An Analysis of Poplar Growth and Quality Traits to Facilitate Identification of Climate-Adapted Plant Material for Sweden

Almir Karacic¹ · Anneli Adler¹ · Martin Weih¹ · Lars Christersson¹

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Abstract

Poplar plantations harbor large potential as a renewable source of biomass for bioenergy and other industrial applications. The overall aim of this study is to analyze growth, phenology, stem form, and branching characteristics of 32 poplar clones grown in a trial in southern Sweden for their suitability to be grown as industrial feedstock. In a linear mixed model, performed for diameter at breast height and stem volume, the precision was improved by the use of two competition indices. The significance of phenology and quality characteristics for growth performance and ranking of poplar clones was evaluated through genotypic correlations, and multivariate hierarchical cluster analysis used to group the material. All traits showed moderate to high broad sense heritability. In general, higher stem volume was positively correlated with later leaf senescence, and uncorrelated with spring phenology. Selection efficiency for stem diameter and height was greatly improved between age 3 and 6 years allowing a better precision in selecting a subset of clones to be further tested in production plots and pilot plantations. Two commercial *Populus maximowiczii* Henry × *trichocarpa* Torr. & Gray cultivars performed best, while some intraspecific hybrids of *P. trichocarpa* are considered useful to genetically diversify commercial plantations in Southern Sweden (Belgian clones) or establish plantations in north-central parts of Sweden (Swedish clones). The cluster analysis emphasized growth traits and the grouping of the clones corresponded to their origin (or parentage). The results will facilitate decisions on the use of studied material in breeding, further testing and commercial deployment of poplar plantations in Sweden.

Keywords Genetic parameters · Growth performance · Multivariate analysis · Phenology · *Populus trichocarpa* · Stem quality

Introduction

Transformation towards sustainable land and material use benefits from an increased availability of fossil-free and regionally produced raw materials such as woody biomass. Fast-growing *Populus* species represent one potentially important biomass source [1, 2] with high biomass productivity [3, 4] and multiple industrial and environmental uses [5, 6]. Currently, Swedish

poplar feedstock is mixed in the pulping process (particularly for textile pulp) with other tree species, while tops and branches are used as fuel in combined heat and power plants (Anders Ekstrand, Södra—personal communication). Nevertheless, the anticipated use of poplar wood is much broader and includes sawn wood, plywood, and refined fuel products for vehicles and aviation. In any case, the economic and technological viability of poplars rests heavily on the access to reliable feedstock supply and its quality characteristics. This precondition greatly depends on availability of highly productive and climate-adapted poplar varieties. Currently, in Sweden, commercially deployable poplar varieties are reduced to clone “OP-42” (*Populus maximowiczii* Henry × *P. trichocarpa* Torr. & Gray) crossed in the 1920s by Stout and Schreiner [7–9]. This clone has been planted since the 1990s on some thousand hectares at latitudes 56°–59° N reaching an annual biomass production of up to 10 Mg ha⁻¹ year⁻¹ [4, 10] within rotations of 18–25 years. However, operating with only one commercial variety represents an obstacle to further expansion of poplar plantations on the potentially available land area (0.5–2.5 million ha [11]), particularly in more harsh environments at higher latitudes.

✉ Almir Karacic
almir.karacic@slu.se

Anneli Adler
anneli.adler@slu.se

Martin Weih
martin.weih@slu.se

Lars Christersson
lars.christersson@slu.se

¹ Department of Crop Production Ecology, Swedish university of Agricultural Sciences, 750 07 Uppsala, Sweden

Breeding and selection of *Populus* in Sweden was first focused on hybrid aspen, whereas poplars have been only occasionally tested [12]. Development of bioenergy market in the 1970s and 1980s attracted renewed interest to poplars as an economically interesting alternative for farmers on the land set-aside from an overproducing agricultural sector. Poplar germplasm, originally introduced mainly from collections in the Netherlands and Germany, was later expanded with Belgian material consisting of *P. trichocarpa* and its hybrids with *P. deltoides* Bartr. Ex Marsh. and with IUFRO [13] material imported mainly from Finland [14]. After initial evaluations, Belgian clones were considered unsuitable for central Sweden, but partly usable in southern Sweden [15, 16]. In 1990s, a short poplar breeding program was started as a result of a growing insight into the importance of adaptation of material for Swedish climate conditions. The focus was entirely on *P. trichocarpa* using parentage from maritime-continental and south-north transects at 45–60° N [17, 18]. A relatively small portion of the resulting progeny population was saved and is presently under field evaluation across the whole Baltic Region. Six clones from this program were included in the trial presented here.

So far, poplar breeding programs have been mainly focused on producing material suitable for temperate climate regions at latitudes between 30° N and 50° N [19–22]. Such material lacks necessary hardiness when planted at higher latitudes (55° N–65° N), which has been confirmed in a number of north European field trials [15, 16, 18, 23–25]. This maladaptation has its cause in phenotypic mismatch, usually related to delayed autumnal transition from growth to dormancy [26, 27]. In *P. trichocarpa*, this transition is mainly governed by photoperiod signals for growth cessation triggered at longer days in northern compared to southern ecotypes [26, 28]. Thus, while highly productive varieties of southern origin tend to set buds too late or inadequately when grown at higher latitudes, there is also a clear trend of prolonged periods of shoot elongation to be correlated with higher biomass production [15, 16, 18, 23–25, 29–33]. Such a trade-off between competitive advantages of a longer seasonal growth and survival due to timely termination of growth is under strong selection pressure in natural populations of *Populus* spp. [31, 34]. Consequently, even the adaptation of poplars outside their natural range will rest on our ability to develop criteria for adequate balance of biomass productivity and phenology timing under the specific photoperiod and temperature conditions in different parts of Sweden.

In many studies on poplar clones, multiple traits have been used to evaluate poplar material using multivariate analytic tools [30, 35–39]. In the present study, we use some quality traits along with growth and phenology variables, adding thus the potential end use value as the evaluation criterion. The overall aim of this study was to analyze growth, phenology, stem form, and branching characteristics of 32 poplar clones grown in southern Sweden for their suitability as industrial

feedstock. The specific aims were to (i) estimate the genotypic components of clonal variation for various traits, (ii) evaluate correlations between phenology and clonal growth performance, (iii) analyze age-dependent correlations of growth traits and their impact on selection efficiency, and (iv) group the material using multiple traits for growth performance, phenology, and quality characteristics. This study will improve our understanding of the importance of phenological and stem quality traits in the selection of poplar clones for Swedish climate conditions.

Material and Methods

Climate and Soil

The trial was located at the Swedish west coast, outside the city of Halmstad (56° 41' N; 12° 56' E), a region with temperate climate, naturally dominated by deciduous broadleaved forests. During the study period, between 2007 and 2018, all important climate parameters corresponded to the average values for the standard reference period 1961–90. The mean annual temperature was 8.2 °C, equaling an average value of 1783 growing degree days, whereas the total annual precipitation was 864 mm, with 371 mm falling during the period of intensive growth in May–August. The temperature-based average length of growing season (SMHI 2020—Open data, Swedish Meteorological and Hydrological Institute) is 210 days beginning in early April and ending in the first week of November. The mean temperature during the growing season was 13.1 °C and the first autumn frosts occurred usually first between October 31 and November 15 or later.

