Combined selection for growth and wood properties is an opportunity for tree improvement. It could simultaneously improve growth rate and relative density (or moisture content) of the wood, without significantly affecting cell length.

Selection concentrated on wood density or moisture content could also give satisfying results.

Even though these conclusions can not be taken as final and general recommendations, further research of balsam poplar genetics is in progress. More reports can be expected (FARMER, 1990). By comparing different studies, from different sites, we will be able to learn more about this native species, whose importance for forestry practice is increasing.

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Growth Rates and Phenology of Fast- and Slow-Growing Families over an Entire Growth Period in *Betula pendula* ROTH

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Abstract

Differences in growth rate and growth rhythm, and their contribution to stem volume were analyzed in fast- and slow-growing full-sib families of silver birch (*Betula pendula*). Observations were made on the basis of a 15-year-old progeny test. Significant differences between fast- and slow-growing family groups were noted for growth rates at almost all development periods over the entire growing season, for growth cessation and for the length of growth period. Growth rates at the middle periods of the growing season and the total length of the growth period were strongly correlated with annual growth or total stem volume. Total stem volume was mainly attributable to growth rates during a certain period in the middle of the growing season, here named "growth efficiency" (GE). It suggests that direct selection for this yield component may be the most efficient way of breeding for high yield.

Key words: Betula pendula, growth rate, growth efficiency, phenology, growth profile.

FDC: 232.11; 181.8; 165.53; 176.1 *Betula pendula.*

Introduction

Selection for high wood production may lead to a prolonged growth period (GP) either through early growth initiation (GI) or late growth cessation (GC) (DIETRICHSON, 1969; CANNELL, 1989; REHFELDT, 1992a and b; WANG and TIGERSTEDT, 1993). However, early budburst or late growth cessation involves increased risks of early or late frost damage, a great concern of tree breeders in Nordic countries. Thus, to achieve genetic gains from tree breeding requires adaptedness to be maintained while economic value is improved. For this purpose, understanding of yield components in morphology, physiology and phenology is imperative. Genotypic or phenotypic correlations between yield and phenological traits have been noted, and relative contributions to total yield by growth rate (GR) and the length of GP have been compared in many tree species, such as *Populus nigra* L. (PICHOT and TEISSIER du CROS, 1988), *Pinus banksiana* (MAGNUSSEN and YEATMAN, 1989), *Pinus taeda* (BRIDGWATER, 1990), *Larix occidentalis* (REHFELDT, 1992a), *Pinus ponderosa* (REHFELDT, 1992b) and *Populus* hybrids (CEULEMANS et al., 1992).

In silver birch (*Betula pendula*) several studies have been made on phenological characteristics. The time of budburst has been documented in Finland since 1896 (HÄKKINEN et al., 1995). Duration of chilling, photoperiod, chilling temperature and ecotype are important to budburst (MYKING and HEIDE, 1995). Environmental factors determining GC have been found to be the joint effects of heat sum and night length (KOSKI and SIEVÄNEN, 1985), GI, GC and GP are significantly different among hybrid families between southern and central Finland, and strongly correlated with total stem volume growth (WANG and TIGERSTEDT, 1993). However, the question of how much of the genetic gain achieved by breeding in this species that can be attributable to (1) an extended GP, (2) a higher GR within a certain growing season, or (3) to other reasons, still need to be scrutinized.

The objective of the present study is to investigate "growth profiles", an integration of GRs and GP, of fast- and slow-growing families over the growing season and then to examine how differences in GR at various periods of the growing season and differences in length of the GP influence yield. At the same time such research sheds additional light on the definition of heterosis in tree breeding.

Materials and Methods

Plant materials

The plant materials for the present study were from progeny test 816/1 involving full- and half-sib families and stand origins in southern Finland (lat. 60° 57' N, long. 24° 32' E and alt. 85 m). It was planted with 2-year-old seedlings in May 1982, spacing at 2 m x 2 m, by the Finnish Forest Research Institute. A randomized complete block design was used in the test with 69 entries, 16 trees (4 x 4) per plot and 6 blocks.

