Growth and Phenology of Hybrid Aspen Clones (*Populus tremula* L. × *Populus tremuloides* Michx.)

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Height, basal diameter, diameter at breast height, bud burst, and leaf development were recorded in a 5-year-old hybrid aspen clonal trial. The field trial consisted of four aspen hybrid clones (*Populus tremula* × *Populus tremuloides*) and one local *P. tremula* seedling source. Phenological traits were observed in the 3rd year. Growth patterns were recorded during the 3rd and 4th years. Phenological traits were explored in relation to hybrid vigor expressed as growth traits. Differences were observed for phenological and growth traits among hybrid clones and *P. tremula*. The growth period varied from 143–158 days for the four hybrid clones, and was 112 days for *P. tremula*. The correlation between growth period and yield was highly significant. The annual growth rate of height for the hybrids was 4.2 cm per 7 days (2.4 for *P. tremula*) in the 3rd year and 6.4 cm per 7 days (2.9 for *P. tremula*) in the 4th year. After 5 years, mean estimated stem volume of the hybrids was 3.9 times that of *P. tremula*. Significant clone by year interaction was observed for height, diameter, and volume growth. The hybrid vigor seems to be mainly attributable to a longer growth period.

Keywords hybrid aspen, growth pattern, growth rate, phenology
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1 Introduction

Populus tremula is a widely distributed species in Finland, often growing in mixed stands with pine, spruce and birch. Recent developments in wood fibre research have allowed short fibres to be used in admixture with coniferous long fibres in high-quality papermaking. The Finnish forest industry has shown a fresh interest in utilising aspen for producing the short fibres. Interest in cultivating selected clones of hybrid aspen has increased. The hybrid between European aspen *P. tremula* L. and North American trembling aspen *P. tremuloides* Michx. has shown superior growth in Finland (Beuker 1989). Genetic gain from aspen breeding programs were demonstrated in the United States (Einspahr 1984) and Europe (Melchior 1985). Interspecific hybrids have grown faster than the progenies of intraspecific crosses (Heimburger 1936, Einspahr and Benson 1964, Melchior and Seitz 1966, Heimburger 1968, Zsuffa 1969, 1973). There is much genetic diversity in aspen, and it can be manipulated through selective breeding, interspecific hybridization and cloning (Li 1995).

Hybrid vigor has been observed in poplar and has been one of the driving forces in poplar breeding (Muhle Larsen 1970). The phenomenon is also well documented for aspen hybridisation in the U.S. (Li and Wu 1996, 1997, Li et al. 1998). This increase in vigor may have many components, including carbon allocation patterns, water and nutrient use efficiency, and shoot growth phenology. Traits that affect Populus performance include phenology (Michael et al. 1990, Ceulemans 1992), leaf and stomatal morphology and photosynthetic capacity. Large clonal differences in phenology, leaf area development, and photosynthetic production have been found (Ceulemans 1987, Orlovic 1998, Thomas et al. 1997). Li et al. (1998) found that interspecific aspen hybrids grew faster than intraspecific hybrids at the juvenile stage. The authors ascribe this to larger internode number and length and leaf number. Heterosis of *P. tremula* × *P. tremuloides* hybrids for stem volume was probably the result of delayed bud set, which gave a longer duration of height growth.

In this paper we compare hybrid aspen clones and local *P. tremula* for yield, growth pattern and phenology. The aim of the study was to obtain better fundamental understanding of hybrid vigor of aspen hybrids. We present results of studies on yield components and their relationship in hybrid aspen clones and local *P. tremula*. The growth patterns were studied mainly from a phenological perspective, in an attempt what has hitherto been loosely termed heterosis of species hybrids.

2 Materials and Methods

The material used in this study was a clonal trial established by the Foundation for Forest Tree Breeding and the University of Helsinki. The trial is located in Viikki, area of Helsinki University (lat. 60°14´ N, long. 25°05´ E, alt 10 m). The trial was planted in May, 1994 with one-year-old plants, and consists of four aspen hybrid clones (*Populus tremula* × *P. tremuloides*) and one *P. tremula* seedling source. Clone 1 was a hybrid between *P. tremula* (Tuusula, south Finland) × *P. tremuloides* (Lake Aleza, B.C. Canada). Clone 2 was a hybrid between *P. tremula* (Tuusula, Finland) × *P. tremuloides* (Maple, Ontario, Canada). Clones 3 and 4 were selected from a mixed plantation of hybrids, between *P. tremula* (Tuusula, or Punkaharju, Finland) and *P. tremuloides* (Lake Aleza or Maple, Canada). Thus their exact pedigrees are unknown. The local aspen seedlings were progenies of single open pollinated superior tree in Karkkila (lat. 60°32´ N, long. 24°15´ E), Finland. Thus they are predominantly half-sib. A randomized complete block design was used with 4 × 4 plants spaced at 2.5 m × 2.25 m per plot and five blocks.

