in relation to the trial mean (Table 4).

Both provenance hybrids of *P. trichocarpa* (T×T_{SLU}) and the hybrids between *P. maximowiczii* and *P. trichocarpa* (M×T) were among the top-ranked clones in southern and central Sweden, Latvia, and western Lithuania, where the sum of growing degree days was above 1562–1787 (Table 1, Figs. 4 and 5, S3–S6).

In contrast, hybrids with a *P. nigra* parent or a *P. maximowiczii* parent were among the best performing clones in the southernmost site at Anykščiai (eastern

Table 5 Results from the mixed linear model analysis of growth and adaptive traits of poplar clones at age of 3–4 years at five sites around the Baltic Sea and at age 7 years in Bodarna. σ_G^2 , clonal variance component, which corresponds to broad-sense heritability as a percent of the total

random variance; $\sigma_{spatial}^2$, spatial variance component; σ_e^2 , residual variance component; R_G^2 , repeatability of clonal means; CV_G , coefficient of genotypic variation; CV_{en} , coefficient of environmental variation

Trait	Site	H_c^2	σ_G^2 (%)	$\sigma_{spatial}^2$ (%)	σ_e^2 (%)	$R_G^2 \pm SE$	CV_G (%)	CV_{en} (%)
<i>dbh</i> ₄	Tierp	0.43	42.9	22.1	35.0	0.57 ± 0.09	21.8	25.1
<i>h</i> ₄	Tierp	0.42	42.2	17.0	40.8	0.59 ± 0.09	19.4	22.8
<i>v</i> _{i4}	Tierp	0.43	42.9	17.2	39.9	0.60 ± 0.09	6.1	9.3
<i>BBR</i> ₂ —date 20100415	Tierp	0.42	41.5	4.6	53.9	0.68 ± 0.08	21.6	25.7
<i>s</i> ₄	Tierp	0.02	1.7	9.8	88.4	0.08 ± 0.05	7.3	55.0
<i>dbh</i> ₇	Bodarna	0.35	35.1	37.1	27.8	0.44 ± 0.10	32.0	43.6
<i>h</i> ₇	Bodarna	0.37	37.2	38.0	24.8	0.46 ± 0.09	21.3	27.7
<i>v</i> _{i7}	Bodarna	0.35	35.3	25.6	39.1	0.50 ± 0.09	9.2	12.5
<i>BBR</i> ₁₀ —date 20190426	Bodarna	0.88	88.0	0.9	11.1	0.97 ± 0.01	31.0	11.5
<i>s</i> ₅	Bodarna	0.12	11.8	32.3	55.9	0.20 ± 0.09	14.4	39.2
<i>dbh</i> ₄	Arlösa	0.79	79.3	9.1	11.6	0.94 ± 0.02	33.7	17.2
<i>h</i> ₄	Arlösa	0.78	78.0	11.5	10.5	0.93 ± 0.02	23.0	12.2
<i>v</i> _{i4}	Arlösa	0.75	75.2	9.9	14.9	0.92 ± 0.02	8.7	5.0
<i>BBR</i> ₄ —date 20100416	Arlösa	0.91	91.0	0.2	9.0	0.97 ± 0.01	16.6	5.3
<i>BBR</i> ₄ —date 20100427	Arlösa	0.88	88.4	1.9	11.4	0.96 ± 0.01	6.2	2.4
<i>s</i> ₃	Arlösa	0	0.00	32.8	68.2	0.00 ± 0.07	0.0	15.8
<i>dbh</i> ₄	Ludza	0.28	27.6	15.7	56.7	0.60 ± 0.04	20.0	32.3
<i>h</i> ₄	Ludza	0.30	30.2	15.9	53.8	0.62 ± 0.03	12.5	19.0
<i>v</i> _{i4}	Ludza	0.27	27.1	14.6	58.3	0.60 ± 0.03	5.8	9.5
<i>BBR</i> ₃ —date 20150422	Ludza	0.68	67.7	0.6	31.8	0.97 ± 0.001	20.6	14.3
<i>BSet</i> ₄ —date 20160915	Ludza	0.31	31.3	9.4	59.4	0.66 ± 0.03	107.6	159.6
<i>s</i> ₄	Ludza	0	0.00	0.0	100.0	0.00 ± 0.01	0.0	12.0
<i>dbh</i> ₄	Šašaičiai	0.28	27.5	13.0	59.6	0.60 ± 0.08	21.4	34.9
<i>h</i> ₄	Šašaičiai	0.32	32.0	18.8	49.3	0.58 ± 0.08	15.2	22.1
<i>v</i> _{i4}	Šašaičiai	0.35	35.2	9.7	55.2	0.70 ± 0.07	8.02	10.9
<i>BBR</i> ₄ —date 20170427	Šašaičiai	0.91	91.3	0.9	7.8	0.98 ± 0.01	28.9	8.9
<i>BSet</i> ₄ —date 20170916	Šašaičiai	0.83	83.1	2.0	14.9	0.96 ± 0.01	103.6	46.7
<i>s</i> ₄	Šašaičiai	0.28	27.6	3.0	69.4	0.78 ± 0.05	22.5	43.5
<i>dbh</i> ₃	Anykščiai	0.23	22.9	15.3	61.9	0.51 ± 0.08	16.8	30.8
<i>h</i> ₃	Anykščiai	0.32	32.2	11.3	56.6	0.65 ± 0.07	12.6	18.3
<i>v</i> _{i3}	Anykščiai	0.22	22.2	120	65.9	0.54 ± 0.08	4.6	8.7
<i>BBR</i> ₄ —date 20170414	Anykščiai	0.86	86.0	1.3	12.7	0.97 ± 0.01	27.5	11.1
<i>BBR</i> ₄ —date 20170428	Anykščiai	0.90	89.9	1.7	8.5	0.97 ± 0.01	28.7	9.6
<i>BSet</i> ₄ —date 20170915	Anykščiai	0.76	76.3	2.8	20.9	0.94 ± 0.02	89.4	49.9
<i>s</i> ₄	Anykščiai	0.14	13.5	7.7	78.9	0.51 ± 0.08	13.4	34.0