The soil has developed on relatively deep postglacial sand (SGU—Geological Survey of Sweden) with sandy loam/loamy sand texture for 0–20 and 20–50-cm layers, respectively. Blocks I and II were located on the northern slope, whilst blocks III and IV were placed at the bottom of the slope where ground water table was occasionally high, decreasing the tree survival in a part of block III. The soil pH was 5.5; there was 2% of organic C within 20 cm topsoil, while the NO₃ and NH₄ nitrogen amounted to approximately 30 kg ha⁻¹.

Trial Design and Plant Material

After appropriate soil preparation and weed treatment the trial was established in June 2007 by planting 1-year-old, containerized seedlings of 32 poplar clones. A randomized 4-block design was applied with a 3 × 3 m planting spacing, 5-trees line plots, totaling 20 trees per clone. The poplar clones originated from four major sources; (i) *P. trichocarpa* and *P. trichocarpa* × *deltoides* bred at Geraardsbergen, Belgium (BELt and BELtd), preliminary evaluated by Christersson [16], (ii) six clones of *P. trichocarpa* bred for central Sweden (58°–62° N,

SLUc—for central Sweden and SLUn—for the southern part of Swedish northern provinces) [14], (iii) 17 progenies of *P. trichocarpa* from Prince George (PG, 54° N) including two additional progenies of *P. balsamifera* from Forth Nelson (FN, 58° N), British Columbia, Canada, and finally (iv) two reference clones (REF) of *P. maximowiczii* × *trichocarpa*, “OP-42” and “OP-41” (Table 1). The Kinship coefficient between the two reference clones is 0.464 (Pär Ingvarsson, SLU, Uppsala, Sweden—personal communication). Considering that the expected value for monozygotic twins is 0.5 and 0.25 for full-sibs, it appears that the clone identified as “OP-41” most probably is “OP-42.” However, we decided to treat them as two different clones in our statistical analysis.

Measurements and Sampling

Diameter at breast height (*D*) and tree height (*H*) were measured repeatedly in 3-year intervals. In 2015, we visually assessed stem form and branching, and measured the occurrence and height of top dominance loss, crooks and forks (Table S1). Phenology of bud burst (BB) was inventoried in 4–6-day intervals between end of March and the beginning of May 2010 by observing six different developmental stages: BB0, closed bud; BB1, initial shoot emergence; BB2 and BB3, the two phases defined by the length of primordial expansion outside the bud scales; BB4, leaves half shed (still rolled), bud scales wide open or shed; and BB5, leaves completely unrolled. Julian day (doy) for bud burst phase BB3 was selected as the starting point of canopy growth. To compensate for inventor’s bias and due to periodic oscillation of temperature between screening occasions, we used all the observations of bud burst to slightly correct

timing of BB3 for each clone (Supplementary Information, S2). Changes in autumn crown color and defoliation were registered between the end of September and mid-November 2018. The color change was screened separately for 1-year-old shoots (TC), and for older parts of crown (CRC) using the 0–2 scale, i.e., 0, green; 1, yellow-green; and 2, yellow. The same scale was used for leaf shed (LS), i.e., 0, less than 33%; 1–33% to 66%; and 2, more than 66% leaves shed (Table 2). Bud burst was inventoried in 2010 and leaf senescence in 2018. Consequently, clone canopy durations (CADU), calculated between BB3 and different autumn variables were hypothetical. Here, we made assumption that relative comparison of CADU among different clones will be meaningful, and also usable to compare the correlations of CADU with growth traits. In some cases, doy of phenological stages was not recorded, so that linear estimates were made for each single tree between two consecutive observations, for example, between BB2 and BB4 or for CRC2 when it was not registered.

Calculations and Statistical Analysis

In January 2019, 39 trees of 13 clones were thinned out from the trial and used to model volume growth based on diameter measurements along the stem in 2-m segments. Obtained parameters were used to estimate stem volume of all clones in the trial at all ages according to following function:

$$V = e^{(b_1 + b_2 \times \ln D + b_3 \times \ln H)} \quad (1)$$

where *V* (dm³, i.e., m³/1000) is stem volume on bark, *D* (cm, i.e. mm/10) is the breast height diameter, *H* (m) is total tree

Table 1 The origin and parentage of the poplar material

Clone	Species	Group	Female parent	Male parent
OP-41	M × T	REF	Japan	Washington
OP-42	M × T	REF	Japan	Washington
15.7	T × T	SLUc	216 (1560) Lincoln Island, Alaska 58°30'N	290, Unknown
21.9	T × T	SLUc	230 (69.094/6) Abbots Ford, BC	236; V235 (Washington) × V23 (Idaho)
23.4	T × T	SLUc	230 (69.094/6) Abbots Ford, BC	Kenai Island, Alaska
26.1	T × T	SLUc	230 (69.094/6) Abbots Ford, BC	299 (910), Washington
70.038/20	T × T	BELt	S.3–31 (Michigan)	V24 (Oregon, Columbia River)
70.038/67	T × T	BELt	S.3–31 (Michigan)	V24 (Oregon, Columbia River)
70.039/24	T × T	BELt	S.192–5 (Idaho)	V24 (Oregon, Columbia River)
44.7	T × T	SLUn	70.039/? (S.192–5 (Idaho) × V24/36 (Oregon)	299 (910) Washington
44.11	T × T	SLUn	70.039/? (S.192–5 (Idaho) × V24/36 (Oregon)	299 (910) Washington
69.037/2	T × D	BELtd	V235 (Washington)	S.620–543 (Michigan)
70.045/1	T × D	BELtd	V235 (Washington)	S.520–225 (Michigan)
PG clones	T	PG	PG1, PG2, ..., PG5 (Prince George, BC)	Unknown
FN clones	B	FN	FN3 and FN5 (Forth Nelson, BC)	Unknown

M, *P. maximowiczii*; *T*, *P. trichocarpa*; *D*, *P. deltoides*; and *B*, *P. balsamifera*

Table 2 List of variables and acronyms used to characterize growth, phenology, and quality of trees grown in a 12-year-old poplar trial in southern Sweden

Variables	Definition
Growth traits	
D, H, V	Cumulative growth of D, diameter at breast height (1.3 m); H, total tree height; V, stem volume at age 3, 6, 9, and 12, i.e., D ₃ , D ₆ , zD, zH, zV
zD, zH, zV	Periodic growth increments of D, H and V for the period 3–6, 6–9 and 9–12 years, or for the period 6–12 years, i.e., zD _{3–6} , zD _{6–9} etc.
Observed phenology traits¹	
BB3	Bud burst stage 3
TC1, TC2	Yellow-green and yellow color of the tree top and 1-year-old parts of the crown
CRC1, CRC2	Yellow-green and yellow color of the older parts of the crown
LS1, LS2	Foliage shedding stage 1 (33–66% leaves shed) and 2 (more than 66% leaves shed)
Constructed autumn phenology traits	
CAV	Color average, i.e., average day's for occurrence of TC1, TC2, CRC1, and CRC2
LSAV	Leaf shed average, i.e., average day's for occurrence of LS1 and LS2
AUAV	Autumn average, i.e., average day's for all variables included in CAV and LSAV
Canopy Duration traits based on BB3 and different autumn phenology variables	
CADU-TC1, CADU-CRC2, CADU-CAV, CADU-AUAV	Canopy duration limited by BB3 in spring and autumn phenology traits TC1, CC2, CAV, and AUAV
Stem form and branching traits (Table S1)	
STR, stem straightness; BRA, branch angle; BRTH branch thickness; BRNS, branchyness	

¹ Phenology variables are expressed as day of year (doy) for the first occurrence of a certain phenology stage or as an average day for the first occurrence of phenology traits included in the constructed variables

height, and $b1 = -3.53769$, $b2 = 1.70873$, and $b3 = 1.35448$ are the estimated equation parameters.