Total height, basal diameter 15 cm from the ground and breast height diameter at height 1.3 m were measured. Measuring positions were marked on the stems to assure that repeated measurements were taken at exactly the same position. Stem volume was estimated as height × basal diameter^2 (Causton 1985, Ceulemans 1992, Li et al. 1998).

Height, basal diameter and breast height diameter were measured in the autumns of the 2nd to the 5th year. For observation of dynamic seasonal growth patterns, the five tallest trees were sampled for measurements of growth traits in each plot in the spring of the 3rd year. Height, basal diameter and breast height diameter were measured at intervals of approx. 2 to 3 weeks over the course of the growing season in the 3rd year (10 measurements) and the 4th year (8 measurements). The growth rates for height, basal diameter and breast diameter were expressed as increments (cm or mm) over a 7 day period. The annual growth rates were calculated by bringing total growth made over the total growth measuring period (days) to a 7 day basis.

Phenological traits were recorded in the 3rd year. Growth initiation was classified into three stages counting from the first of May: 1) the day when the bud emerged 5 mm beyond the bud scale, 2) the day leaves unfolded, 3) the day the leaves attained full size. Likewise, three stages of growth cessation were distinguished: 1) the day when half of the leaves yellowed, 2) when all of the leaves yellowed, 3) when all leaves defoliated. "Bud emerged" and "half of the leaves yellowed" were taken as indicators of growth initiation and growth cessation. The length of the growth period was estimated as the number of days from growth initiation to growth cessation. Each individual was observed from the same direction and from about the same relative position with respect to the tree crown, every other day in the spring, and every third day in the autumn.

All calculations were based on plot means. The difference between the hybrid clones and the *P. tremula* were established by an analysis of variance (ANOVA) using the PROC GLM procedure of the SAS statistical software package (1989; SAS Institute, Cary, NC) with the type III estimation of sum of squares. Means of phenological and growth traits were separated by Tukey's multiple range test at $p \leq 0.05$ probability level of significance. Pearson correlations were calculated to assess the linear relationships between the studied traits. Data from all the four years were combined and the following statistical model was used:

$$X_{ijkl} = \mu + C_i + Y_j + B_{k(j)} + C_iY_j + C_iB_{k(j)} + \varepsilon_{ijkl}$$

where X_{ijkl} is an observation on the lth tree from the ith clone in jth year and kth block, μ is the overall mean, C_i is the effect due to the ith clone, Y_j is the effect due to the jth year, $B_{k(j)}$ is the effect due to the kth block in the jth year, C_iY_j is the interaction of the ith clone and jth year, $C_iB_{k(j)}$ is the interaction of the ith clone and kth block in the jth year and ε_{ijkl} is random error. Clonal effects were considered to be fixed, while the year and block were treated as random effects.

3 Results

3.1 Growth

Highly significant differences in growth traits (height, basal and stem volume) were observed among the blocks, clones, years and their interactions (Table 1). All hybrid clones had outperformed the *P. tremula* by the end of the 5th year. The best clones were clone 2 and 1, with stem production volumes of 17.82 dm^3 and 17.57 dm^3, respectively (Fig. 1). Clonal ranking in the 5th year remained nearly the same as in the 2nd year. Clone 3 was shorter than clone 4 at the end of the 5th year, but because of its larger diameter, it had a larger stem volume (Table 2).

Growth patterns of mean height, basal and breast diameter of the hybrid clones and *P. tremula* in the 3rd and the 4th year are shown in Fig. 2. The hybrids displayed superior growth for all traits during the entire growth period (Table 3).

The growth rate of height, basal and breast height diameter was highest from the beginning of June to the end of July in the 3rd year. The same pattern for the basal and breast height diameter was found in the 4th year. However, for height growth, the highest growth rate occurred during mid August. The growth rate of hybrid aspen clones had two peaks, the first in mid-July, and the second in mid-August. For the local *P.*

Table 1. Analysis of variance for height (cm), basal diameter (cm) and stem volume (dm^3).