Lithuania) in terms of their v_i (Table 1, Figs. 4 and 5, S7). Most of the top-ranked clones had early spring phenology and late or intermediate autumn phenology (S7) in relation to the trial mean (Table 4). The exception was a *P. nigra* × *P. deltoides* hybrid (AF34) with late spring and autumn phenology (S7).

Comparison of growth (v_i) of the 5 common clones in all six trials (S2–S7) revealed that growth of poplars as an early-successional alluvial species was significantly correlated with

precipitation during the actual growing seasons (Table 1, the Pearson correlation coefficient $r = 0.67$ at $p < 0.0001$).

Discussion

Improved growth of commercial woody crops requires that the trees use effectively a short growing season at northern latitudes. The northward transfer of poplar clones with

Table 6 Genotypic correlations among growth and adaptive traits of hybrid poplar clones at individual trials after 3–4 years of growth at Tierp, Arlösa, Ludza, Šašaičiai, and Anykščiai (sandy loam) and after 7 years of growth at Bodarna (silty clay). The number after the abbreviations

denotes the age of the trees at the time of inventory, e.g., h_4 = height at 4 years. Correlations are significant at $p < 0.05$ (*), $p < 0.005$ (**), or $p < 0.0001$ (***)

Trait	Tree height, h	Stem volume index, v_i	Bud burst, BBR		Bud set, $BSet$	Survival, s
Tierp. central Sweden						
dbh_4	0.86***	0.95***	-0.10			0.09
h_4		0.89***	-0.15			0.07
v_{i4}			-0.12			0.1
BBR_2 —date 2010/04/15						-0.25
Bodarna. central Sweden						
dbh_7	0.97***	0.88***	-0.40*			0.68***
h_7		0.88***	-0.35*			0.70***
v_{i7}			-0.32			0.55*
BBR_{10} —date 2019/04/26						-0.05
Arlösa. south-west Sweden						
dbh_4	0.97***	0.98***	Date 2010/04/16	Date 2010/04/27		0.97***
h_4		0.96***	-0.17	-0.03		1.00***
v_{i4}			-0.20	-0.08		0.96***
BBR_4 —date 2010/04/27			-0.23	-0.07		0.96***
BBR_4 —date 2010/04/16			0.69***			-0.08
BBR_4 —date 2010/04/16						-0.20
Ludza. eastern Latvia						
dbh_4	0.95***	0.99***	-0.12		0.57***	0.03
h_4		0.97***	-0.13		0.53***	-0.02
v_{i4}			-0.14		0.56***	0.00
BBR_3 —date 2015/04/22					-0.18	-0.03
$BSet_4$ —date 2016/09/15						0.03
Šašaičiai. western Lithuania						
dbh_4	0.90***	0.96***	0.46*		-0.26	0.59**
h_4		0.93***	0.51*		-0.26	0.54**
v_{i4}			0.46*		-0.23	0.58**
BBR_4 —date 2017/04/27					-0.22	0.28
$BSet_4$ —date 2017/09/16						-0.43*
Anykščiai. eastern Lithuania						
dbh_3	0.89***	0.98***	Date 2010/04/14	Date 2010/04/07		0.07
h_3		0.93***	0.30	0.36	0.31	0.07
v_{i3}			0.42*	0.50*	0.42*	-0.09
BBR_4 —date 2017/04/14			0.38	0.44*	0.34	-0.006
BBR_4 —date 2017/04/28				0.96***	-0.09	-0.05
$BSet_4$ —date 2017/09/15			0.95***	0.93***	-0.19	0.03
$BSet_4$ —date 2017/09/15			-0.09	-0.17		-0.23

southern origin results in a relatively late bud set in relation to the place of origin and subsequently longer canopy duration [12, 16, 32]. The commercial deployment of southern clones at northern latitudes is an attractive strategy among land-owners but is coupled with the risk for frost damage in the autumn as photoperiod-dependent bud set occurs in the north at daylengths when ambient temperatures are occasionally below zero. Similarly, spring leaf flush of southern clones at northern latitudes is likely to be delayed as temperature sums

needed for bud burst occur several weeks after the growing season begins at northern latitudes. Genetic improvement of poplars for different climatic regions in Northern Europe would offer a possibility to increase the pool of renewable raw materials for circular economies and sustainable environments. A considerable genetic variation in growth and phenology traits is a prerequisite for genetic improvement by breeding. Here we studied phenotypic variation of growth and phenology of poplar clones with different origin to estimate the