Variance analysis of phenology variables was performed using mixed model procedure with the restricted maximum likelihood method to estimate the effects of fixed and random components. *Z* and *F* tests were used to determine significance of random and fixed effects respectively. The following linear model was used for analyses of all phenology variables:

$$Y_{jkl} = \mu + C_j + B_k + e_{jkl} \quad (2)$$

where Y_{jkl} represents an observation on the l^{th} line plot (average value of the five individuals in a line plot) on a j^{th} clone within k^{th} block, μ is the overall mean, and e_{jkl} is random error. The random clonal component was assumed to have normal distribution with the expectation of zero and corresponding σ_c^2 and σ_e^2 . The analyzed variables are presented in Table 2.

In the analyses of D, H, and V, and the corresponding periodic increments (zD, zH, zV) additional random spatial components were introduced in the mixed model representing row-column within-block matrices. Two competition indices were also calculated and used as covariates, i.e., sum of line lengths (SLL) [40] and neighbor plots (NP). The competition indices compensated for differences in growing space caused by early mortality and the edge

effects. SLL was calculated for every single tree, then averaged for each line plot entry:

$$SLL_i = \sum_{j=1}^8 \frac{D_i}{D_i + D_j} \times RDist \quad (3)$$

where SLL_i is the competition index value of a target tree, D_i is the breast height diameter of a target tree, D_j is the breast height diameter of a neighbor tree, and $RDist$ is the relative distance to the neighbor trees in a quadratic design, equaling 1 for perpendicular and 1.41 for diagonal neighbors. The NP index was emphasizing the competition effects of the two nearest neighboring line plots using the mean values per plot and was calculated as

$$NP_{tp} = \frac{D_{tp}}{D_{np1} + D_{np2}} \quad (4)$$

where NP_{tp} is the index value for the target plot, D_{tp} is the mean breast height diameter of the target plot, and D_{np1} and D_{np2} are the mean breast height diameters of the nearest line plots on both sides of the target line plot.

Analysis of variance for growth variables at different ages was performed using a mixed model procedure with the following basic linear model:

$$Y_{ijkl} = \mu + C_i + B_j + r_{k(j)} + c_{l(j)} + SLL + NP + e_{ijkl} \quad (5)$$

where Y_{ijkl} represents the estimated value of clone i , block j in row $k(j)$, and column $l(j)$, and e_{ijkl} is random error, while C_i , $r_{k(j)}$, and $c_{l(j)}$ were entered as random variables in the model. The competition indices, SLL and NP, were entered as covariances always representing the relationships among neighbor trees and plots from the end of the previous 3-year period, i.e., in the model for D_6 (D at age 6) we used competition indices calculated for trees and plots at the age of 3 years. The model runs for the first 3-year period did not include competition indices as they were negligible at this stage with the 3×3 m spacing applied here. The competition indices were omitted from the analysis for H and zH , as the effect of competition on height increment could not be clearly anticipated. Block effects were omitted in the analysis of variance for stem form and branching as well as competition indices except for applying SLL for branchiness and branch thickness.

Variance components of random effects were derived from the mixed models runs for each trait. Genetic relatedness (Table 1) was not taken into account and clones were treated as independent genotypes. The genotypic clonal variance component, here corresponding to broad sense heritability, was calculated as

$$\sigma_G^2 = \sigma_c^2 / (\sigma_c^2 + \sigma_e^2) \quad (6)$$

where σ_c^2 is the clonal variance component and σ_e^2 is the residual variance. The genotypic coefficient of variation was calculated as follows:

$$CV_G = \sqrt{\sigma_c^2} \times 100 / \hat{\mu}, \quad (7)$$

where $\hat{\mu}$ is the predicted grand mean in the mixed model. The repeatability of clonal means was estimated as follows:

$$R_c^2 = \sigma_c^2 / (\sigma_c^2 + \sigma_e^2 / k) \quad (8)$$

where k represents the harmonic mean number of replications per clone, i.e., harmonic mean number of line plots. The standard errors of repeatability estimates were calculated according to following formula [41]:

$$seR_c^2 = \sqrt{\frac{2(n-1)(1-R_c^2)^2[1 + (k-1)R_c^2]^2}{k^2(n-N)(N-1)}} \quad (9)$$

where N is the number of clones and n the total number of entries. The Pearson correlation coefficient was calculated for a large number of traits, while the relative selection efficiency of a trait Y (RS_y) as related to the direct selection of the target trait X (S_x), in this case V_{12} :

$$RS_y / S_x = H_y r_G / (H_x), \quad (10)$$

where H_y and H_x equal square root of broad sense heritability for the indirect trait Y (σ_{GY}) and the directly selected trait X (σ_{GX}), whereas r_G is the genotypic correlation between traits X and Y [42].

Hierarchical cluster analysis was used to visualize the structuring of the tested material according to selected traits. The analysis included four variables for growth performance (D_{12} , H_{12} , zD_{6-12} , zH_{6-12}), two for phenology (BB3 and CRC2), one for stem form (STR) and one for branchiness (BRNS). Prior to analysis all eight variables were standardized at the range -1 to 1 . Euclidian distance was used as a measure of similarity that was fixed at 70 and complete linkage was applied as a clustering algorithm. The cluster analysis and all other statistical runs were performed in Minitab 18.

Results

Superior Performance of Reference Clones

The two reference clones (REF) established their dominance during the period between age 3 and 6 years reaching at age 12 a mean diameter of 260 mm and a height above 20 m (Fig. 1). Belgian (BELt) and Swedish (SLUc) clones achieved on average 70% of REF stem volume by the age of 12 years. Across the 12-year period, BELt material was steadily closing the gap to REF, while SLUc decreased their relative performance from the initial 94% of REF at age 3 (Fig. 1d). The superior performance of REF clones is reflected by a sustained better diameter growth (Fig. 1a), along with good height growth performance except during the last 3-year period (age 9–12 years, Fig. 1c). The Belgian $T \times D$ (Table 1) clones (BELtd), Swedish SLUn, and four best PG clones (PG4best) reached only 40% of REF stem volume at age 12 years. Apart from REF, the best performing new clone was “21.9” (SLUc) with 18% lower mean stem volume compared to “OP-42.” The broad sense heritabilities (σ_G^2) for the growth variables were high (cumulative D , H , and V) or moderate to high (periodic growth increments zD , zH , and zV), ranging from 0.43 for zD_{9-12} to 0.87 for H_{12} . The (σ_G^2) values increased slightly with age for cumulative growth and decreased for periodic increments. The exception from this trend was σ_G^2 for zV that stayed unchanged during the period 3–12 years (Table 3).

