# GENETICS AND PERFORMANCE OF BELGIAN POPLAR CLONES TESTED IN SWEDEN

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## ABSTRACT

In 1989 an exchange of genetic poplar material started within the International Energy Agency, I.E.A. Participating countries were Belgium, Canada, Finland, Sweden, United Kingdom and USA. The Department of Forest Genetics, SLU, Sweden received 104 poplar clones from Belgium: 65 clones *P. trichocarpa*, one *P. maximowiczii* and 38 hybrids. The material grew well during the first growth periods, 1989–91, with height means at age 3 of 5.5 m for the highest clones. In spite of poor budset, with repeated flushes, the frost damage these years was not severe. In 1991 18 clones were selected, new clonal trials established and assessments were made for the years 1993–94. Altogether around 25 traits were studied. Variance components and broad and narrow sense heritabilities were calculated. In the trial with the selected clones the frost damage was severe. The meteorological statistics indicate that the circumstances of importance for the frost damage these years were sudden frost attacks that occurred rather early in the autumns of 1992 and 1993. The conclusion is that these genotypes originating from latitudes more than 10 degrees south of the test areas have too poor or too late budset and inwintering. We need a more hardy material, inwintering according to daylength and early enough for the trees to be well prepared for sudden frost attacks during autumn.

Key words: *Populus trichocarpa*, poplar hybrids, clonal tests, genetic variation, growth rhythm, frost hardiness

## INTRODUCTION

In Sweden poplars have mostly been used as ornamental trees, and in the most southern part as wind shelters, especially around fruit orchards (NITZELIUS 1958, GUSTAVSSON & INGELÖG 1994). A few clones and a few experimental plantations have shown rather promising growth and stem quality.

There are several significant reasons for investigating the possibilities for poplar cultivation in Sweden:

- The poplars' great production and breeding potential and the breeding progress achieved in Western North America and in South and Central Europe (CEULEMANS et al. 1992, HEILMAN & STETTLER 1985, STEENACKERS 1992, WEBER et al. 1985, WU et al. 1992).
- The increasing possibilities for using poplars, both as a raw material for energy, pulp and boxboards and for high quality purposes such as panels, veneer, or modern composite materials (DEXIN 1991, DOUGLAS 1988, GRANFELT 1989, WANG et al. 1992).
- The difficulties in finding economically attractive uses for the surplus of agriculture land (ANON. 1992).
- Bred, adapted, poplars may be suitable alternatives to *Picea abies* on former agricultural land, now infected with root rot (*Heterobasidion annosum*).

- *P. tremula* × *P. tremuloides,* hybrid aspen, is highly susceptible to hypoxylon canker (*Hypoxylon mammatum*). Moreover the canker easily spreads to *P. tremula* and occasionally certain other poplar hybrids (TERRASSON et al. 1988). As resistance breeding is difficult or uncertain (VON MOHRDIEK 1983), breeding of poplars of section *Tacamahaca* (balsam poplars) and *Aigeiros* (black poplars) is considered preferable (OSTRY et al. 1989, ILSTEDT & GULLBERG 1993).

In Geraardsbergen, Belgium, poplar breeding has been going on since the late 1940's. Priority has always been given to disease resistance. Artificial infection with known bacterial strains of poplar canker, *Xanthomonas populi,* has enabled juvenile selection of resistant new poplar clones. Besides resistance the new varieties have an essentially improved stem and wood quality and a remarkable production capacity. Several of these clones have an annual volume increment per hectare double and more that of the old variety Robusta (STEENACKERS 1990).

At the end of the 1980's it was questioned whether it might be possible to use selected poplar clones from Geraardsbergen, some of them bred for high altitudes in the Ardennes, for cultivation in Sweden. This testing could be done within the framework of the I.E.A. cooperation. Participating countries, besides Belgium, were Canada, Finland, Sweden, United Kingdom and

USA (STEENACKERS et al. 1990).