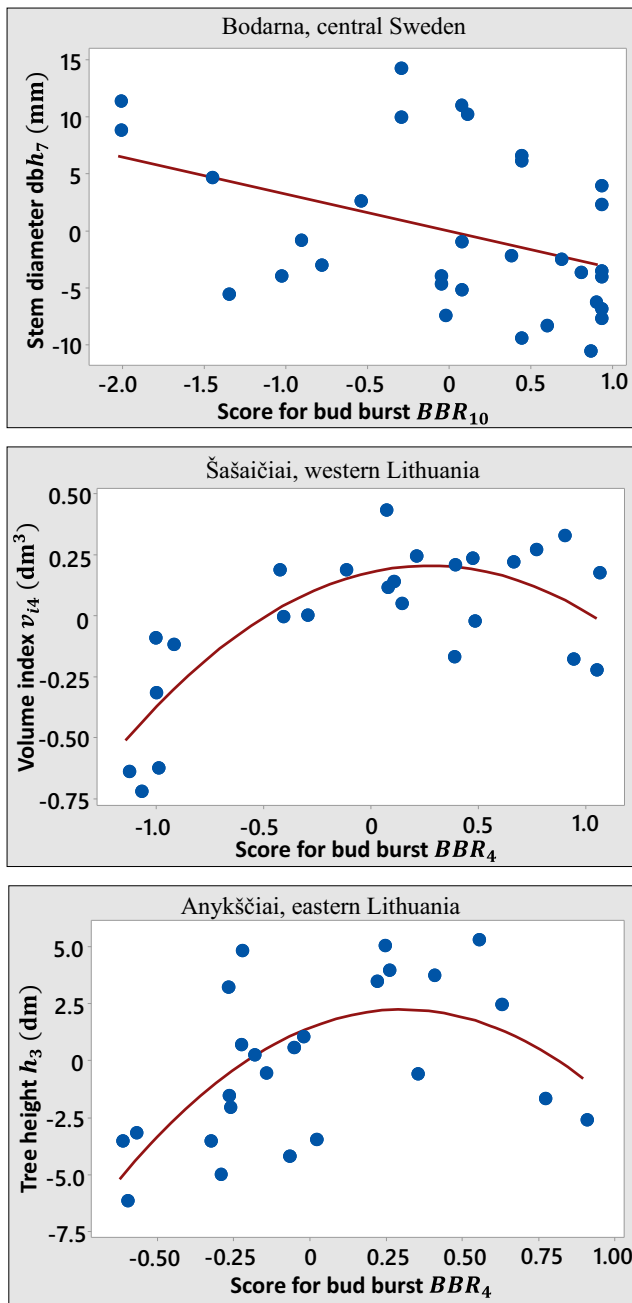


Fig. 2 Spearman correlation between BLUP values of score for bud burst (BBR_{yr}) and growth at Bodarna, central Sweden ($r = -0.35$ at $p < 0.05$; $N = 32$), at Šašaičiai, western Lithuania ($r = 0.51$ at $p < 0.05$; $N = 25$) and at Anykščiai, eastern Lithuania ($r = 0.46$ at $p < 0.05$; $N = 25$)

genotypic component of clonal variation in boreo-nemoral climates in Northern Europe [33–35]. We have shown that both bud burst and bud set have a significant effect on early growth of poplars in the Baltic Sea Region. The high heritability of phenology traits enables an early selection of locally adapted poplar clones with sufficient growth. We suggest three major breeding zones for poplar clones according to the pattern of the genotype-by-environment interactions of volume index and phenology in the Baltic Sea Region.

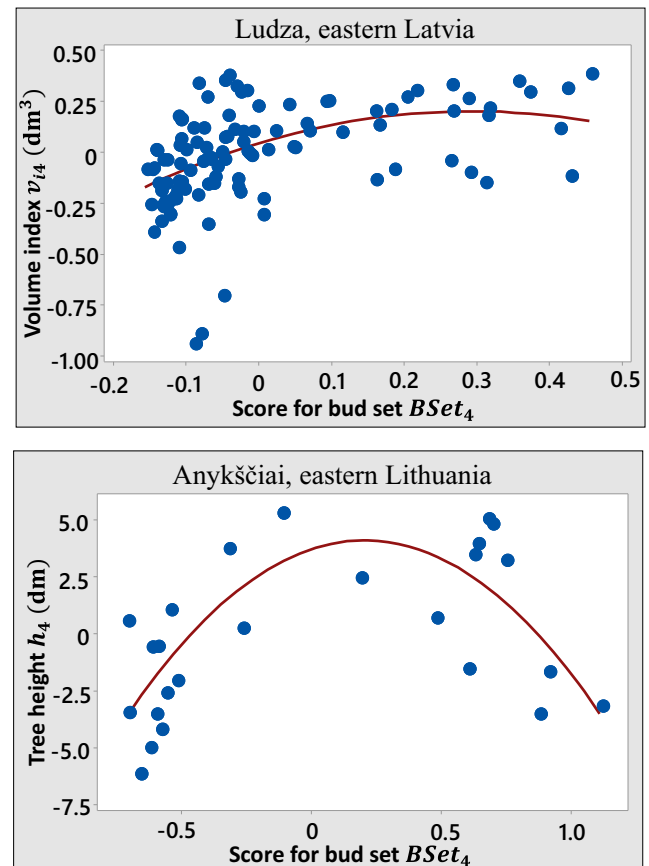


Fig. 3 Spearman correlation between BLUP values of score for bud set ($BSet_4$) and volume index (v_{14} , log-transformed) at Ludza, eastern Latvia ($r = 0.56$ at $p < 0.0001$; $N = 108$) or stem height at Anykščiai, eastern Lithuania ($r = 0.50$ at $p < 0.05$; $N = 25$)