Strong Age–Age Correlations Enabled Early Selection of Clones

The correlations between values of traits at different ages, known as age $\times$ age correlations (r_G), were 0.81 and 0.90 for $D_3 \times D_{12}$, and $H_3 \times H_{12}$ respectively. Initial growth variables, i.e., D_3 and H_3 , were moderately to strongly correlated with

Table 3 Results of the linear mixed model analysis of growth, phenology, stem form, and branching properties of poplar clones grown in southern Sweden. Variance components for random effects were divided between the clone effects (σ_G^2 , corresponding to broad sense heritability) and error (σ_e^2), which includes both random error and within-block variance component that was relatively small in most

cases. R_c^2 is repeatability of clonal means, CV_G and CV_e are coefficients of variation of σ_G^2 and σ_e^2 ; SLL and NP are the competition indices; F and p values are provided for the effects of block and two competition indices used as covariance in some models. The variables were described in Table 2

Trait	σ_G^2	σ_e^2	$R_c^2 \pm SE$	CV_G	CV_e	SLL		NP		Block		R_{adj}^2
						F	p	F	p	F	p	
D ₃	0.75	0.25	0.92 ± 0.02	17.9	10.5	*	*	*	*	1.65	0.226	93.94
D ₆	0.79	0.21	0.93 ± 0.02	28.6	14.8	0.7	0.405	8.04	0.006	9.9	0.002	99.44
D ₉	0.83	0.17	0.95 ± 0.01	24	11	5.31	0.024	8.33	0.005	6.49	0.01	95.69
D ₁₂	0.82	0.18	0.95 ± 0.02	24.7	11.6	17.8	0	7.11	0.009	4.44	0.033	95.89
H ₃	0.79	0.21	0.93 ± 0.02	12.1	6.4	*	*	*	*	2.01	0.162	97.34
H ₆	0.79	0.21	0.93 ± 0.02	22.3	11.6	*	*	*	*	7.26	0.005	99.48
H ₉	0.83	0.17	0.95 ± 0.01	20.9	9.4	*	*	*	*	9.33	0.004	98.12
H ₁₂	0.87	0.13	0.96 ± 0.01	21.8	8.5	*	*	*	*	9.46	0.002	99.99
V ₃	0.74	0.26	0.92 ± 0.02	*	*	*	*	*	*	1.79	0.199	95.79
V ₆	0.82	0.18	0.95 ± 0.02	17.3	8.1	4.35	0.042	12.94	0.001	11.76	0.001	99.24
V ₉	0.83	0.17	0.95 ± 0.01	32.7	14.6	0.68	0.412	6.59	0.012	8.14	0.004	97.80
V ₁₂	0.84	0.16	0.95 ± 0.01	31.6	13.6	12.73	0.001	6.36	0.014	6.23	0.013	98.67
zD ₃₋₆	0.76	0.24	0.92 ± 0.02	27.5	15.7	0.55	0.459	6.85	0.01	13.49	0.001	92.50
zD ₆₋₉	0.63	0.37	0.87 ± 0.03	18.9	14.5	38.04	0	1.62	0.207	7.25	0.003	95.92
zD ₉₋₁₂	0.43	0.57	0.74 ± 0.06	20.5	23.7	88.23	0	0.02	0.881	0.54	0.658	99.35
zH ₃₋₆	0.69	0.31	0.90 ± 0.03	21.5	14.4	*	*	*	*	9.15	0.002	99.54
zH ₆₋₉	0.65	0.35	0.88 ± 0.03	22.3	16.5	*	*	*	*	8.98	0.005	91.64
zH ₉₋₁₂	0.53	0.47	0.81 ± 0.05	25.3	23.8	*	*	*	*	4.13	0.038	93.16
zV ₃₋₆	0.81	0.19	0.97 ± 0.01	34.2	16.6	4.66	0.037	12.86	0.001	13.85	0.001	98.66
zV ₆₋₉	0.82	0.18	0.97 ± 0.01	31.5	14.7	2.78	0.1	4.82	0.031	8.03	0.005	96.91
zV ₉₋₁₂	0.80	0.20	0.93 ± 0.02	30.6	15.3	31.76	0	4.03	0.048	4.21	0.04	99.08
BB3	0.90	0.10	0.97 ± 0.01	2.9	0.9	*	*	*	*	4.43	0.006	92.63
TC1	0.73	0.27	0.91 ± 0.02	3.3	2.0	*	*	*	*	1.52	0.214	79.50
CRC1	0.71	0.29	0.90 ± 0.03	2.9	1.9	*	*	*	*	3.69	0.015	78.29
CRC2	0.83	0.17	0.95 ± 0.01	3.8	1.7	*	*	*	*	0.4	0.75	87.31
LS1	0.72	0.28	0.91 ± 0.03	3.3	2.1	*	*	*	*	2.9	0.039	78.31
LS2	0.84	0.16	0.95 ± 0.01	4.0	1.7	*	*	*	*	5.42	0.002	88.02
CAV	0.84	0.16	0.95 ± 0.01	3.3	1.4	*	*	*	*	0.45	0.721	88.09
LSAV	0.83	0.17	0.95 ± 0.01	3.7	1.7	*	*	*	*	5.37	0.002	87.36
AUAV	0.86	0.14	0.96 ± 0.01	3.4	1.4	*	*	*	*	2.03	0.115	89.55
CADU-CRC2	0.82	0.18	0.95 ± 0.02	5.7	2.7	*	*	*	*	*	*	88.60
CADU-TC1	0.71	0.29	0.90 ± 0.03	5.0	3.3	*	*	*	*	*	*	77.25
CADU-CAV	0.82	0.18	0.95 ± 0.01	5.1	2.4	*	*	*	*	*	*	87.77
CADU-AUAV	0.85	0.15	0.96 ± 0.01	5.3	2.3	*	*	*	*	*	*	90.45
STR	0.58	0.42	0.84 ± 0.04	14.1	12.1	*	*	*	*	*	*	80.84
BRA	0.62	0.38	0.86 ± 0.04	13.9	10.9	*	*	*	*	*	*	75.63
BRTH	0.60	0.40	0.85 ± 0.04	20.4	16.6	30.70	0	*	*	*	*	85.94
BRNS	0.80	0.20	0.94 ± 0.02	25.3	12.6	41.44	0	*	*	*	*	92.02

subsequent periodic 3-year increments ranging from 0.57 to 0.90 (Table S2A). The merit of early selection in relation to the target trait (i.e., V₁₂, stem volume at age 12) was calculated

as selection efficiency (eq. 10). This value was high already after 3 years (0.80–0.83) and increased towards the target age, particularly for *D* and *V* that already at age 6 reached a value of

Fig. 1 The periodic diameter, height and stem volume (a, b, and c) increment of poplar clones grown in southern Sweden. The standard error bars were omitted to increase the readability of the graph. The cumulative growths were presented as relative to REF clones (d). The

clones were grouped according to Table 1 except for PG4best representing the values of the four best performing PG clones with respect to stem volume at age 12 (V_{12})

0.94 and 0.95 (Fig. 2). The selection efficiency calculated for the subset of 17 best performing clones had lower values initially (i.e., 0.59 for D_3), increasing to 0.88 for D_6 (Fig. 2). Thus, the precision of an early estimate increased substantially between age 3 and 6 years and was generally higher for D and V compared to H . However, despite a high selection efficiency at age 6 there were substantial changes in clonal rank within the subset of the 17 best clones between age 6 and 12 (Fig. 3). These changes were caused by differential growth development of different groups of clones (see SLUc and BELt in Fig. 1d) also reflected in lower correlation coefficients between cumulative and periodic growth traits (Table S3).

Advantageous Stem Form and Branching Can Be Combined with High Growth Performance

The stem straightness (STR) was > 2 for most of the PG and the two REF clones, and < 2 for the SLU and BELt clones. The score for branch angle (BRA) in the best producing clones was low (i.e., obtuse angle) except for “69.037/2” and “70.038/67” with higher scores of 2.4 and 2.3 respectively. Both branch thickness (BRTH) and branchiness (BRNS) were lowest for the SLU material (Table 4). The variance components of clonal effect (σ_G^2) were moderate to strong, being largest (0.80) for BRNS (Tables 3 and 4).