Under Nordic conditions growth rhythm is of decisive importance for survival and good growth (e.g. ERIKSSON 1982). Thus early flushing and late inwintering may be most harmful. Studies of growth rhythms of trees are of prime importance for identifying genotypes well suited to the Nordic growth conditions.

The purpose of the present study has been to investigate the possibility for immediate use of the selected Belgian clones under southern Swedish conditions and their potential in a long-term breeding program.

## MATERIAL AND METHODS

### Clones

The cuttings from Belgium consisted of 65 clones of Populus trichocarpa, one clone of P. maximowiczii and 38 hybrids between P. trichocarpa as the one parent and P. maximowiczii, P. deltoides or P. nigra as the other. The parents originate from areas more than 10 degrees of latitude further south than the test areas (Table 1).

The mating design is given in Table 2. The clonal mixture sent to the participating countries was described in STEENACKERS & SMETS (1990 a). Only two families, VI and VII, consisting of 16 clones, are purely coastal. All the other families are crosses between coastal and continental provenances, intended to increase frost hardiness. 'Family VIII' consists of the one clone of P. maximowiczii.

### Trials and selection

In June 1989 a clonal trial of the Belgian clones was established at the Swedish University of Agricultural Sciences, Ultuna, Uppsala, at latitude 59°50'. The spacing between cuttings was 0.5 × 1.8 m, which should allow normal competition during the first three years from the results of AUCLAIR (1992) and XU (1995). The trial consisted of four complete randomized blocks with two-tree plots. In the first year, 1989, only one plant per plot was recorded. Because of an accident we had to dismiss the fourth block from the third year's calculations.

In 1991 a new trial was established with 18 clones, 14 P. trichocarpa and 4 hybrids, selected from the

Table 1 The origin of the parents in the Belgian material and the reference clones

| A. Belgian material | | | |
| --- | --- | --- | --- |
| clone | Sex | Species | Origin |
| V.21 | ♂ | P. trichocarpa | Montana, U.S.A. |
| V.23 | ♂ | P. trichocarpa | Idaho, U.S.A. |
| V.24 | ♂ | P. trichocarpa | Oregon, U.S.A. |
| V.26 | ♀ | P. trichocarpa | Washington, U.S.A. |
| V.235 | ♀ | P. trichocarpa | Washington, U.S.A. |
| S.190-3 | ♀ | P. trichocarpa var. hastata | Shoshone county, Idaho, U.S.A. |
| S.192-5 | ♀ | P. trichocarpa var. hastata | Shoshone county, Idaho, U.S.A. |
| V.5 | ♀ | P. deltoides | Iowa, U.S.A. |
| S.333-44 | ♀ | P. deltoides | Michigan, U.S.A. |
| Essene 2 | ♀ | P. nigra | Belgium |
| Max. 495 | ♂ | P. maximowiczii | Japan |
| S.122-3 | ♂ | P. maximowiczii | Hokkaido, Japan |

| B. P. trichocarpa reference clones at Vittinge grown for one generation in Sweden | | | | |
| --- | --- | --- | --- | --- |
| Clonal number | Sex | Earlier number | Transit country | Origin |
| 230 | ♀ | 69094/6 | England | Abbots Ford B.C. |
| 235 | ♂ | V. 235 × V. 23 | Belgium | Washington × Idaho, U.S.A. |
| 236 | ♂ | V. 235 × V. 23 | Belgium | Washington × Idaho, U.S.A. |
| 239 | ♂ | S.190-3 × V. 24 | Belgium | Idaho × Oregon, U.S.A. |
| 278 | ♂ | – | Norway | Kenai Island |
| 209 | ♂ | – | – | Origin unknown. Imported by Swedish Match Co. 1924. Label marked "Rush Mush" |