Phenotypic and genotypic variations

Considerable phenotypic and genotypic variation in growth and adaptive traits characterized the tested poplar material. We found that tree growth correlated significantly with spring or autumn phenology in all Baltic trials and in one trial in central Sweden at Bodarna. Significant negative correlation between early spring phenology and growth, measured as lifetime increment of stem diameter at breast height, was also reported by Richards et al. [36] who studied variation in the timing of leaf phenology at both ends of two growing seasons in a 14–15 years old poplar trial close to Bodarna in central Sweden. Although observations of bud set were not available for our Swedish trials, the significant effect of other leaf phenology traits on tree growth, such as leaf senescence and autumn leaf coloring, indicate that bud set may also have a significant effect on poplar growth in Swedish climates [37].

Clones with their origin from breeding programs for Central Europe, which were tested only in Šašaičiai and Anykščiai, showed mismatch to local growing conditions in the Lithuanian climate. For example, many of the *P. nigra* × *P. deltoides* (N×D) hybrids with poor growth had late bud

Table 7 Type B genotypic correlations (r_{Gxy}) of BLUPs for growth and adaptive traits between pairs of locations. Non-significant correlations indicate a genotype-by-environment interaction. The number after the abbreviations denotes age of the trees at the time of inventory

Trial 1	Trial 2	Number of common clones, N	r_{Gxy}	p
Volume index, v_i				
Arlösa, v_{i4}	Bodarna, v_{i7}	27	0.80	<0.0001
Arlösa, v_{i4}	Tierp, v_{i4}	27	0.66	<0.005
Bodarna, v_{i7}	Tierp, v_{i4}	28	0.51	Ns
Arlösa, v_{i4}	Ludza, v_{i4}	18	0.43	Ns
Bodarna, v_{i7}	Ludza, v_{i4}	14	0.68	Ns
Anykščiai, v_{i3}	Ludza, v_{i4}	11	-0.46	Ns
Šašaičiai, v_{i4}	Ludza, v_{i4}	11	0.25	Ns
Anykščiai, v_{i3}	Šašaičiai, v_{i3}	25	0.40	Ns
Bud burst (date)				
Arlösa, BBR_4 (2010/04/27)	Bodarna, BBR_{10} (2019/04/26)	27	0.68	<0.001
Arlösa, BBR_4 (2010/04/27)	Tierp, BBR_2 (2010/04/15)	25	0.36	Ns
Bodarna, BBR_{10} (2019/04/26)	Tierp, BBR_2 (2010/04/15)	28	0.50	Ns
Arlösa, BBR_4 (2010/04/27)	Ludza, BBR_3 (2015/04/22)	18	0.61	Ns
Bodarna, BBR_{10} (2019/04/26)	Ludza, BBR_3 (2015/04/22)	14	0.59	Ns
Anykščiai, BBR_4 (2017/04/28)	Ludza, BBR_3 (2015/04/22)	11	0.82	Ns
Šašaičiai, BBR_4 (2017/04/27)	Ludza, BBR_3 (2015/04/22)	11	0.82	<0.05
Anykščiai, BBR_4 (2017/04/28)	Šašaičiai, BBR_4 (2017/04/27)	25	0.98	<0.0001
Bud set (date)				
Anykščiai, $BSet_4$ (2017/09/15)	Ludza, $BSet_4$ (2016/09/15)	11	0.82	Ns
Šašaičiai, $BSet_4$ (2017/09/16)	Ludza, $BSet_4$ (2016/09/15)	11	0.87	<0.05
Anykščiai, $BSet_4$ (2017/09/15)	Šašaičiai, $BSet_4$ (2017/09/16)	25	0.92	<0.0001