Seven F_2 full-sib families, including 4 fast-growing, 3 slow-growing, and 1 stand origin used as the control were selected for the study. Selections of the fast- and slow-growing families was on the basis of average-height of the family observed in 1991. The parents of these full-sib families were selected (for better growth) F_1 individuals produced by crossing plus trees. Information of cross combinations was described in our previous study (WANG et al., 1995b). The stand origin was from a seed mixture involving two natural stands. All individuals in each plot were observed using the 3 best blocks of the test regarding soil conditions and survivals. All measurements were taken in 1994.

Observations of growth rates and phenological characters

Growth rates (GR) of stem volume at ten development periods over the entire growing season, defined in *table 1*, were observed by measuring changes of girth at breast height at each period and converting to stem volume by using the model developed by LAASASENAHO (1982), whereas the increment of stem volume was the accumulated increase at the observing date since the first observation (May 10) in the year. The growth efficiency (GE) was the sum of GRs over the periods 4 to 7. These periods reflect highest growth rates in all cases (*Fig. 1*).

Table 1. – Definition of development periods.

Period	Date of the observation	Length of period (Days)	Period	Date of the observation	Length of period (Days)
0	May 10		6	Jul. 29	23
1	May 19	9	7	Aug. 14	16
2	May 26	7	8	Sep. 3	19
3	Jun. 2	7	9	Sep. 27	24
4	Jun. 16	14	10	Oct. 10	13
5	Jul. 6	20			

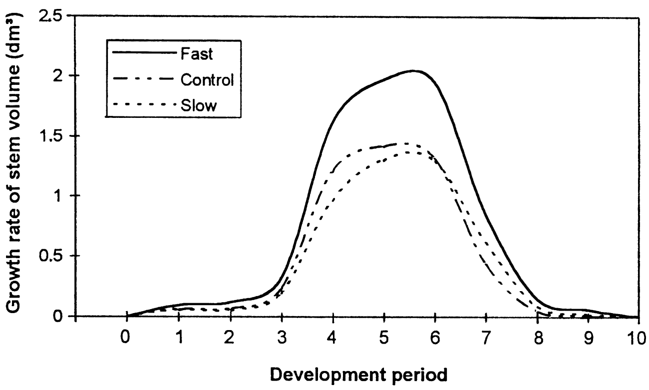

Figure 1. – Growth profiles of the fast- and slow-growing family groups and the control.

The measuring position was smoothed and marked around the stem to assure that repeated measurements were taken at exactly the same position. All measurements were taken between 9:00 and 11:30 in the morning. The influence of temperature and water content was found to be insignificant during the period of measurement.

Phenological characters, including GI (leaf unfolding), GC (leaf decoloration) and GP (the days between growth initiation and cessation) (see WANG and TIGERSTEDT, 1993) were also observed on the same material. Observations were started on May 6 at 3 days interval for GI and on September 27 at 5 days interval for GC. The number of days for the attainment of GI and GC from the first date of the observation were recorded.

Statistical analyses

Differences between fast- and slow-growing family groups, and the control were examined using analysis of variance (ANOVA). Groups and blocks were treated as fixed effects in the ANOVA. Multiple range tests of Tukey was used for the means of groups. Phenotypic correlation between traits were analyzed based on family means.

To compare the contributions of GE and GP to annual growth or total stem volume, regression analyses were made at the individual level. The procedure GLM (type III) in SAS was used to specify the predictable proportion of variance by those 2 variables. To make the parameters of regression comparable, independent variables were standardized.

Results

Stem volume

Differences in total stem volume were highly significant among fast- and slow-growing groups and the control ($P<0.001$) (*Table 3*). The fast-growing family group was 76% higher and the slow-growing family group 6% lower in stem volume than the control, while the difference between the slow group and the control was not significant. Stem volume of the best family (no. 11) was 100% higher than the stand control, whereas the poorest family (no. 20) was 14% lower in stem volume than the control. This skew distribution around the control indicates that 2 generations of selection has effectively pulled the breeding population towards higher yields.

Growth profile of stem volume growth

Growth profiles of the fast- and slow-growing family groups and the control are shown in *figure 1.*

Generally, growth initiation and cessation were observed at period 1 and period 9 (there might be minor growth at period 10, but not detectable). High GRs appeared between periods 4 and 7. Of the annual increment 90% was achieved within this period, i.e., between early June and mid August. Thus, GE was defined as the sum of GRs over these periods.