Crooks occurred frequently (26%), but only 8% and 10% of the trees had discontinuous stems (loss of apical dominance in the tree crown) and forks (Table 5). Crooks and forks occurred usually at 50–60% of tree height at age 9 (Fig. S1, supplement) and were more frequently found on Swedish and Belgian material compared to the reference clones. The

Fig. 2 The change of selection efficiency with time for diameter (D), height (H), and stem volume (V) in the whole set of 32 clones (solid lines and filled symbols), and in the subset of 17 best clones (dashed lines, open symbols). The selection efficiency (eq. 10) expresses the precision of estimates of volume at age 12 years (V_{12} , Table 3) by values of D , H , and V at age 3, 6, and 9 years

Fig. 3 The relationship between clone ranking for stem volume at age 12 and 6 years presented for the subset of 17 best growing poplar clones in the trial in southern Sweden. The dashed line represents the correlation coefficient of 1 between the ranks at different ages. The corresponding Pearson correlation coefficient between the two traits was 0.89 and the selection coefficient (RS_V/S_V) for V_6 against V_{12} was 0.88 (see Fig. 2). Clonal rank for clones above the 1/1 line decreases, while the opposite applies to the clones below the 1/1 line

crooks were particularly often recorded on clones “23.4” (87%), “70.038/67” (44%), and “70.038/20” (58%). Forks were most frequently found on Belgian T × D hybrid “70.045/1” (27%), on two reference clones (20% and 23%) and on some PG clones.

The assessed stem form and branching characteristics were in general positively correlated to each other indicating that trees with thicker and denser branching had less straight stems with branches attached at a sharper angle. The same correlation pattern was also found within the two subsets of clones. Out of all the branching characteristics, particularly BRNS was negatively (low score for BRNS = less branchy appearance) correlated to volume and height. Also, BRTH and BRA were negatively correlated with growth, but significantly only for some of the growth variables. The correlations between STR and growth were not significant. Weak to moderate negative correlations of stem form and branching to growth indicated that desirable quality characteristics were generally found in better growing clones (Table S3 A and B).

Larger Clonal Variation in Autumn Leaf Phenology than in Bud Burst

The broad sense heritabilities (σ_G^2) for phenology variables and canopy duration varied between 0.71 (CRC1) and 0.90 (BB3, Table 3). Bud burst (BB3) differed 13 days (Fig. 4g–i, values on X-axes) between the earliest (“PG5–2”) and the

latest flashing clone (“69.037/2”). Most of the clones reached BB3 within 5 days (i.e., day 99–104) except the two BELtd clones reaching BB3 6 and 8 days later than any other clones. The clonal range for autumn leaf phenology traits varied from 35 (CRC1) to 52 (LS2) days. This range was strongly affected by a single clone (“FN3–20”) and after its exclusion the range was between 24 (LS1) and 37 (LS2) days (Fig. 4a–c, values on X-axes). Canopy duration was calculated between BB3 and different autumn leaf phenology variables ranging from 163 days for “FN3–20” to 209 days for “OP-41” (Fig. 4d–e, values on X-axes calculated for number of days between BB3 and CRC2).

Canopy Duration and Leaf Senescence, but Not Bud Burst, are Strongly Correlated to Growth

Correlations among all analyzed variables were performed for (i) the whole set of 32 clones (Table S2 A and B), (ii) a subset of 17 best performing clones, and (iii) a subset containing only PG clones (Table S3 A and B). The same general pattern of positive, mostly significant, correlations between growth, leaf phenology, and canopy duration was present for the whole set and within the two subsets, where correlation coefficients were weaker and in many cases non-significant, particularly in the PG subset of clones. In contrast, growth and bud burst (BB3) were uncorrelated (Fig. 4). Coefficients for correlation of growth to autumn leaf phenology and canopy duration increased with age (Fig. 5). This trend was particularly consistent for both cumulative and periodic volume increment. The correlations between growth and autumn leaf phenology variables were stronger for the subset of 17 best clones compared to the PG subset (Fig. 5a, c). The strong correlations obtained between growth and phenology traits are presented by the slope of regression lines in Fig. 4a–e. For example, the values of diameter (D_{12}) and height (H_{12}) at age 12 increased by 3.5 mm and 2.8 dm (i.e., mm/100) respectively for each day of prolonged growth until the leaf coloring stage (CRC2, i.e., day for leaves turning yellow). The slope of regression lines of growth traits in relation to canopy duration (CADU) were almost identical (see equations presented in Fig. 4a–e).

Hierarchical Cluster Analysis Visualizes the Links Between Genetic Background, Growth, and Quality Characteristics

The resulting dendrogram from hierarchical cluster analysis was presented in Fig. 6. It divides the studied poplar material into two main branches with high performing clones in one branch (clusters 1, 2, 5, and 7) and all PG material including the SLUn and BELtd clones contained within the other branch. The four clusters of the first branch were separated mainly on the basis of cumulative and periodic growth for D

Table 4 The quality assessment scores for stem straightness, branch angle, branch thickness, and branchiness presented for five different poplar clone groups tested in southern Sweden

Quality characteristic	Clone group	Mean	St dev	CoefVar	Range	Source	Var comp % /F value	P value
Stem straightness (STR)	BEL	2.0	0.26	13.4	0.9	Clone	57.5	0.001
	FN	2.1	0.22	10.6	0.5	Row (B) ¹	4.02	0.129
	PG	2.2	0.41	18.8	1.6	Column (B) ¹	8.54	0.063
	REF	2.2	0.18	7.9	0.5	Error	29.5	0
	SLU	1.9	0.33	17.9	1.3	$R_{adj}^2\%$	80.84	
	All	2.1	0.28	13.7	1.0			
Branch angle (BRA)	BEL	2.1	0.33	15.9	1.2	Clone	61.9	0
	FN	2.0	0.08	4.0	0.2	Row (B)	2.3	0.197
	PG	2.2	0.33	15.2	1.7	Column (B)	1.7	0.376
	REF	1.8	0.23	12.7	0.5	Error	33.5	0
	SLU	1.7	0.27	15.5	0.8	$R_{adj}^2\%$	75.6	
	All	2.0	0.25	12.7	0.9			
Branch thickness (BRTH)	BEL	1.9	0.44	23.2	1.6	Clone	60.3	0
	FN	1.8	0.81	45.0	1.9	Row (B)	0.6	0.426
	PG	1.9	0.51	26.3	2.0	Column (B)	11.4	0.047
	REF	2.2	0.21	9.8	0.5	Error	27.7	0
	SLU	1.3	0.34	26.3	1.0	CI_{stlile}	30.7 ²	0
	All	1.8	0.46	26.1	1.4	$R_{adj}^2\%$	85.94	
Branch number, branchiness (BRNS)	BEL	2.3	0.45	19.7	1.7	Clone	80.1	0
	FN	2.2	0.68	30.0	1.5	Row (B)	6.72	0.03
	PG	2.4	0.45	18.6	1.7	Column (B)	0.52	0.384
	REF	2.3	0.15	6.6	0.5	Error	12.63	0
	SLU	1.2	0.35	28.1	1.1	CI_{stlile}	41.44 ²	0
	All	2.1	0.41	20.6	1.3	$R_{adj}^2\%$	92.02	

¹ The effects of plot random position in a row-column matrix within the block

² F value of covariance

and *H* (Table 6). The division of clones into clusters is based on their proximity of cluster centroids with a strong tendency to reflect the common genetic origin of the clones. However, clone “23.4” (one-clone cluster 2) was separated from its half-sibs in cluster 1 based on growth characteristics, but also by the differential influence of its phenology (CRC2, BB3) and stem form (STR). Clustering of PG material provided more specific insights into this group of clones. Cluster 10, for example, contains the clones “PG2–22” and “PG5–5” with relatively weak diameter growth, but a high values for H_{12} and zH_{6-12} . A low score for STR and BRNS in cluster 10 stands in a sharp contrast to the four highly producing clones (in terms of V_{12}) of clones in cluster 9 that had poor scores for the two quality variables.