**Table 2 Parents, families and clones of poplar in the IEA exchange material from Belgium**

| Parent | V.23 | V.24 | V.26×V.23 | V.235×V.24 | (V.25×V.21) × (V.26×V.23) | Max.495 | S.122-3 | V.235 ×Max.495 | (V.26 ×V.23) ×Max.495 |
|---|---|---|---|---|---|---|---|---|---|
| V.235 | I:1–10 (1) | VI: 72–88 (1) | II:11–13 (1) | VII:89 | IX:90–94 (2) | X:96–104 | XI: 105 | XII:106 –116 | |
| V26×V23 | | III:17–42, 61–71 (7) | | | | | | | |
| S190–3 var. *hastata* | | IV:14–16 | | | | | | | |
| S192–5 var. *hastata* | | V:48–60 (4) | | | | | | | |
| S333–44 P. *deltoides* | | | | | | | XIII:117 | | XIV:118 –120 (2) |
| Essene2 P. *nigra* | | XV:121 –128 | | | | | | | |

Crossings within the shaded fields are pure *P. trichocarpa*. Number of selected clones within parentheses.

**Table 3 Description of certain traits and procedure used at recording**

| | |
|---|---|
| **Growth rhythm** | |
| Early growth | growth, cm, spring 1990, until June 12 |
| Date of growth cessation | when receiving the same reading at three consecutive recordings |
| Bud burst | scale 0–5, where 1 = development visible and 5 = growing |
| Bud set (at Ultuna) | scale 0–7, where 1 = leaf in a point and 7 = bud is full |
| Bud set (at Vittinge) | code; 1 = no bud, 2 = flushed bud and 3 = bud set |
| Reflushing stage | scale 0–3, where 1 = one leaf breaks and 3 = growing |
| Number of reflushes | number of slushed buds on main leader after first bud set |
| Polycyclic growth | lenght, cm, from the first to the last bud the same autumn |
| | |
| **Morphological characters** | |
| Straightness | graded 1–5, where 1 = straight |
| Leaf size | graded 1–5, where 1 = 20% least expanded and 5 = 20 % most expanded |
| Bud shape | grade 1 = thin, 2 = elliptical and 3 = bulb-shaped |
| Several leaders | 1 = one leader, 2 = two leaders and 3 = more than two leaders |
| | |
| **Damage** | |
| Rust November 9, 1990 | graded 1–5 |
| Frost damage Oct. 12, 1989 (at Ultuna) | percent of the leaves damaged |
| Frost damage Sept. 23, 1993 (at Vittinge) | 1 = only leaf damage, 2 = damage affecting apical bud, 3 = severe damage, apical bud destroyed |
| Frost damage October 23, 1993 and November 17, 1994 | cm of the leader destroyed by frost |

Ultuna trial and six control clones selected after 20 years growth in Sweden (Table 1). In both cases the selection criteria were hardiness, growth capacity and stem quality. The new trial was established at Vittinge, 30 km west of Uppsala, at the same latitude as the Ultuna trial, with around 20 cm rooted cuttings and with a spacing of 3.5 × 3.5 m. It consisted of eight complete randomized blocks with six-tree plots.

Both the trials are situated within that area in southern Sweden where we consider that Swedish poplar breeding should be concentrated in the first place.

## Sites

Both trials, at Ultuna and Vittinge, are located on the upper part of a south slope towards an open field area and with forest to the north. The soil at Ultuna was a light sandy clay, and at Vittinge a medium clay. Sand and moraine influenced the soil from the upper parts. Both trials were subjected to cold air streams from the north-west, but they were also sheltered from wind by the forest. The sites were not fertilized.

## Assessments

The final height was measured at Ultuna at ages 1–3 and at Vittinge at ages 3 and 4. For the first two years at Ultuna the height was measured twice a week, from the middle of August until every tree gave the same reading at three consecutive recordings. The third year we measured the height once a month during the growing season. The Vittinge trial was not recorded the first two years because of transplanting stress caused by drought.