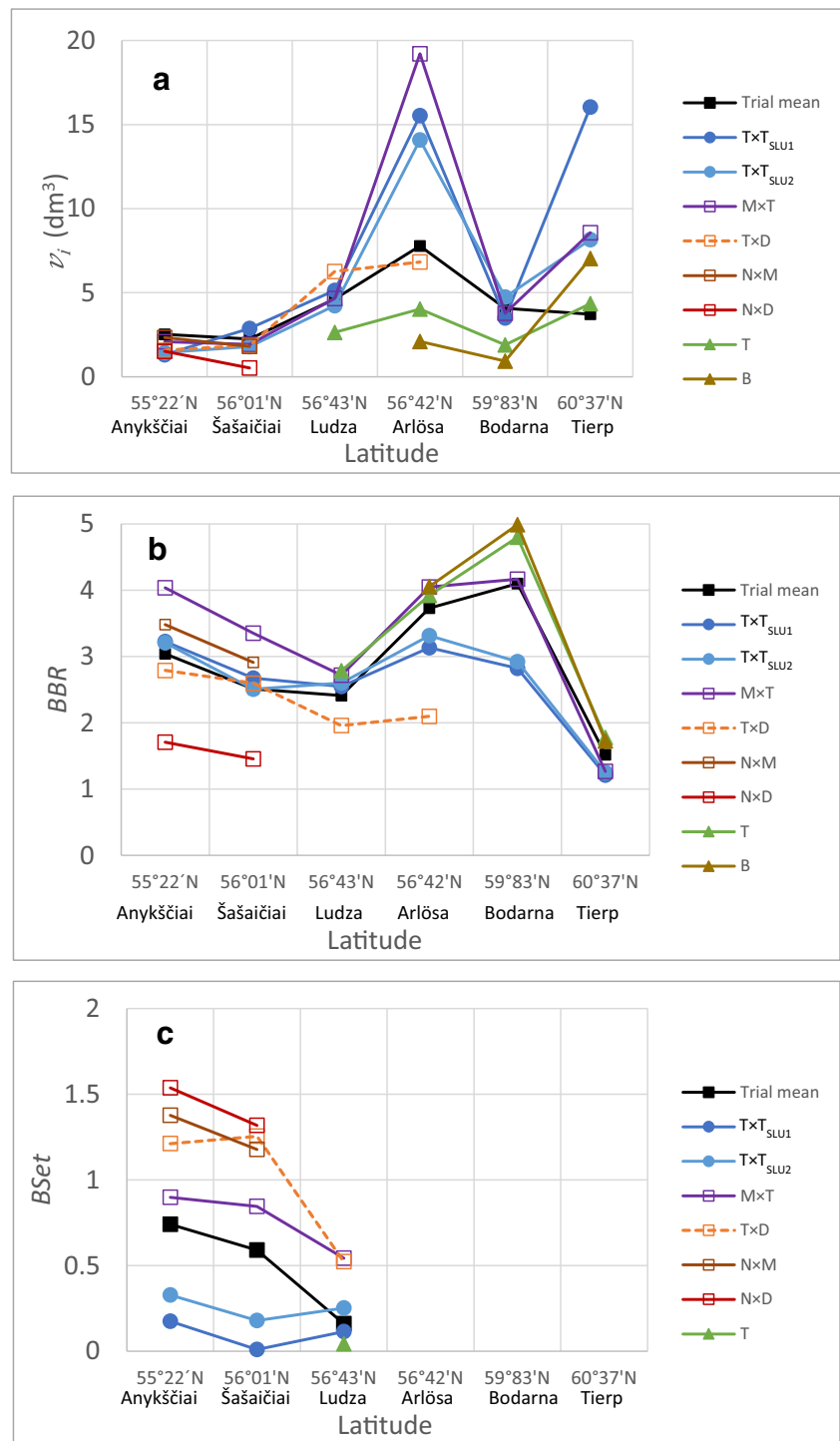
burst and late bud set compared to the trial means (Fig. 4). These observations are in accordance with Olson et al. [38] who showed that trees adapted to southern latitudes needed a greater temperature sum accumulation before bud flush than trees adapted to northern latitudes. The hybrids between *P. maximowiczii* × *P. trichocarpa* (M×T) showed better adaptation to the climate in our southernmost trials in the Baltic Sea Region. The M×T hybrids were characterized by earlier bud burst and a few days later bud set compared to the trial mean, which resulted in sufficient growth of these hybrids in southernmost trials (Anykščiai, Šašaičiai, Arlösa) in the current study. Our results are in concordance with a study from a geographically close location in northern Poland (N 54° 4' 26", E 20° 30' 4"), where “OP42” planted at similar spatial density as in our study, had significantly higher 6th-year biomass than N×D hybrids from southern and central Europe [39].

However, different strategies for growth rhythm may result in sufficient growth. For example, at Ludza, the clones with

intermediate bud set (i.e., the clonal values not significantly different from the trial mean), such as the provenance hybrids within *P. trichocarpa* (T×T_{SLU}), “26.1” and “23.4”, were among the top-performing clones as well as those with relatively late bud set (e.g., T×D hybrids; S5). However, the short testing period (4 years) without early autumn frosts might have been favorable for the hybrids with late bud set (M×T, T×T_{REF}, T×D, and *P. tremula* × *P. tremuloides*; S5). In addition, we might have missed out some portion of variability in bud set as the majority of clones had reached final stages of growth cessation at the time of inventory. This, however, would not significantly affect the main conclusions from this work. Despite relatively late inventories of bud set in the Baltic trials, the genotypic variation in bud set between clones was considerably higher than the genotypic variation in bud burst and growth. Furthermore, the relatively high residual variance component $\sigma_e^2 = 59.4\%$ for bud set reflects the large effect of environmental cues, e.g., autumn temperatures, on this phenology trait in Ludza (Table 5). Therefore, clones with

Fig. 4 Average clonal values of **a** volume index, v_i , **b** score for bud burst, *BBR*, and **c** score for bud set, *BSet* of different hybrid/species groups of poplar clones in six trials in Baltic Sea Region along a latitude gradient.