The fast group kept a significantly higher GR than the slow group over the periods between 2 and 9, and a significantly higher GR than the control at 2 late periods 8 and 9 (*Table 2* and *Fig. 1*). Differences among groups and the control were not significant at the first period. Consistently, the fast group had also a significantly higher GE than both the slow group and the control. The largest absolute differences in growth rate between the fast and slow or control occurred at periods 5 or 6 respectively, indicating their importance to the total annual growth. However, the relative differences between the fast group and the control or between the fast and slow groups had a peak at the early period 2 and increased after period 7 (*Fig. 2*). It indicates a general feature of the fast-growing families; earlier growth initiation in spring and delayed growth cessation in autumn. However, variation exists among families, for instance, family 18 had the highest growth rate over the first three periods and a relatively high growth rate after period 7, whereas family 11 had a relatively low growth rate over the first three periods, but had the outstandingly highest growth rate over the following 3 periods (4 to 6) (*Table 2*).

The differences in the increment of stem volume among groups became significant at the end of period 2 (May 26) and continued until the end of growing season (*Table 3* and *Figure 3*). However, there was a fluctuation in the ranking of families in the fast group, for instance, family 18 had the highest increment of stem volume from the beginning up to the end of period 3 (June 16), and was then overtaken by family 11. The fast group was continuously increasing its leading position with the elapse of time over the cumulative growth period.

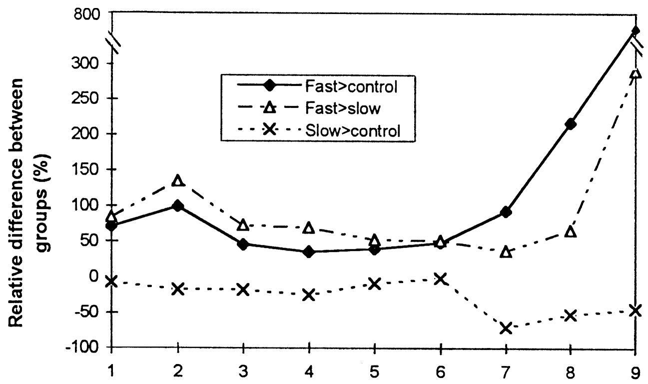

Figure 2. – Relative differences in growth rates (GRs) of stem volume among the fast- and slow-growing family groups and the control at different development periods.

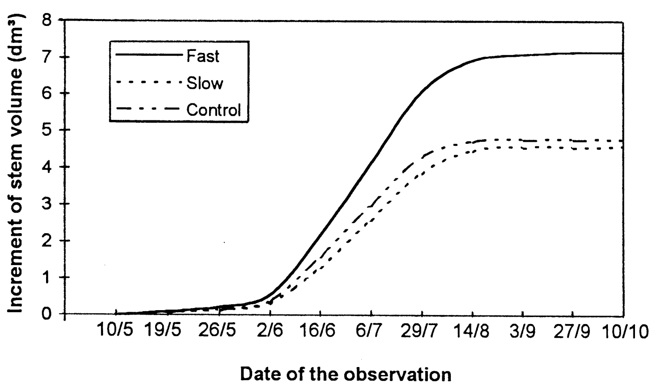

Figure 3. – Increments of stem volume of the fast- and slow-growing family groups and the control at different dates.

Table 2. – Growth rates (GRs) of stem volume (cm^3) at different development periods for selected families and groups.

Group	Family	Development period									GE
		1	2	3	4	5	6	7	8	9	
Fast	11	67	87	281	1677	2287	2152	879	17	41	6422
	18	121	192	358	1649	1927	1612	934	144	105	5239
	35	84	56	348	1618	1861	2068	89	164	32	5883
	40	115	153	320	1533	1814	1990	702	138	67	5699
	Means	*97*	*122a*[1]	*326a*	*1619a*	*1972a*	*1955a*	*851a*	*154a*	*61a*	*5834a*
Slow	49	67	71	255	1077	1290	1326	590	66	17	2865
	20	68	36	151	834	1318	1330	668	96	28	3584
	31	23	50	160	963	1281	1236	607	117	2	3986
	Mean	*53*	*52b*	*189b*	*958b*	*1296b*	*1298b*	*622b*	*93b*	*16b*	*3862b*
Control	Stand	*57*	*61ab*	*224ab*	*1196ab*	*1412ab*	*1321ab*	*442ab*	*49b*	*7b*	4274b
Significance (P)	*Group*	*0.0853*	*0.0336*	*0.0184*	*0.0006*	*0.0068*	*0.0124*	*0.0174*	*0.0027*	*0.0003*	0.0001

[1]) Means followed by the same letter are not significantly different at 0.05 level.