Growth cessation and budset did not seem to be sufficient to describe the differences in winter hardiness. To get a better perception of the growth rhythm and how winter hardiness is built up and possibly find a selection criterion for frost hardiness, we tried to follow the Ultuna trial all year round assessing different expressions for the growth rhythm.

Bud burst was recorded May 18 1990. During spring 1991 more or less all the trees responded rapidly to a sudden change in temperature, causing difficulties in distinguishing clonal differences. Rust damage was frequent only during the autumn of 1990, and was classified according to severity and leaf area infested. For a description of the traits and procedure used, see Table 3.

## Statistical approach

In the analysis the fathers of family X, XI and XII, Table 2, are pooled together and denoted family XII. The models used in the GLM analysis are (SAS 1993):

$$Y_{ijklm} = \mu + b_j + s_j + g_{k(j)} + c_{l(jk)} + p_{ijkl} + e_{ijklm} \qquad [1]$$

where: $\mu$ = overall mean, $b_i$ = effect of block $i$, $i$ = 1, 2, 3, 4; $s_j$ = effect of species $j$, $j$ = 1,..., 5; $g_{k(j)}$ = effect of family $k$, $k$ = 1,..., $k_j$, $k_1$ = 7, $k_2$ = 1, $k_3$ = 1, $k_4$ = 2 and $k_5$

= 1; $c_{l(jk)}$ = effect of clone $l$, $l$ = 1,...,$ljk$; $p_{ijkl}$ = effect of plot $ijkl$; $e_{ijklm}$ = error term.

The same model was used for Vittinge, but the number of blocks was 8 and the kinds of genetic materials 3, namely $P.$ $trichocarpa$ from Belgium, hybrids from Belgium and $P.$ $trichocarpa$ from Sweden. Family effect was not included in this model because of too few families.

The effect of parents was calculated according to the following model:

$$y_{ijk} = \mu + b_i + f_j + m_k + e_{ijk} \qquad [2]$$

Effects not presented above are: $f_j$ = effect of female parents $j$, $j$ = 1,...6; $m_k$ = effect of male parents $k$, $k$ = 1,...7.

To test the interaction between sites and clones the following model was used:

$$Y_{hilm} = \mu + s_h + b_{i(h)} + c_l + sc_{hl} + p_{hil} + e_{hilm} \qquad [3]$$

Effects not presented above are: $s_h$ = effects of site $h$, $h$ = 1, 2; $b_{i(h)}$ = block within sites; $s_{chl}$ = interaction effect between site and clone; $p_{hil}$ = plot effect.

All factors, except for species, are considered random. Restricted maximum likelihood (REML) was used to estimate the variance components. For the Vittinge trial model 2 was not used. The family relationships of the clones at Vittinge do not allow any accurate estimates of female and male effects (cf Table 2). The Duncan method described in SAS 1993 was used for testing differences between species.

The broad sense heritability, $H^2 = V_G / V_P$, and the narrow sense heritability, $h^2 = V_A / V_P$, where the genotypic variance $V_G = V_{(fam.)} + V_{(clone)}$, the additive variance $V_A = V_{(male)} + V_{(female)}$ and $V_P$ is the phenotypic variance (FALCONER 1981).

## RESULTS

### Height development

The height development at Ultuna during the first three years was good (Fig. 1–3), with the highest trees being more than six meters at age 3, and with means at 5.5 m for the highest clones of $P.$ $trichocarpa$ and hybrids (Fig. 4). The differences between the $P.$ $trichocarpa$ and the hybrids according to the Duncan test are not significant, either when the hybrids are treated as a group or when the different hybrids are separated. There was, however, a difference between the hybrids $P.$ $trichocarpa$ × $P.$ $deltoides$ and $P.$ $trichocarpa$ × $P.$ $nigra$, the former being 33 % higher. The family within-species variation for height (Fig. 2) is obviously