Source		Height[a]		Basal diameter		Stem volume	
	df	MS	Pr > F	MS	Pr > F	MS	Pr > F
Clone	4	779.3	0.0006	76.79	0.0002	1543.6	0.0351
Year	3	5390.0	0.0001	529.63	0.0001	9574.3	0.0001
Block (Year)	16	81.7	0.0001	6.23	0.0001	251.0	0.0001
Clone × Year	12	71.5	0.0141	5.81	0.0107	418.4	0.0001
Clone × Block (Year)	64	30.4	0.0001	2.37	0.0001	90.1	0.0001
Error	1332	3.7		0.54		14.9	

[a] Sums of squares are multiplied by 10^{-3}

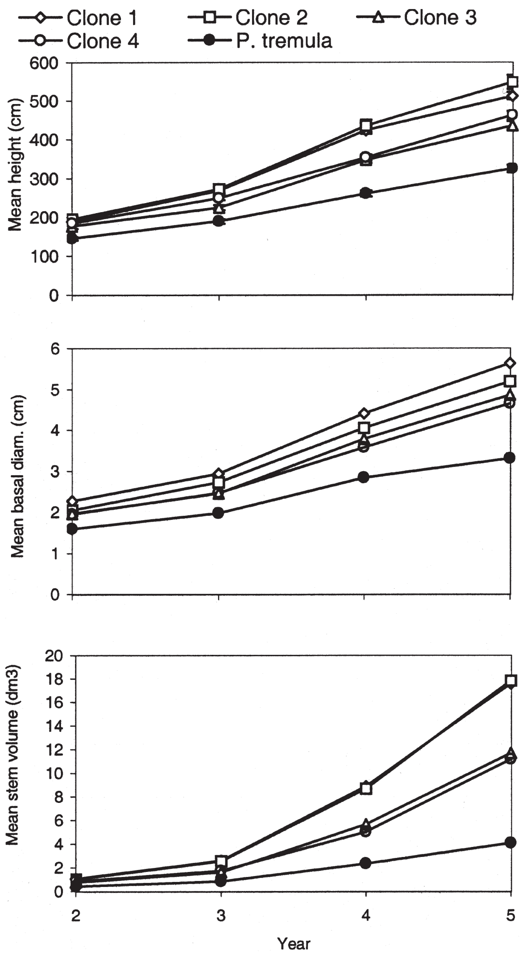

Fig. 1. Mean total tree height, basal diameter, and total stem volume at the end of each of the four growing seasons for aspen hybrid clones and *P. tremula*.

tremula, however, there was only one peak of growth in mid-June. (Fig. 2).

The growth patterns were different for different clones. Even for the same clone, the growth patterns for basal and breast diameter differed from the pattern for height growth. Clone 3 had the highest growth rate for basal diameter in mid-July in the 3rd year, but ranked third for height and breast height diameter (Fig. 2).

The growth patterns in the 3rd and the 4th year were different (Fig. 2). Compared with hybrid clones in the 3rd year, the annual growth rate of the *P. tremula* was 56% for height, 73% for basal diameter and 71% for breast height diameter. The respective values in the 4th year were 45%, 67% and 56%, respectively (Table 3a, 3b).

3.2 Phenology

Hybrids flushed earlier and grew longer than *P. tremula* (Table 4). The mean time for each stage of growth initiation of the hybrids was earlier than for *P. tremula*: 9 days for bud emerged, 7 days for leaves unfold, 7 days for full size leaves. The ranges of variation of growth cessation varied from clone 3 to the *P. tremula* : 4–41 days for half leaves yellowed, 11–45 days for all leaves yellowed, and 16–54 days for all leaves defoliated. For the hybrids, averaged half leaves yellowed, all leaves yellowed and all leaves defoliated were all 32 days later than for *P. tremula*. Hybrids had a growth period of between 158–143 days compared to 112 for *P. tremula*. The mean of the growth period of hybrids was 41 days

Table 2. Mean height, basal diameter, breast height diameter and stem volume of four hybrid aspen clones and one local *P. tremula* seedling source at the end of 2nd and 5th year of growth.

Clone	Year 2				Year 5			
	Height (cm)	Basal diameter (cm)	Breast height diameter (cm)	Stem volume (dm^3)	Height (cm)	Basal diameter (cm)	Breast height diameter (cm)	Stem volume (dm^3)
Clone 1	187.8a	2.3a	1.2ab	1.07a	512.3a	5.6a	4.3a	17.57a
Clone 2	194.2a	2.1ab	1.4a	1.03ab	548.6a	5.2ab	4.3a	17.82a
Clone 3	176.5a	2.0b	1.0bc	0.78b	435.4b	4.9bc	3.8b	11.69b
Clone 4	184.5a	1.9b	1.1b	0.83ab	462.1b	4.7c	3.6b	11.19b
P. tremula	144.7b	1.6c	0.9c	0.41c	324.9c	3.3 d	2.3c	4.09c

Note: Means in vertical sequence not followed by the same letter are significantly different at P < 0.05 according to Tukey' s test.