Table 3. – The increment of stem volume (cm³) at different observing dates for selected families and groups.

Group	Family	Date of the observation									Total stem volume
		May 19	May 26	Jun. 2	Jun. 16	Jul. 6	Jul. 29	Aug. 14	Sep. 3	Sep. 27 [1]	
Fast	11	67	154	434	2111	4398	6550	7429	7599	7639	52248
	18	121	313	671	2320	4247	5859	6793	6937	7042	41419
	35	84	140	487	2105	3966	6035	6925	7089	7121	45006
	40	115	268	587	2121	3935	5925	6626	6765	6831	46406
	Mean	*97*	*218a* [2]	*545a*	*2164a*	*4136a*	*6092a*	*6943a*	*7097a*	*7158a*	*46270a*
Slow	20	68	103	255	1088	2407	3737	4405	4501	4525	22874
	31	23	67	227	1190	2471	3707	4313	4430	4420	24410
	49	67	138	393	1470	2760	4086	4676	4742	4743	26769
	Mean	*53*	*103b*	*291b*	*1249b*	*2546b*	*3843b*	*4465b*	*4558b*	*4563b*	*24684b*
Control	Stand	*57*	*118ab*	*342ab*	*1538ab*	*2.951ab*	*4271ab*	*4714ab*	*4762ab*	*4768ab*	*26068b*
Significance (P)	*Group*	*0.0853*	*0.0237*	*0.0020*	*0.0006*	*0.0015*	*0.0028*	*0.0037*	*0.0036*	*0.0031*	*0.0002*

[1]) Annual growth of stem volume
[2]) Means followed by the same letter are not significantly different at 0.05 level.

Phenology

Differences in GI, GC and GP were significant among groups (*Table 4*). The fast group had a significantly earlier GI than the slow group, and a significantly later GC than both the slow group and the control. Consequently the fast group had a significantly longer GP than both the slow group and the control.

Table 4. – Growth initiation (GI), growth cessation (GC) and growth period (GP) for selected families and groups.

Group	Family	GI (days)	GC (days)	GP (days)
Fast	11	2.71	7.32	144.61
	18	2.38	4.41	142.03
	35	4.35	5.38	141.03
	40	4.47	6.98	142.51
	Mean	*3.48a* [1]	*6.02a*	*142.54a*
Slow	20	3.21	1.07	137.86
	31	5.56	3.33	137.78
	49	4.82	3.82	139
	Mean	*4.53b*	*2.74b*	*138.21b*
Control	Stand	*4.18ab*	*1.58b*	*137.4b*
Significance (P)	Group	0.0005	0.0001	0.0001

[1]) Means following with the same letter are not significantly different at 0.05 level.

Relationships among yield, growth rate and phenology

Annual stem volume growth was strongly correlated (R=0.9861, P=0.0001) with total stem volume at the end of the growth season (*Table 5*), indicating that at the age of 15 years development had been consistent.

The phenotypic correlations between annual growth or total stem volume and the GRs at different periods were increasing between period 1 and 6, and decreasing at later periods. The correlations were significant between periods 3 and 8 (*Table 5*). However, the strongest correlation was between annual growth or total stem volume and GE, indicating that the higher total stem volumes of the fast-growing families were achieved during the intensive growing period rather than at early or late growing season.

Both annual growth and total stem volume were positively correlated with GC and GP, but not correlated with GI. Among the phenological characters, GI was neither correlated with GC, nor with GP. Growth cessation, however, was positively correlated with GP (*Table 5*).

Linear regressions of annual growth and total stem volume on GE and GP were highly significant (*Table 6*). Of the total variances of annual growth and total volume 98.7% and 88.9% could be explained by the regression models respectively. Both GE and GP had significant contributions to the models. However, 99% of their joint contribution could be attributable to GE.

Discussion

Differences in phenological characters in the present study were smaller than we expected. In our previous study (WANG and TIGERSTEDT, 1993) the extreme differences in growth period (GP) among families was 29 days, whereas it was only 6 days in the present study. Parents of all families involved in this study were from southern Finland, while the previous study included hybrid families by crossing parents from southern and

Table 5. – Correlations among annual growth, total stem volume, growth rates (GRs) at different development periods, growth efficiency (GE), and growth initiation (GI) and cessation (GC), and growth period (GP). Correlation coefficients in bold, P-values italics.