Cluster 3 contains the full-sibs “44.7” and “44.11” (SLU) characterized by a considerable height growth and the most favorable STR and BRNS. The two BELtd hybrids were separated within cluster 4 by late bud burst, a relatively early autumn leaf coloring, and a poor height compared to diameter growth, i.e., low *H/D* value.

Discussion

In this study, we compared two commercial *P. maximowiczii* × *trichocarpa* clones with new, potentially promising, material of *P. trichocarpa* and *P. trichocarpa* × *deltoides* bred (SLU) or selected (BEL) specifically for Swedish photoperiod and climate conditions. This clone evaluation presents results after 12 years of growth, whereas a majority of comparable studies on poplars are from younger trials. Growth data from 3-year periods allowed us to estimate age-dependent correlation coefficients for growth performance, and to establish correlations between single-year phenological observations and growth at different ages. Growth performance was additionally emphasized by using 6-year periodic increments (zD_{6-12} and zH_{6-12}) in a hierarchical cluster analysis. The correlation analysis performed for slower growing progenies from British Columbia revealed that some general correlation patterns present in the material of broader geographic origin can also be observed within a single geographic origin

Table 5 Occurrence of stem deviations in 9-year-old poplar clones tested in Arlösa, southern Sweden. For definition of clone groups see Table 1

Characteristics of stem deviations	Clone group	Total count	N of trees (% of clone group count)	Mean height (dm), (% of tree height at age 9)	St. dev mean height (dm)	Min height (dm)	Max height (dm)
Discontinuous stem in tree crown	BEL	88	4 (4.5)	69 (56)	38.7	12	96
	FN	22	2 (9.1)	76 (70)	1.41	75	77
	PG	301	24 (8.0)	74 (68)	17.17	36	106
	REF	32	4 (12.5)	119 (68)	13.92	105	131
	SLU	110	7 (6.5)	106 (72)	17.8	78	124
	All	553	41 (7.9)	83 (68)	18.3	50	109
Crotches	BEL	88	29 (33.0)	73 (52)	22.75	28	124
	FN	22	4 (18.2)	59 (52)	11.8	51	76
	PG	301	30 (10.0)	57 (49)	21.54	19	101
	REF	32	7 (21.9)	96 (58)	11.75	79	111
	SLU	110	38 (34.5)	78 (53)	19.45	45	129
	All	553	108 (25.9)	71 (52)	20.13	35.64	116.75
Forks	BEL	88	8 (9.1)	74 (57)	12.98	55	94
	FN	22	0 (0)		*	*	*
	PG	301	18 (6.0)	62 (55)	21.75	25	106
	REF	32	7 (21.9)	91 (52)	19.28	54	112
	SLU	110	7 (6.4)	91 (57)	17.31	65	118
	All	553	40 (9.5)	74 (55)	18.79	43	107

(Table S3). Fast growth and a substantial phenological variation provided good prerequisites to reveal correlation patterns among growth, phenology, and branching traits.

In addition, the analysis of variations in stem form and branching represents an important, but rarely described aspect of the selection of poplar clones.

Fig. 4 The genotypic values for timing and range of leaf coloration (CRC2), canopy duration (CADU), and bud burst (BB3) of poplar clones grown in southern Sweden as related to cumulative diameter (D_{12}), height (H_{12}), and stem volume (V_{12}) at age 12 years. Dashed line represents linear regression line of growth traits as related to the clonal genotypic

values for CRC2, CADU, and BB3. The slope of increasing Y over X is provided in equations for CRC2 and CADU. Clones were grouped according to clustering from the multivariate analysis presented in Fig. 6 and Table 6

Fig. 5 The change with time of correlation coefficients between growth and phenology. Cumulative growth (“Cum”) and periodic growth increment (“Per”) were shown in separate panels in relations to average autumn leaf phenology (“COL&SH”) and canopy duration (“CADU”). The coefficients for correlations with periodic increments (“Per”) at 3, 6,

9, and 12 years represent the periods 0–3, 3–6, 6–9, and 9–12 years. The subsets of the 17 best clones (“17best”) and PG clones (“PG”) were shown separately. COL&SH is the average of correlation coefficients to TC1, CRC2, LS1, and LS2. CADU is the average to CADU-TC1, CADU-CRC2, and CADU-CAV

High Heritability Values and Strong Age–Age Correlations Increase the Precision of Early Clonal Selection

First, it needs to be stressed that the high broad sense heritability values (σ_G^2 , hereafter “heritability”) obtained in this

study for the growth traits were likely biased upward (i.e., overestimated). For instance, (i) heritability obtained from single-site trials lacks separation between genetic and genetic $\times$ environment effects present in the studies where the trial design includes replications on several locations. Thus, in this study the potential genetic $\times$ environment variance was

Table 6 Cluster centroids (CC) and mean cluster values for the eight variables included in hierarchical cluster analysis of 31 poplar clones grown in southern Sweden

Variable	Cluster1	Cluster2	Cluster3	Cluster4	Cluster5	Cluster6	Cluster7	Cluster8	Cluster9	Cluster10	Cluster11
D ₁₂ (CC)	0.90	1.29	−0.31	0.36	1.10	−0.67	2.16	−1.24	0.01	−0.58	−1.54
D ₁₂ (mm)	212	219	161	191	218	152	260	131	179	153	119
H ₁₂ (CC)	1.52	1.13	0.58	0.10	1.04	−0.58	1.33	−1.54	−0.53	0.01	−1.46
H ₁₂ (dm = m $\times$ 10)	204	193	177	163	190	143	199	116	145	161	118
zD _{6–12} (CC)	0.60	1.47	−0.49	0.05	1.35	−0.47	1.70	−1.32	0.10	−0.28	−1.94
zD _{6–12} (mm)	107	119	91	99	118	89	123	79	100	94	70
zH _{6–12} (CC)	1.18	0.32	0.16	−0.12	1.54	−0.45	1.06	−1.77	−0.20	0.36	−1.67
zH _{6–12} (dm = m $\times$ 10)	98	86	84	80	103	75	96	56	79	86	58
CRC2 (CC)	1.21	−0.02	0.01	−0.08	1.63	−0.67	1.71	−1.03	−0.42	−0.26	−1.12
CRC2 (doy)	304	292	293	292	308	286	309	283	288	290	282
BB3 (CC)	0.49	−0.71	0.16	3.16	0.12	−0.60	−0.35	−0.46	−0.49	0.17	0.78
BB3 (doy)	103	100	102	111	102	100	101	101	101	103	104
STR (CC)	−0.70	0.69	−1.43	−0.16	−0.61	−0.26	0.49	1.02	1.63	−0.79	−0.51
STR (score)	1.9	2.3	1.7	2.0	1.9	2.0	2.2	2.4	2.5	1.9	2.0
BRNS (CC)	−1.71	−1.56	−1.70	0.30	−0.13	0.33	0.03	0.97	1.13	0.07	−0.37
BRNS (score)	1.2	1.3	1.3	2.3	2.1	2.3	2.2	2.7	2.8	2.2	2.0