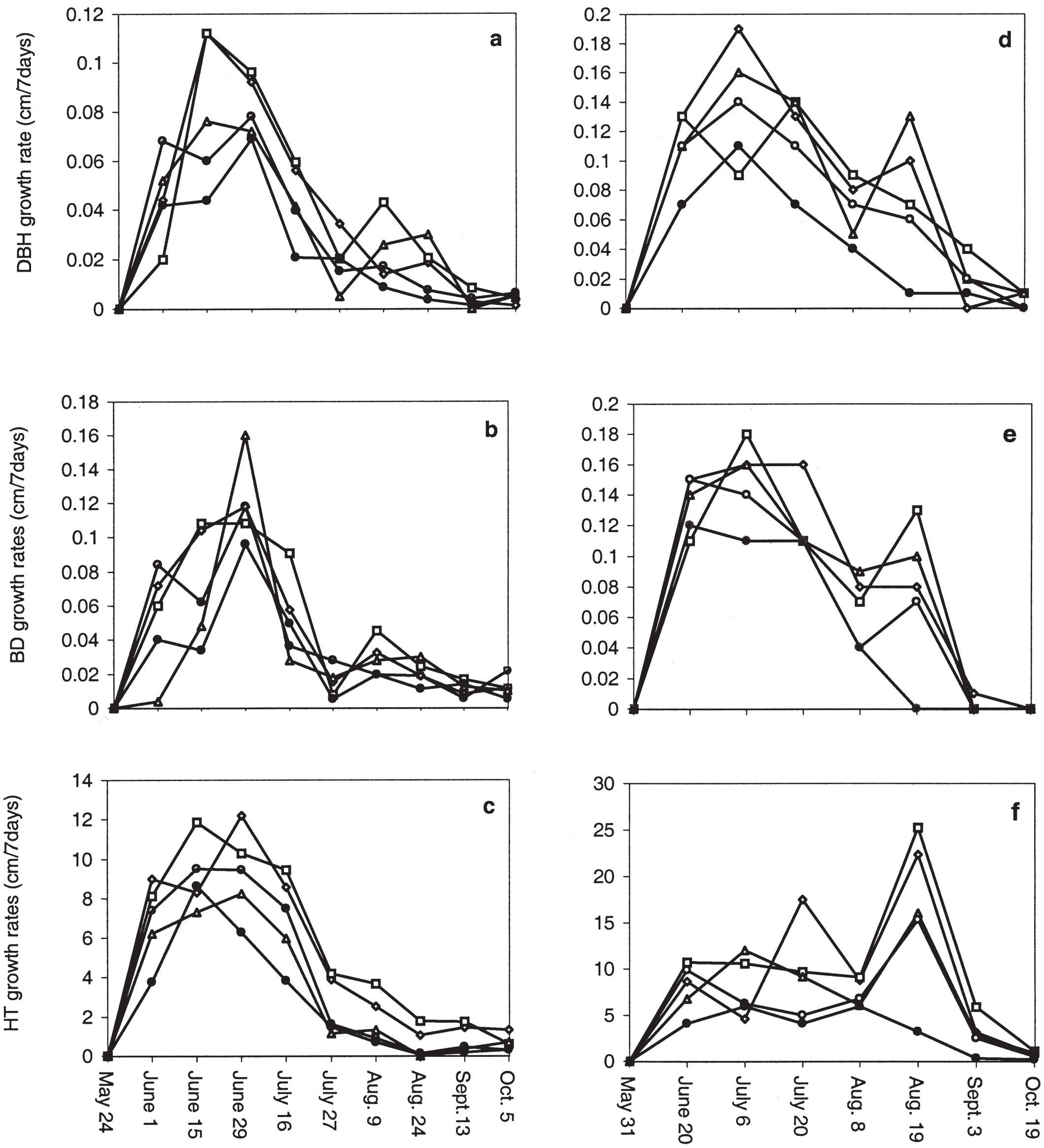

Fig. 2. Growth pattern of diameter at breast height (DBH), basal diameter (BD) and height (HT) in the 3rd (Figs. a,b,c) and 4th year (Figs. d,e,f) for the hybrid clones and *P. tremula*. For key to symbols, see Fig. 1.

longer than for *P. tremula*, the four hybrids all fell within a 15 day range.