Table 4 Variance components in percent for family within species and clone within family and plot, and broad sense heritability at Ultuna, 1989–1991

| Character | Fam (spec) | Clone (spec,fam) | Plot (spec, fam) | Error | $H^2$ |
|---|---|---|---|---|---|
| **Plant heights** | | | | | |
| Year 1 [1] | 0 | 21*** | – | 75 | 0.21 |
| Year 2 [1] | 6*** | 9* (16***) | 39*** (39***) | 43 (41) | 0.14 (0.16) |
| Year 3 | 3 | 18*** | 17*** | 62 | 0.21 |
| **Growth rhythm** | | | | | |
| Early growth spring 1990 | 23*** | 1 | – | 76 | 0.24 |
| Date of growth cessation 1990 | 9** | 10* | 28*** | 52 | 0.20 |
| Budset, October 10, 1989 | 7* | 0 | – | 66 | 0.07 |
| Budset October 22, 1990 | 14*** | 2 | 39*** | 25 | 0.15 |
| Reflushing stage October 22, 1990 | 8*** | 0 | 39*** | 42 | 0.08 |
| Number of reflushes autumn 1990 | 12** | 11** | 29*** | 43 | 0.23 |
| Polycyclic growth autumn 1990 | 6 | 10** | 23*** | 58 | 0.17 |
| Bud burst, spring 1990 | 7 | 8 | – | 84 | 0.14 |
| **Morphological characters** | | | | | |
| Straightness autumn 1989 | 3 | 9 | – | 88 | 0.11 |
| Leaf size, Sept. 3, 1989 | 5 | 4 | – | 83 | 0.10 |
| Bud shape, Oct. 22, 1990 | 0 | 1 | 27*** | 58 | 0.01 |
| **Damage** | | | | | |
| Rust damage, Nov. 9, 1990 | 0 | 0 | 35*** | 20 | 0 |
| Frost damage, Oct. 12, 1989 | 6 | 12* | – | 82 | 0.18 |

[1] Figure if the family effect is neglected, within parenthese

less than that within families (Fig. 3–4, Table 4–5). The broad sense heritability ($H^2$) was estimated at 0.21 for age 1 and 3, and 0.14 for age 2. The narrow sense heritability ($h^2$) varied between 0.12 and 0.51 for the three years.

At Vittinge the mean heights of the different Belgian clones after four growth periods never exceeded two meters and the variation among clones was much smaller than at Ultuna (Fig. 4–5). Also the heritabilities for heights were lower, $H^2 = 0.06$ and 0.12 and $h^2 = 0.12$ and 0.16 for the two years. According to the Duncan grouping (Table 7) the four hybrids did not differ in height from the *P. trichocarpa*, but, at age 4, the comparison clones selected in Sweden were significantly taller (16%) than the Belgian clones.

The heights of the Belgian clones at Vittinge after four growing seasons were compared with the same clones at Ultuna after three growing seasons (Figure 5). The variance of heights at age 2 and 3 at Ultuna and

age 3 and 4 at Vittinge are compared in Table 8. The best growing clones at Ultuna are the poorest at Vittinge and vice versa. The ANOVA, however, did not reveal any significant clone × site effect. The site effects are great, especially when data from age 3 at Ultuna are included.

Table 9 shows that positive Pearson correlations exist between heights at ages 1–3 at Ultuna on the one hand and early growth, leaf area index, total polycyclic growth and growth cessation on the other hand.