	Development period									GE	GI	GC	GP	Annual growth	Total stem volume
	1	2	3	4	5	6	7	8	9						
Annual growth	**0.6478**	**0.5822**	**0.8381**	**0.9625**	**0.9727**	**0.9352**	**0.8452**	**0.8567**	**0.6750**	**0.9975**	**-0.5262**	**0.8537**	**0.9490**	------	**0.9861**
	0.0831	*0.1300*	*0.0094*	*0.0001*	*0.0001*	*0.0006*	*0.0082*	*0.0066*	*0.0663*	*0.0001*	*0.1804*	*0.0070*	*0.0003*	------	*0.0001*
Total stem volume	**0.5984**	**0.5473**	**0.8024**	**0.9445**	**0.9613**	**0.9634**	**0.7718**	**0.8395**	**0.6033**	**0.9872**	**-0.4324**	**0.9146**	**0.9627**	**0.9861**	------
	0.1171	*0.1604*	*0.0166*	*0.0004*	*0.0001*	*0.0001*	*0.0249*	*0.0091*	*0.1133*	*0.0001*	*0.2847*	*0.0015*	*0.0001*	*0.0001*	------
GI	**-0.5272**	**-0.4394**	**-0.3387**	**-0.4561**	**-0.6179**	**-0.3436**	**-0.6015**	**-0.3636**	**-0.6573**	**-0.5189**	------	**-0.1345**	**-0.5265**	**-0.5262**	**-0.4324**
	0.1794	*0.2761*	*0.4118*	*0.2560*	*0.1026*	*0.4047*	*0.1147*	*0.3760*	*0.0765*	*0.1875*	------	*0.7509*	*0.1801*	*0.1804*	*0.2847*
GC	**0.4413**	**0.4945**	**0.6895**	**0.8065**	**0.8121**	**0.8739**	**0.6263**	**0.7736**	**0.4546**	**0.8518**	------	------	**0.9133**	**0.8537**	**0.9147**
	0.2737	*0.2128*	*0.0585*	*0.0156*	*0.0143*	*0.0046*	*0.0967*	*0.0243*	*0.2578*	*0.0073*	------	------	*0.0015*	*0.0070*	*0.0015*
GP	**0.5952**	**0.6046**	**0.7310**	**0.8797**	**0.9510**	**0.8913**	**0.7847**	**0.8134**	**0.6601**	**0.9445**	------	------	------	**0.9490**	**0.9627**
	0.1196	*0.1123*	*0.0394*	*0.0040*	*0.0003*	*0.0030*	*0.0211*	*0.0141*	*0.0749*	*0.0004*	------	------	------	*0.0003*	*0.0001*

Table 6. – A summary of GLM regression of annual growth and total stem volume on growth efficiency (GE) and growth period (GP).

Dependent	Source	DF	SS	MS	Partial R^2	R^2	F	Significance (P)
Annual growth	Model	2	3341.83	1670.92		0.9873	11004.53	0.0001
	Error	284	43.12	0.15				
	Total	286	3384.95					
	GE	1	2118.26	2118.26	0.9870		13950.69	0.0001
	GP	1	0.8793	0.8793	0.0003		5.79	0.0167
Total stem volume	Model	2	116761.92	58380.96		0.8888	1134.69	0.0001
	Error	284	14612.03	51.45				
	Total	286	131373.95					
	GE	1	68649.77	68649.77	0.8852		1334.28	0.0001
	GP	1	467.65	467.65	0.0036		9.09	0.0028

central Finland. This must have increased the span of the growth period to some extent, but a difference of the magnitude mentioned above can not be explained only by distant crosses in the previous study. We suggest that weather conditions (heat and moisture) may also be crucial factors. Particularly the time of leaf decoloration may be strongly influenced by droughts during the summer. Also the present material has undergone two generations of selection for fast growth which must have had considerable directional effect on phenology as reported, e.g., by REHFELDT (1992a and b). Although the present study may underestimate the effects of GP on yields, it is actually more realistic considering the materials used in birch breeding programs in Finland and it indicates other important causes of growth differences among families.