3.3 Correlations

Significant correlations were observed among phenological and growth characters. The three stages of growth initiation were negatively correlated with stages of growth cessation. Growth traits were positively correlated with growth cessation and growth period, but negatively correlated with growth initiation (Table 5). This means that late starters generally stopped grow-

Table 3. Mean annual growth rates, increment of height, basal diameter and breast height diameter at different observational dates among hybrid clones and *P. tremula* in 3rd year (a) and 4th year (b).

a)

		May 24	June 1	June 15	June 29	July 16	July 27	Aug. 9	Aug. 24	Sept.13	Oct. 5	Annual growth rate (/7 days)
Height (cm)	Clone 1	227.5ab	236.4a	253.0a	277.4a	298.2a	304.3a	309.0a	311.3a	315.4a	319.6a	5.10a
	Clone 2	242.9a	251.0a	274.7a	295.3a	318.2a	324.8a	331.6a	335.4a	340.4a	342.4a	4.65a
	Clone 3	208.9ab	215.1ab	229.6ab	246.1ab	260.6ab	262.4ab	264.9ab	264.2ab	265.2ab	267.4ab	3.23bc
	Clone 4	223.7ab	231.0ab	250.0ab	268.9ab	287.1ab	289.7ab	291.4ab	291.6ab	292.9ab	293.8ab	3.89bc
	P. tremula	172.5b	176.3b	193.6b	206.1b	215.4b	217.8b	219.0b	219.1b	219.6b	220.6b	2.47c
CV%		14.5	13.8	12.6	12.8	13.8	14.2	14.8	15.1	15.4	15.7	29.2
Breast height diameter (mm)	Clone 1	13.0ab	13.5a	15.7ab	17.6ab	18.9ab	19.5ab	19.7ab	20.1a	20.2ab	20.2ab	0.39a
	Clone 2	17.1a	17.3a	19.5a	21.4a	22.9a	23.2a	24.0a	24.4a	24.7a	25.1a	0.35a
	Clone 3	11.6ab	12.1ab	13.6bc	15.1bc	16.1abc	16.2bc	16.6bc	17.3ab	17.3bc	17.4bc	0.29a
	Clone 4	12.3ab	13.0ab	14.2bc	15.7abc	16.7bc	16.9abc	17.2abc	17.4ab	17.5abc	17.7bc	0.32a
	P. tremula	7.8b	8.2b	9.0c	10.4c	10.9c	11.2c	11.4c	11.5b	11.5c	11.7c	0.24a
CV%		23.2	21.3	19.1	20.0	20.2	20.6	20.9	20.8	20.6	19.99	24.3
Basal diameter (mm)	Clone 1	25.1a	25.8a	27.9a	30.2a	31.6a	31.9a	32.5a	32.9a	33.1a	33.5a	0.46a
	Clone 2	25.7a	26.3a	28.5a	30.6a	32.8a	33.0a	33.8a	34.3a	34.8a	35.2a	0.44ab
	Clone 3	23.7a	23.8a	24.7a	27.9a	28.6a	28.9a	29.4a	30.0a	30.4a	30.7a	0.35bc
	Clone 4	21.9ab	22.8a	24.0a	26.4a	27.2ab	27.7a	28.0ab	28.4ab	28.6ab	29.3a	0.40abc
	P. tremula	16.8b	17.2b	17.8b	19.8b	21.0b	21.0b	21.4b	21.6b	22.0b	22.2b	0.31c
CV%		13.3	11.6	10.9	11.2	12.2	12.1	11.9	12.1	11.9	12.06	13.4

b)

		May 31	June 20	July 6	July 20	Aug. 8	Aug. 19	Sept. 3	Oct. 19	Annual growth rate (/7 days)
Height (cm)	Clone 1	327.4a	353.5ab	363.4a	398.4a	422.2a	457.3a	464.0ab	468.7ab	6.97ab
	Clone 2	353.4a	385.5a	408.3a	427.6a	452.4a	492.1a	504.7a	512.4a	7.83a
	Clone 3	278.6ab	294.8abc	320.6ab	339.0ab	355.6ab	380.7ab	386.8bc	393.1bc	5.64ab
	Clone 4	295.1ab	324.8bc	338.4ab	348.4ab	366.8ab	390.8ab	396.2abc	399.3abc	5.14bc
	P. tremula	228.8b	241.9c	254.0b	262.2b	278.6b	283.6b	284.3c	285.6c	2.92c
CV%		15.0	14.7	13.9	15.2	14.4	14.1	14.4	14.4	20.6
Breast height diameter (mm)	Clone 1	21.7a	25.6ab	29.7a	32.2a	34.4a	35.9a	35.9a	36.3ab	0.72a
	Clone 2	26.5ab	30.5a	32.5a	35.3a	37.8a	38.8a	39.6a	40.0a	0.67a
	Clone 3	19.4abc	22.7abc	26.7a	28.8a	3.00a	32.1a	32.6a	33.1ab	0.68a
	Clone 4	18.2bc	21.4bc	24.4ab	26.7ab	28.ab	29.5ab	29.9a	29.8b	0.57a
	P. tremula	12.2c	14.5c	16.8b	18.3b	19.4b	19.6b	19.7b	19.8c	0.37b
CV%		18.2	18.5	19.4	20.1	16.8	16.3	16.1	16.0	15.9
Basal diameter (mm)	Clone 1	34.7ab	39.1a	42.5a	45.6a	47.8a	49.0a	49.2a	49.2a	0.72a
	Clone 2	36.1a	39.5a	43.4a	45.5a	47.5a	49.5a	49.2a	49.5a	0.68a
	Clone 3	30.9ab	35.0a	38.5a	40.7a	43.0a	44.5a	44.5a	44.8a	0.69a
	Clone 4	28.4bc	33.0ab	36.0ab	38.2ab	39.4ab	40.5ab	40.6ab	40.6ab	0.60ab
	P. tremula	22.0c	25.5b	27.9b	30.0b	31.0b	31.0b	31.0b	31.2b	0.45b
CV%		11.7	12.1	11.9	11.9	11.3	11.7	11.7	14.3	17.0