Abbreviations of the various hybrid/species groups are described in Table 2. Following clones are included in this figure: $T \times T_{SLU1}$ (26.1; 44.11; 23.4); $T \times T_{SLU2}$ (21.9; 15.7); $M \times T$ (OP42; OP41); $T \times D$ (70045/1; 69.037/2); $N \times M$ (Max1, Max3, Max4); $N \times D$ (AF13, AF34; AF6; AF7; AF3); T (PG2-25; PG2-28; PG2-22); B (FN5-4; FN3-20). SE of clonal values for each clone is presented in S2–S7



too late bud set in relation to the trial mean do not have improved growth compared to the clones with intermediate bud set and should not be planted in commercial plantations.

Provenance hybrids of *P. trichocarpa* ($T \times T_{SLU}$), such as clones “23.4” and “26.1,” which were characterized by intermediate bud burst and intermediate bud set compared to the trial means and reference clones (S2–S7), had superior growth in the northernmost trials at Tierp and Bodarna, central

Sweden and at Ludza in eastern Latvia. These provenance hybrids show optimal adaptation to a relatively short growing season at latitudes around 60° N by an optimal use of growing season that is 177–210 days long with a sum of growing degree days between 1471 and 1787 at the base temperature of 5°C.

The adaptability of clones to grow in different environments is not necessarily defined only by their phenology

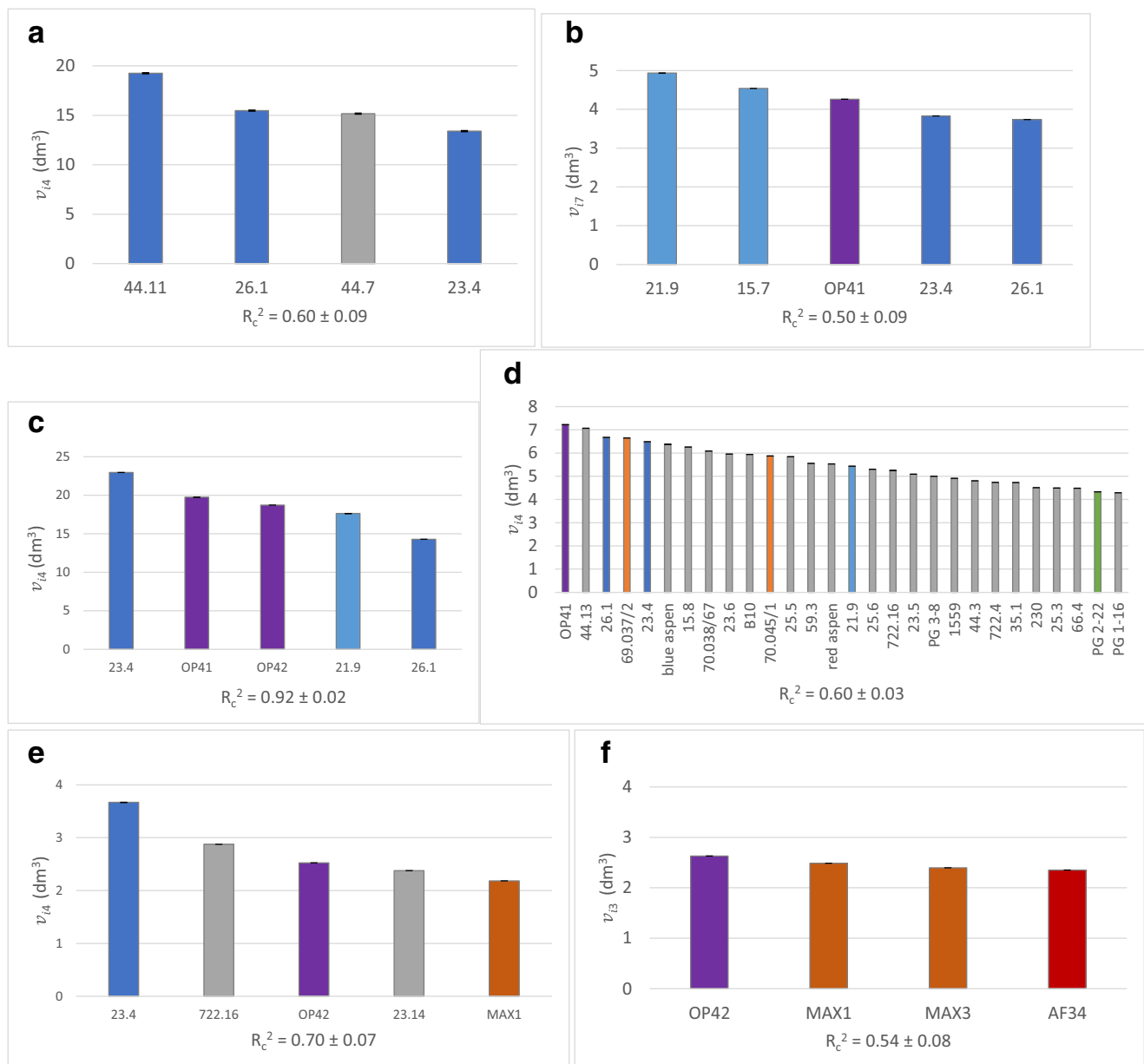


Fig. 5 Ranking of clones according to their clonal values for volume index (v_i) in Swedish and Baltic clonal trials. Clones with significantly higher volume indices compared to the respective mean values for specific trials are presented. Figures are grouped according to latitudes in this study: northernmost (**a - Tierp**, **b - Bodarna**), middle (**c - Arlösa**,

d - Ludza), and southernmost (**e - Sasaiciai**, **f - Anyksčiai**) trials. R_c^2 is the repeatability of the clonal means. The different color, identifying clones from specific hybrid/species groups, follow the color pattern in Fig. 4. The clones not involved in Fig. 4 are presented in gray

[40] but also by their physiological and morphological parameters [41], which were not examined here. For example, the T×D hybrid “69.037/2,” a clone with relatively late bud burst and bud set, allocated relatively more biomass to roots than wild *P. trichocarpa* clones from continental parts of Canada in Prince George in an outdoors pot experiment in Central Sweden, where plant responses to water and nutrient stress were studied [42]. The authors predicted the suitability of this particular clone for sandy soils, as was the case at our Ludza trial in eastern Latvia and at Arlösa in southern Sweden (Table 1; S1).