We found significant differences among the fast- and slow-growing family groups for growth rate (GR) at almost all periods of development periods and for stem volume increment at almost all observing dates over the entire growing season. Generally, the higher the stem volume, the higher the GR over all periods. However, exceptions exist. The highest yielding family 11 was ranked fourth until period 4. High GR only occurred over period 5 and 6, indicating that high annual growth can be achieved in a short but intensive period within the growing season and not necessarily by an extended GP. Similar results have been noted in *Pinus banksiana* (MAGNUSSEN and YEATMAN, 1989), the superior height growth of two interprovenance hybrid families was attributed to higher growth rates rather than a longer growth period. Such "growth efficiency" (GE) may be clear indications of heterosis, while an extended growth period is just manipulation of adaptation.

Our results indicated that among the three phenological characters observed, GP was most strongly correlated with annual growth or total stem volume. Growth cessation had stronger correlation with GP and with stem volume growth than GI. These findings were concordant to our previous study mentioned above and to some other studies, such as, *Populus nigra* (PICHOT and TEISSIER, 1988) and *Pinus banksiana* (MAGNUSSEN and YEATMAN, 1989). Although there was a strong positive correlations between GP and growth in this study, the correlation between annual growth or total stem volume and GRs at various periods of the growing season were significant only for middle periods, but not for the very early and late periods, where differences in growth rhythm among families were supposed to take effect to enlarge differences among families. This indicated that extended growth period had a weak direct-effect on growth, probably due to the minor differences among families and suboptimal environmental conditions (light and temperature) at such times. However, high relative differences in growth rate between fast- and slow-growing families at the early and the late periods implied the quick response in spring and delayed growth cessation in autumn.

A positive correlation between yield and growth period, implying that strong selection for growth may increase growth period, has been noted in several tree species; *Pinus banksiana* (MAGNUSSEN and YEATMAN, 1989), *Pinus taeda* (BRIDGWATER, 1990), *Larix occidentalis* (REHFELDT, 1992a), *Pinus ponderosa* (REHFELDT, 1992b) and *B. pendula* (WANG and TIGERSTEDT, 1993). In the present study, although the same correlation exists, results of regression show that over 99% of the joint contribution of the 2 variables (GE and GP) to the model was attributable to GE alone. Even with relatively large differences in growth period among the materials in our previous study, a number of fast-growing families, including the best family in the whole test, had an intermediate growth period (WANG and TIGERSTEDT, 1993). Similar results have been reported in other studies. MAGNUSSEN and YEATMAN (1989) have found large differences in the rate of shoot elongation among families with almost equal growth duration, which allows genetic improvement in height growth without changing growth period in *Pinus banksiana*. CEULEMANS et al. (1992) have noted a weak correlation between growth period and stem volume ($R=0.521$, $P=0.07$) in some *Populus* hybrid clones, suggesting that these phenological characters can only partly explain observed differences in growth. On the other hand, the length of growth period can also be the main cause of the difference in growth in some species (REHFELDT, 1992a and b), especially among provenance materials (FARMER, 1993). We suggest that this depends on the light and temperature conditions prevailing. Here evergreen conifers may react differently from deciduous trees.

The higher growth efficiency in this study can be explained by the higher leaf area indices and higher net photosynthetic efficiencies of the upper crown leaves of the fast-growing families (WANG et al., 1995a and b). Particularly the latter factor must be seen as a directly heterotic effect.

We conclude that higher yields of the fast-growing families are mainly caused by higher GE. Thus it should be possible to improve growth by direct selection for high GE without changing the growth period. It may be advantageous to select for GE rather than GP as the extended growth period clearly introduces higher risks due to early and late frost. As the breeding material in this study is the results of 2 generations of selection for high yields; (1) a phenotypic plus-tree selection and (2) a genotypic selection between and within families, it suggests following interpretation. These 2 generations of selection for high yields have curtailed the GP-variation. Further generations of forward selection, based on progeny testing seems to have only minor effects on GP. However, its effects are now mainly attributable to changes in effective growth rate (GE). Such "2-stage" selection becomes even more evident when the tree breeder starts with provenance selection and proceeds to intraprovenance selection in the second round. Our results suggest, that in advances breeding of fast-growing birch, the emphasis should be on maximizing growth efficiency (GE), in other word, special combining ability or heterosis.

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