Note: Means in vertical sequence not followed by the same letter are significantly different at $P < 0.05$ according to Tukey's test.

Table 4. Mean values and coefficient of variation of the traits among the hybrid clones and *P. tremula* seedling source.

Clone	Growth initiation (days)			Growth cessation (days)			Growth period (days)
	Bud emerged	Leaf unfolded	Full size leaves	Half leaves yellowed	All leaves yellowed	All leaves defoliated	
Clone 1	5 d	7 d	13 c	29 c	43 b	45 b	148 b
Clone 2	6 c	10 c	13 c	37 ab	42 b	46 b	154 a
Clone 3	6 c	10 c	13 c	41 a	45 a	54 b	158 a
Clone 4	13 b	16 b	18 b	35 b	42 b	45 a	143 b
P. tremula	16 a	18 a	21 a	4 d	11 c	16 c	110 c
CV (%)	6.9	6.4	12.7	8.8	3.8	4.47	1.8

Means followed by the same letters are not significantly different at P < 0.05 (Tukey's HSD test).

Table 5. Correlation coefficients (r) among the phenological and growth traits in the 3rd year.

	Growth traits			Growth initiation			Growth cessation		
	Height (cm)	Basal diameter (cm)	Breast height diameter (cm)	Bud emerged (days)	Leaf unfolded (days)	Full size leaves (days)	Half leaves yellowed (days)	All leaves yellowed (days)	All leaves defoliated (days)
Basal diameter	0.91***								
Breast diameter	0.95***	0.98***							
Bud emerged	–0.66***	–0.76***	–0.72***						
Leaf unfolded	–0.68***	–0.77***	–0.73***	0.99***					
Full size leaves	–0.67***	–0.76***	–0.73***	0.96***	0.95***				
Half leaves yellowed	0.58**	0.60**	0.62***	–0.71***	–0.65***	–0.74***			
All leaves yellowed	0.65***	0.69***	0.69***	–0.78***	–0.73***	–0.80***	0.95***		
All leaves defoliated	0.57**	0.66***	0.65***	–0.79***	–0.79***	–0.80***	0.95***	0.98***	
Growth period (day)	0.60***	0.91***	0.67***	–0.83***	–0.79***	–0.85***	0.97***	0.95***	0.95***

ing early, and thus had a short growth period. This must be ascribed to the different parental origins of the F1 hybrids.

4 Discussion

In our study, the superiority of the hybrid clones was best illustrated by stem volume. Hybrid clones had a significantly greater wood production than *P. tremula*. In spite of obvious superiority in hybrid yield, hybrids varied considerable for stem volume and annual growth rate. The hybrid clones showed significantly higher growth rates and yields than *P. tremula* at most observation dates over the entire growth season in the 3rd and 4th years (Table 3). Generally, the higher the yield, the higher the growth rates over all periods. However, growth rate of height showed a strong cross over during the summer in 3rd and 4th year (Fig. 2), which indicates clonal genotype × environment interaction. In the 3rd year (1997), the growth rate of height for *P. tremula* had one peak in the mid-June. It then decreased constantly through the rest of the growth period. We conclude that the fast growth of hybrids can be partly explained by the second growth peak in mid-August. However, the hybrid clones normally had another growth peak in mid-August, especially the height growth. In the 4th year (1998), *P. tremula* shows a slight tendency to form a second peak, but the hybrids behave far more erratically, responding strongly to a period of warm weather in late summer. This indicates that the hybrid genomes are adapted to two different parental environments. The late flushing and early cessation of the local aspen is considered to be an adaptation to the short summers in the far north.