The heritability estimates and coefficient of genotypic variation are used in breeding for comparison of genetic variation in traits and to evaluate the possibility for selection in different environments [43]. The heritability estimates for bud burst and bud set in the current study were higher than those for growth traits, which is in accordance with earlier studies on growth and adaptation of poplar hybrids [18, 26, 36, 37, 44]. The importance of spring phenology for the fitness of the trees in the Lithuanian climate is reported also by Pliura et al. [18]

with higher broad-sense heritabilities for spring phenology than for autumn leaf senescence.

Genotype-by-environment interactions

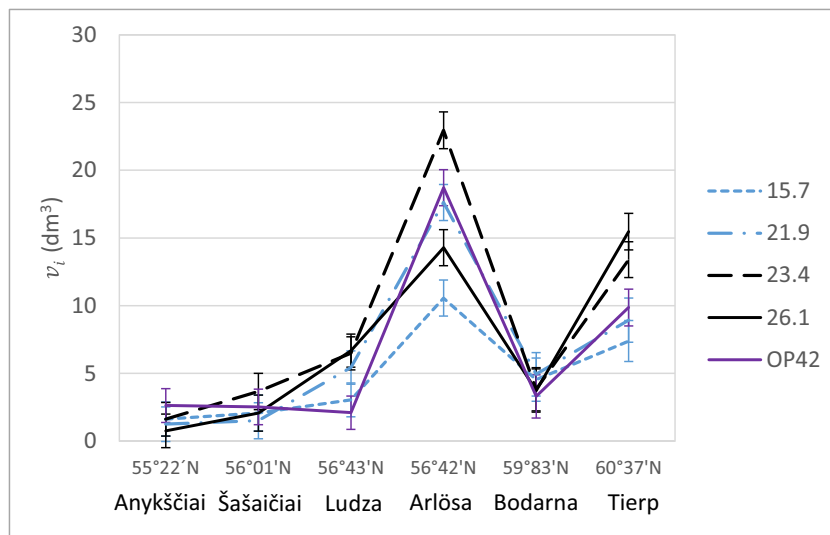
Evaluation of clonal trials with poplars and selection of clones that are adapted to local climates is a prerequisite for commercial deployment [41, 45–48], which aims to support local markets with woody biomass [49]. Genotype-by-environment interactions in biomass growth and phenology of poplar clones [16, 17, 48, 50–52] are important information for optimal development of adapted clonal material to specific growth environments. Our trials had variable climatic and edaphic conditions, indicating, as in earlier studies, that in addition to proper adaptation to local climate, rainfall during the actual growing season and soil type have significant impact on growth of poplars [53, 54].

Pairwise comparison of the six trials in different climates in the Baltic Sea region identified significant $G \times E$ interactions. These interactions were illustrated here as change in rankings of poplar clones that were common to pairs of trials (Table 7) and to all six trials (Fig. 6). Two main breeding strategies are used to deal with $G \times E$ interactions in breeding programs: (1) selection of clones with stable growth and broad adaptation across the environments and (2) selection of clones that are well adapted to each climatic region [55, 56]. Cost-efficient cultivation of woody crops requires maximized growth and survival of planted material per area in combination with high value of the harvested biomass for local industries. Consequently, matching clones with specific climatic regions would maximize yield of this woody crop in northern Europe with variable climatic zones along the latitude cline. Evaluation of clonal trials, as here, gives a hint about clones that should proceed to final evaluation in yield trials. Based on

the growth response of individual clones, we could identify three distinct breeding zones.

The largest breeding zone consists of the areas in southern Sweden, central Sweden (up to the Bodarna trial), Latvia and western Lithuania, where intermediate bud burst combined with intermediate bud set results in better growth (breeding zone 1). The southernmost region in this study—eastern Lithuania (Anykščiai)—represents a separate breeding zone for poplars (breeding zone 2). In this region, which is the northern margin of the natural distribution of *P. nigra*, clones with relatively early bud burst and intermediate bud set were superior in terms of volume growth. The separation of eastern Lithuania as a different breeding zone is a contrasting result to our previous study, which showed consistent ranking of poplar clones in the Baltic Sea Region by using data on leaf phenology and ambient air temperature [57]. All the trials analyzed in the last-mentioned study, belong to the breeding zone 1 identified in the current study, except the trial at Anykščiai. The difference between the two studies is that current study (1) uses also growth in addition to phenology as a criterion to rank poplar clones and (2) the number of analyzed clones is higher in the pairs of trials in current study, compared to the number of analyzed clones in all six trials analyzed by Vico et al. [57]. In addition, (3) the type B genotypic correlations, as a method to compare clonal rankings in current study, take into account also different heritabilities of traits and different harmonic means of replications per clone in pairs of trials. As rankings of clones in Anykščiai and Ludza regarding both phenology and growth were not correlated (Table 7), we suggest Anykščiai region (eastern Lithuania) as a separate breeding zone. Finally, the northernmost region of central Sweden, Tierp, outlines as a third breeding zone, where combination of intermediate bud burst and early bud set in relation to the trial means resulted in better growth (breeding zone 3).