Fig. 6 Dendrogram of hierarchical cluster analysis performed using eight traits for 31, 12-year-old poplar clones, grown in southern Sweden. Eleven clusters were cut-off at similarity 70 (horizontal line) are indicated on dendrogram branches, as well as the six groups of clones compared for growth and stem and branching characteristics. The analysis was

confounded with genetic variance in the numerator of eq. 6. For this reason, more accurate estimates of heritability require larger material, replicated in several edaphic and climatic environments where poplars are intended to be grown [43]. Other potential sources of upward bias were (ii) relatively homogeneous and favorable growing conditions allowing the full expression of genetic potential reducing the spurious environmental effects; (iii) large heterogeneity of tested material; (iv) possible competition effects, which we tried to accommodate for by using competition indices as covariates; (v) exclusion of genetic relatedness of clones as a term in the model; and (vi) the use of line plot values as entries in the analysis, thus disregarding the variation present among individual trees within line plots. The heritabilities calculated on the basis of line plots are difficult to compare with individual tree heritabilities but are useful for the purpose of clonal selection as it was applied in the present study [44]. We did not use family terms in the model due to a complexity already imposed by the inclusion of raw-column matrices within blocks as well as the competition indices.

In this study, the heritability values ($\sigma_G^2 = 0.74\text{--}0.87$) for cumulative growth (D , H , V) were similar or higher than values reported from other single-site *Populus* trials. However, some authors reported repeatability of clonal means as a measure of heritability (R_c , eq. 8, Table 3). The R_c values calculated for growth variables presented in Table 3 were higher (0.81–0.97) than the corresponding values (0.65–0.91) reported from two 3-year-old Lithuanian poplar trials planted with more than a 100 clones of different origin [18]. Heritabilities similar or lower (0.38–0.89) to those obtained in our study were reported from

Clones

performed based on two cumulative growth variables (D_{12} , H_{12}), two periodic growth variables for age 6–12 (zD_{6-12} , zH_{6-12}), two phenology variables (BB3, CRC2), and two variables describing stem form (STR) and branchiness (BRNS)

two Swedish poplar trials, 10 and 14 years old [23, 24], as well as from several, 8–9 years old, hybrid aspen trials (0.23–0.63) [42]. For D and H , heritability increased between age 6 and 9 years, while staying constant for V after the initial increase between age 3 and 6 years (Table 3). Other authors compared heritabilities for cumulative growth variables in conifer species reporting either changing or approximately constant values with increasing tree age [45–48]. Stener and Karlsson [42] accounted the increase of heritability values with age in hybrid aspen trials exclusively to competition effects. On the other hand, heritabilities of periodic increments (zD and zH) in our study decreased with increasing age, while zV remained constant after an initial increase between age 3 and 6 years. If competition was the main source of increasing heritability for a cumulative growth trait, we would have expected this to be reflected also in increasing heritabilities of periodic volume increments. This was not the case in our analysis, and one possibility is that the competition effects for volume increments were compensated for by competition indices, SLL (sum of line lengths) and NP (neighbor plots). Brodie and DeBell [40] found competition indices particularly useful as a tool for re-ranking the clonal performance from mixed clonal plots to better fit the expected results in monoclonal plots. The linear character of zD , for example, implies that similar zD corresponds to different zV in the trees of different sizes. Consequently, a better estimate of heritability for periodic clonal growth should be achieved by analyzing zD^2 or, as in our cases, the stem volume increment (zV), for which heritability values did not decrease in our study, but remained constant for the period 3–12 years (Table 3).

A higher heritability of a trait implies a better precision of clonal estimates and indicates good possibilities for an effective clonal selection [33]. A successful early selection depends also on traits at selection age being strongly correlated with the selection traits at the target age [43, 44]. In our case, with V_{12} as a target trait, both these components increased with age (i.e., D_9 and V_{12} were better correlated than D_3 and V_{12}), but a relatively high selection efficiency could be reached already at age 6 (Fig. 2). Diameter appeared to be a better early selection criterion than height, which can also be explained by its stronger allometric influence on volume compared to height [49]. The most important implication of a high selection efficiency should be contained in a relatively high accuracy at an early clonal selection. However, the correlations of clonal ranks for volume between age 6 and 12 show that substantial changes occurred during this period despite high age–age correlations and correlation efficiency. Clone “70038/24,” for example, improved its rank from 13 to 9 between age 6 and 12, but was a top-three clone with regard to zD_{9-12} and zH_{9-12} . Also, two other BELt clones gained on SLUc clones during this period. Thus, it could be argued that an early clonal selection in this type of trials needs to target a larger proportion of the tested material and is most effective as a mean to select sets of clones for production trials and pilot plantations, rather than single out very few clones to be deployed commercially on a large scale.

The clonal variance component (σ_G^2), i.e., heritability, of spring and autumn phenology traits was high in the present study, being highest for BB3, CRC2, and LS2. CRC2 and LS2 were similarly defined in the recent study on *P. trichocarpa* in central Sweden [50] showing also the highest heritability among other traits of autumn leaf phenology. Medium to high heritability values obtained for stem form and branching characteristics suggest that these traits are strongly genetically determined and can be selected for in order to improve the value of produced poplar biomass. Similar characteristics of stem form and branching were reported in 7-year-old poplar trials in southern Sweden [24], with heritability values between 0.35 for branch thickness and 0.59 for the number of branches. The corresponding values in this study were 0.60 and 0.80 (branchiness). Somewhat lower heritabilities (0.21–0.29) for these characteristics were reported in a study of 10-year-old hybrid aspen [42], while Karlsson et al. [23] obtained values of 0.50 and 0.30 for straightness and branching type in 14-year-old poplar trials with a set of clones grown in central Europe.

Correlations and Hierarchical Cluster Analysis

Our study confirmed the positive correlations between autumn phenology and growth reported in other studies [18, 29, 33, 51–55]. High heritability values for both growth and autumn

phenology traits indicate that there is enough variability to adapt poplars to photoperiods at higher latitudes in Sweden. If selection is entirely based on growth, there will be a tendency to deploy clones that run increased risk of frost damage if planted at harsher localities or higher latitudes. The selection for an earlier autumn phenology, on the other hand, will tend to decrease biomass production. As poplar plantations are based on the qualities of selected individual genotypes, the selection can be directed to the outliers from these general trends. Thus, to select suitable clones for higher latitudes, we would need to look for genotypes with high performance under shorter growing seasons or clones that partly can compensate an earlier autumn phenology with an earlier bud burst in spring. Based on our results, one such clone could be SLU:s “23.4,” which had 15 days earlier leaf coloration and shedding compared to “OP-42” (Fig. 4). This clone still produced 69% of the stem volume of “OP-42” by the age 12 years and performed equally well as other SLU and BEL clones with autumn phenology similar or delayed compared to “OP-42.”

Contrary to autumn phenology the variation in spring phenology was lower and was not correlated with growth (Fig. 4). A tendency of weak negative correlations were found within “PG” subset indicating that PG clones with an early bud burst tended to perform better. Pliura et al. [18] reported an early bud burst to have significantly positive effect on poplar growth in a large material covering several poplar species and hybrids. Also, Yu et al. [56] found earlier-flushing hybrid aspen to achieve a better growth compared to a local and later-flushing aspen material. Other studies mostly report weak or non-existing direct correlations between bud burst and growth performance [32, 54].