The significant clone-by-block interaction for growth performance illustrated how sensitive aspen clones are to microsite differences (Ceulemans et.al 1992). By the end of the 5th year, block 5 in the trial produced only 48% of what block 1 produced. This must have been due to a considerable variation in soil conditions across the trial. Li and Wu (1997) found significant genotype × environment interaction for growth traits of inter and intra-specific aspen crosses in two contrasting environments.

The ranking of clones for stem volume was not consistent from the 2nd to the 5th year. Significant clone by year interaction in growth performance probably indicates differences in hybrid reaction to the climate (Table 2). Zsuffa et al. (1993) found that the ranking of poplar clones (*P.* × *euramericana*) by height changed considerably during the first 6 years of growth. Our study showed similar results. Stem volume of clones 3 and 4 were the same in the 2nd year, 0.8 dm^3. Because basal diameter of clone 3 increased faster than clone 4, the stem volume of clone 3 was larger than that of clone 4 in the 5th year. In the 2nd year, the stem volume of clones 1 and 2 were 1.1 dm^3 and 1.0 dm^3, respectively, but after the 5th year, the stem volume were 17.6 and 17.8 dm^3, respectively. This suggests that, for proper clonal selection several cumulative growth periods must be observed, perhaps over as long as 10 years.

The range in growth initiation was usually smaller than it was for growth cessation. The bud emerged of the hybrids started 8.85 days earlier than for *P. tremula* in the spring, whereas half leaves yellowed of the hybrids occurred 31.63 days later in the autumn. Compared to growth initiation, the environmental control of growth cessation is more site-specific. This may be due to the interaction of edaphic and weather conditions in causing rust damage. The leaf decoloration may have been indirectly affected by cold and wet weather in the 4th year. *P. tremula* and clone 1 had suffered from a strong infection of leaf rust, which may have affected the timing of defoliation and growth cessation.

There was a strong correlation between growth period and yield growth, which indicates that the fast growth for the hybrid can be largely explained by the expanding growth period. However, when *P. tremula* was removed from the data, there was no correlation between growth period and yield growth in the hybrid material ($r = -0.002$). Yield is a complex character, and may well be determined by other factors than the growth period. Li et al (1998) noted that hybrid vigor in aspen hybrids (*P. tremula* × *P. tremuloides*) was associated with delayed bud set resulting in longer duration of growth in first year. However, by the second year, no relationship was found between bud set and stem growth in either the intra- or inter-specific crosses.

Strong selection for growth may increase the growth period (Wang and Tigerstedt 1996). Late active growth may render the hybrids liable to frost damage in fall and winter (Rehfeldt 1979, and Li and Adams 1993, Li et al. 1998). Li (1998) proposes the use of local aspen as female parents in intraspecific crosses, in order to improve frost hardiness of the hybrids.

The fast overall growth of the aspen hybrids is largely explained by their longer vegetative period. This response is not true heterosis as has been commonly assumed in hybrid aspen. It must be borne in mind that an extension of the vegetative period of about 40 days in the hybrids may drastically increase the risk of frost damage at both ends of the growth period.

The considerably extended growth period may also upset a "natural" balance between the aspen and its pests and diseases. Thus, the increased yield is likely to involve an increased risk. This situation should be carefully assessed before large-scale cultivation of cloned hybrids can take place.

Our analyses were based on a small number of clones measured over only five years. The results of the study need to be followed up by larger and longer experiments. The superiority of hybrids over their non-hybrid counterparts, and the underlying cause for such superiority are unclear (Stettler et al. 1996). Valid estimates require a sufficient number of parents and their progenies to be tested in sufficient numbers of trials, replicated in space and time (Stettler et al. 1996). It remains to be found out, if on top of the extended vegetation period, there is in addition a sign of true heterosis that could be detected by molecular markers for heterozygosity (Aravanopoulos and Zsuffa 1998).

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References

Aravanopoulos, F.A. & Zsuffa, L. 1998. Heterozygosity and biomass production in Salix eriocephala. Heredity 81: 396–403

Beuker, E. 1989. Breeding of aspen and poplar in Finland. Proceedings of the Meeting of the Nordic Group for Tree Breeding in Finland. p. 23–27.

Causton, D.R. 1985. Biometrical, structural and physiological relationships among tree parts. In: Cannell, M.G.R. & Jackson, J.E. (eds.). Attributes of trees as crop plants. Titus Wilson & Son Ltd., Cumbria, Great Britain. p. 137–159.