Fig. 6 Volume index (v_i) of five common clones in all six trials in the Baltic Sea Region along a latitude gradient



Breeding goals for the North European market

In Sweden, the production systems with fast-growing trees are designed to deliver wood in dimensions that are suitable for the existing pulping industry. *Populus* hybrids reach high growth rate in terms of mean annual increment (MAI = 15 m³ ha⁻¹) at a plantation age of 9 to 10 years in southern Sweden at 55° N [58] and 6 m³ ha⁻¹ in Northern Sweden at latitude 63° N [59]. MAI continues to increase after this age, and culminates with MAI = 20–30 m³ ha⁻¹ year⁻¹ after 20 years in Southern Sweden [3–5, 60]. During the rotation time of 20 years, the dimensions of poplars reach suitable sizes to produce assortments for diverse markets: pulpwood for pulp industry or biorefineries at first hand and secondly, tops and branches for bioenergy. In the Baltic States, the industry that manufactures wood fibreboards prevails. Poplar wood has also potential as a feedstock for production of liquid biofuels [61]. Recent advances in bioenergy research in Scandinavia are also investigating possibilities to use woody biomass for production of ethanol [62]. Innovative processes for a pulp industry are developing, which aim at more efficient biomass fractionation for future biorefineries to produce lignin oils and textile fiber from fast-growing deciduous trees [63, 64]. Fast-growing poplars would be attractive as raw material for all of these industries. A modeling study suggests that an increased area planted with fast-growing *Populus* species in medium rotations would improve both volume production and profitability to the same or higher level as the cultivation of long-rotation Norway spruce (*Picea abies* (L.) Karst.) in Sweden [65]. Regardless of the end-use of poplar as raw material, a future breeding program for this fast-growing woody crop needs to focus on high production capacity of stemwood. Our study confirms earlier findings that bud burst and bud set are likely controlled by different genes, as these adaptive traits within our trials were not correlated [36]. This finding paves a reliable ground for breeding poplars for regions with different photoperiods. Our investigation contributes to the emergence of a specific breeding program for the Baltic Sea Region by identifying large genotypic variation in growth and phenology traits in available material in local climates. Several new clones, identified in the current study, are suitable for commercial deployment in colder climates in central Sweden and in the Baltic States. Furthermore, the current study found some evidence that in addition to the major commercial hybrid poplar clone “OP42” in southern Sweden [66], there are several alternative clones suitable for establishment of large-scale plantations in different climates in Sweden and in the Baltic countries.

Future studies should follow up if the preliminary division into three different breeding zones—(1) southern and central Sweden, Latvia, western Lithuania, (2) eastern Lithuania, and (3) coastal areas of central Sweden (Tierp)—is correct at later stages of this woody crop. As clonal site suitability may also

vary with rotation length [67], this evaluation after 4 years' growth needs to be complemented with growth assessments at later stages of these trials. Several earlier studies have shown, however, that top clones according to initial growth were also the top clones at greater age, although the ranking of initial top clones changed [45, 50, 68]. On an area basis, the changes in relative clonal rankings in stem volume growth and survival play a significant role in total wood production per planted area. Hence, this evaluation of single-tree plots needs to be complemented by evaluation of yield trials with monoclonal plots, as estimates of volume yields from such plots reflect better the biomass production potential on an area basis and the magnitude of difference in volume production between different clones [69].

To conclude, commercial deployment of poplars requires clones that effectively use the short growing season at northern latitudes. Relocation of clones with southern origin to northern latitudes does not result in effective use of the growing season in the north owing to the mismatch of both spring and autumn phenology of these clones at northern latitudes. Relatively late bud burst and bud set of genotypes of southern origin do not result in better volume growth in the north compared to poplar hybrids with intermediate/early bud burst and bud set matched for northern climate by breeding.

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Author contribution Anneli Adler: establishment and inventory of the clonal trials, development of the concept, analyses of data, writing the original draft, reviewing and editing, funding acquisition. Almir Karacic: establishment and inventory of the clonal trials, development of the concept, co-writing the introduction, reviewing and editing, funding acquisition. Ann-Christin Rönnerberg Wästljung: support to statistical analyses and result generation, development of the concept, reviewing and editing, funding acquisition. Ulf Johansson: establishment and inventory of the clonal trials, development of the concept, reviewing and editing. Kaspars Liepins: establishment and inventory of the clonal trials, development of the concept, reviewing and editing. Audrius Gradeckas: establishment and inventory of the clonal trials, development of the concept. Lars Christersson: initiator of poplar testing on Northern latitudes, development of the concept, reviewing and editing the manuscript.

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Data availability The data analyzed in this manuscript are available from the corresponding author upon request.

Declarations

Conflict of interests The authors declare no competing interests.

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