In the present study, the length of clonal canopy duration (i.e., effective growth season length) can only be regarded as hypothetical as it was calculated on bud burst and autumn leaf phenology from different years. In addition, the year of leaf phenology screening (2018) was unusual due to an extremely warm summer, which might have affected leaf phenology, exaggerating the differences between vigorous and more suppressed clones. Thus, the strong relationships between autumn phenology, canopy duration, and growth (Fig. 4) need to be considered in the light of the possibility that the timing of autumn leaf phenology did not only reflect the phenological trait, but might also have been affected by the tree (clonal) vigor in 2018. More frequent inventories of phenological traits are necessary to reveal the true strength of these correlations. However, the relative timing of phenology events in *Populus* seems to be reasonably stable across different years and sites. This is particularly true for bud burst [34], while reports on relative stability of autumn phenology vary in this respect [33, 56, 57]. We assumed that the projected length of canopy duration for a clone may hold for correlations with cumulative and periodic growth, i.e., general trends, and not for modeling of biomass growth in any particular year. Positive correlations

with growth were the overall trend for canopy duration also present in the two subsets of clones (Fig. 5). Thus, our results confirm previous reports of moderate to strong correlations between growth and canopy duration (length of seasonal growth) in *Populus* [18, 32, 58–61]. Correlation coefficients between cumulative growth, canopy duration, and autumn leaf phenology increased with time in our data (Fig. 5), which might be related to the cumulative nature of this growth trait. The increase of correlation coefficients of periodic increments can have several different causes such as increased competition, an improved ability with age to express genetic potential or the cumulative effect of previous biomass growth that was not accounted for in the mixed models. The increase of correlation coefficients between autumn phenology respective canopy duration and zV was much steeper for the full set of 32 clones compared to the subset for 17 best clones, which suggests that the composition of the material plays a substantial role for modeling of trends in this type of correlations. For the subset of PG clones, i.e., within the material of a single geographic origin, these correlations confirm that delayed autumn phenology provide a competitive advantage with regard to growth. It is thus expected that there will be a selection pressure at lower latitudes or in a changed climate to favor genotypes adapted to warmer autumns allowing for prolonged period of growth. The lack of significant correlations between bud burst and autumn phenology indicates that different sets of genes regulate these traits, and that they may be bred for separately [43]. Different stages of leaf senescence were all well correlated in our data set and also correlated with canopy duration. It has been shown earlier that clones with late start in spring, initiated on high temperature sums [18], may lose a substantial part of growing season, which must be regarded disadvantageous at higher latitudes.

The correlations between growth, stem form, and branching characteristics were presented in Table S2 and S3. Initially, diameter (D_3) and the branching scores were negatively and significantly correlated suggesting that trees with more favorable branching characteristics grew better. By the age 12 years, however, these correlations weakened, while the correlations between height and branching stayed negative and significant throughout the 12-year period. It can be expected that an extensive branchiness or thick branches may have positive effect on diameter development. The quality aspects have been studied more often in other species where discordances between diameter growth and quality characteristics are often handled by putting additional emphasize on height growth [43]. This, presumably unfavorable correlation between growth and quality imposes additional difficulties on defining poplar ideotypes, with imperative to satisfy a broad spectrum of possible end uses. However, our data clearly confirmed that height growth and stem form (STR) were negatively affected by branch number (BRNS) and thickness (BRTH), suggesting that the selection for biomass performance needs to be balanced by quality characteristics.

As selection of suitable clones is dependent on growth, climate adaptation, and quality traits, we used multivariate analysis for grouping and evaluating clones. The hierarchical clustering is useful for selecting clones with similar characteristics, provides an overview of the material and represents a valuable aid for the decisions about further testing of clones or their deployment in pilot plantations. The clusters can also be useful for the composition of clonal mixtures to be deployed commercially, particularly when site-specific studies on clonal performance are not yet available. Deployment of clones in mixtures is regarded as advantageous in terms of risk avoidance and ecological services and has been applied in Sweden for both hybrid aspen and poplars [62]. Hierarchical clustering is more efficient when underlying traits are characterized by high heritability and clear correlation patterns. In our case, four out of eight variables characterized growth, a deliberate choice to emphasize growth where cumulative growth represented a feature of overall clonal performance, and the periodic increment at age 6–12 years characterizing clonal development after the anticipated time for the first selection at the age of 6 years. The use of bud burst and leaf coloring as phenological variables is governed by their high heritabilities (i.e., large variation in the studied material) and importance in the delimitating the length of canopy duration. Stem straightness and branchiness, on the other hand, have shown high heritability values in this study and are important for the characterization of clones and their suitability for use in different types of growing systems.

The results of present study implicate a superior performance of the two commercial clones “OP-41” and “OP-42” (Cluster 7). *P. maximowiczii* × *trichocarpa* hybrids have been frequently reported as high performing in other studies from central and northern Europe and in comparison with the material of varying origin [17, 18, 33, 37, 63–65]. These hybrids are undoubtedly of interest for northern Europe and should be included in the future breeding programs targeting geographical regions at high latitudes. The BELt and SLUc clones performed less, but can be of interest for further testing in southern Sweden (particularly BELt clones, cluster 5) and as an alternative at latitudes 57–59° N (cluster 1). Clone “23.4” was separated into a single-clone cluster (cluster 2) due to its distinct characteristics of high diameter increment, lower height increment in the period between age 6 and 12 years, earlier autumn phenology, earlier bud burst, and less advantageous stem form (Fig. 6, Table 6). Thus, clone “23.4” belongs to the branch of high producing clones (SLUc, BELt, and REF clones; Fig. 6) while phenologically having potential to be transferred to the north at much lower risk compared to REF clones. In general, SLUc and BELt clones had more favorable stem form and branching traits compared to REF clones at the expense of productivity. However, high-producing clones with smaller crowns, such as “21.9,” may potentially be interesting for growing systems established with denser initial planting distances and thinning schemes. The multivariate

analysis was also useful for structuring PG clones, which potentially can be of interest in breeding for higher latitudes. For example, clones belonging to cluster 9 were best in terms of volume growth, but are also characterized unfavorable values for STR and BRNS. Thus, extensive branching may have contributed to overestimate the measured stem diameter and volume while signaling decreased value related to harvest and industrial processing of biomass. Contrary, the clones “PG2–22” and “PG5–5” separated within cluster 10 seem to be good candidates for inclusion in germplasm of Swedish poplar breeding population, as they have straight stems, relatively thin branches and the best height increment among PG material.

Conclusions

- The commercial clones “OP-42” and “OP-41” have shown superior performance, but unfavorable stem form and branching compared to the Swedish and Belgian *P. trichocarpa* clones selected for this study.
- Some Swedish *P. trichocarpa* clones demonstrate potential to be deployed at higher latitudes, where growth of “OP-42” implies an increased economic risk.
- Late autumn phenology and longer canopy duration correlate positively with productivity. Thus, the selection of clones for deployment at higher latitudes needs to be based on their relative phenological characteristics.
- Stem straightness and height growth are negatively influenced by extensive branching.
- Hierarchical cluster analysis provides a valuable tool for clonal evaluation based on growth, phenology, stem form, and branching characteristics. The material is separated in clusters that reflect the origin and parentage of the material, while providing a visual overview of differences and similarities among the material. The method is useful for decision making with regard to clonal deployment and building up a poplar breeding population for northern latitudes.

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Data availability The data are available from the corresponding author upon request.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no competing interests.

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