Ceulemans, R., Impens, I. & Steenackers, V. 1987. Variation in photosynthetic, anatomical, and enzymatic leaf traits and correlation with growth in recently selected Populus hybrids. Canadian Journal of Forest Research 17: 273–283.

— , Scarascia-Mugnozza, G., Wiard, B.M., Braatne, J.H., Hinckley, T.M. & Stettler, R.F. 1992. Production physiology and morphology of populus species and their hybrids grown under short rotation. I. Clonal comparisons of 4-year growth and phenology. Canadian Journal of Forest Research 22: 1937–1948.

Einspahr, D.W. 1984. Production and untilization of triploid hybrid aspen. Iowa State Journal of Research 58: 401–409.

— & Benson, M.K. 1964. Production and evaluation of aspen hybrids. Journal of Forestry 62: 806–809.

Heimburger, C. 1936. Report on poplar hybridization. Forestry Chronicle 12: 285–290.

— 1968. Poplar breeding in Canada. In: Growth and utilization of poplars in Canada. Canadian Department of Forestry and Rural Development, Toronto, Canada, No. 1205. p. 88–100.

Li, B. 1995. Aspen improvement strategies for western Canada-Alberta and Saskatchewan. Forestry Chronicle 71: 720–724.

— & Wu, R. 1996. Genetic cause of heterosis in juvenile aspen: a quantitative comparison across intra- and inter-specific hybrids. Theoretical and Applied Genetics 93: 380–391.

— & Wu, R. 1997. Heterosis and genotype × environment interactions of juvenile aspens in two contrasting sites. Canadian Journal of Forest Research 27: 1525–1537.

— , Howe, G.T. & Wu, R. 1998. Developmental factors responsible for heterosis in aspen hybrids (Populus tremuloides × P. tremula). Tree Physiology 18: 37–43.

Li, P. & Adams, W.T. 1993. Genetic control of bud phenology in pole-size trees and seedlings of coastal Douglas-fir. Canadian Journal of Forest Research 23: 1043–1051.

Melchior, G.H. 1985. Breeding of aspen and hybrid aspen and important for practical use. Allgemeine Forst- und Jagdzeitung 1956(6/7): 112–122.

— & Seitz, F.W. 1966. Einige Ergebnisse bei Testanbauten mit Aspenhybriden. Silvae Genetica 15: 127–133.

Michael, D.A., Dickmann, D.I., Isebrands, J.G. & Nelson, N.D. 1990. Photosynthesis patterns during the establishment year within two Populus clones with contrasting morphology and phenology. Tree Physiology 6: 11–27.

Muhle Larsen, C. 1970. Recent advances in poplar breeding. International Review of Forest Research 3: 1–67.

Orlovic, S., Guzina, V., Krstic, B. & Merkulov, L. 1998. Genetic variability in anatomical, physiological and growth characteristics of hybrids poplar (Populus × euramericana Dode (Guinier)) and eastern cottonwood (Populus deltoides Bartr.) clones. Silvae Genetica 47: 183–190.

Rehfeldt, G.E. 1979. Ecological adaptations in Douglas-fir (Pseudotsuga menziesii var. glauca) populations in north Idaho and northwest Washington. Heredity 43: 383–397.

SAS Institute Inc. 1989. SAS/STAT® user's guide. Version 6, 4th edition, volumes 1–2. Cary, NC, USA.

Stettler, R.F., Zsuffa, L. & Wu, R. 1996. The role of hybridization in the genetic manipulation of Populus. In: Stettler, R.F., Bradshaw, H.D. Jr.,

Heilman, P.E. & Hinckley, T.M. (eds.). Biology of Populus and its implications for management and conservation. Part I, chapter 4. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. p. 87–112.
Thomas, B.R., Macdonald, S.E. & Dancik, B.P. 1997. Variance components, heritabilities and gain estimates for growth chamber and field performance of Populus tremuloides: gas exchange parameters. Silvae Genetica 46: 309–326.
Wang, T.L. & Tigerstedt, P.M.A. 1996. Growth rates and phenology of fast- and slow-growing families over an entire growth period in Betula pendula Roth. Silvae Genetica 45: 124–129.
Zsuffa, L. 1969. Poplar breeding in Canada. Forestry Chronicle 45: 402–408.
— 1973. A summary review of review of interspecific breeding in the genus Populus. In: Proc. 14th Mtg. Canadian Tree Improvement Association, Fredericton, Canada. p. 107–123.
— , Sennerby-Forsse, L., Weisgerber, H. & Hall, R.B. 1993. Strategies for clonal forestry with poplars, aspens and willows. In: Ahuja, M.R. & Libby, W.J. (eds.). Clonal forestry II. Conservation and application. Springer-Verlag, Berlin. p. 91–86.

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