**Frost damage and survival**

There was no loss recorded at Ultuna that could be attributed to frost damage. Severe frost damage only occurred on one occasion, at the end of October 1990, when 5% of the ramets had their buds killed. None of the damaged ramets were from the 18 clones finally selected.
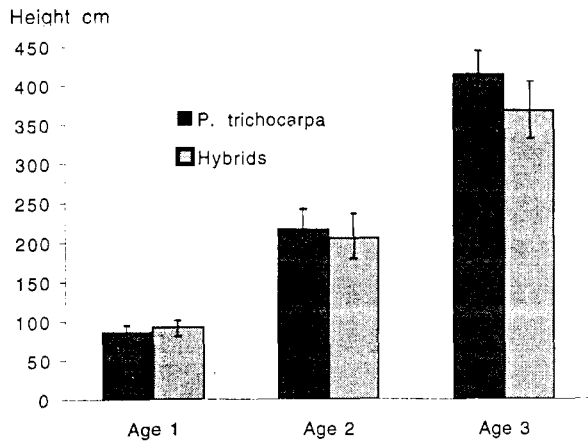
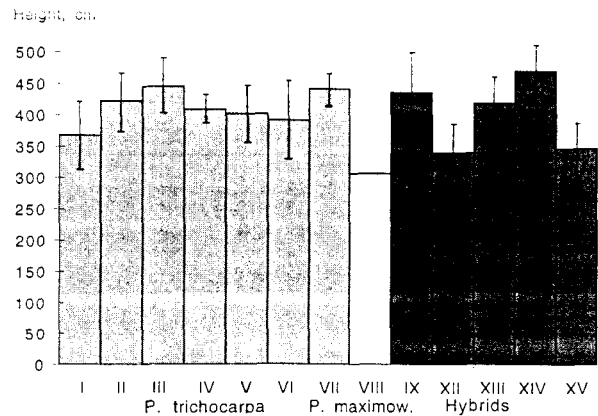Figure 1 Mean height of *P. trichocarpa* and hybrids, Ultuna



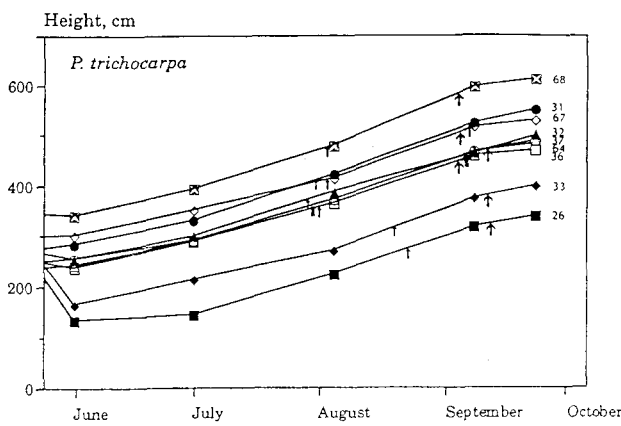Figure 2 Family mean heights at age 3, Ultuna



Figure 3 Monthly growth at Ultuna during the third growth period. Clones in the *P. trichocarpa* family 111. ‡ indicate 50 % and 90 % of the growth
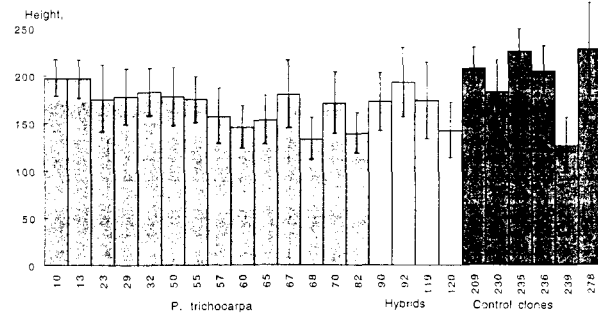


Figure 4 Clone mean heights at age 4, Vittinge

At Vittinge the frost damage was severe at three occasions, with accumulated totals of 15% dead trees at age 3 and 22% at age 4, whereas no loss was recorded for the reference clones selected in Sweden.

Figure 6 shows the frost damage at Vittinge at four different occasions at ages 2–4. The most severe frost damage, October 1993, caused an approximate die back of 40 cm in the leaders. No severe spring frost damage was recorded. The correlation coefficients between late autumn frost damage at age three and four was 0.49***, and between early and late frost damage the same autumn at age three 0.30*** (Table 10). There are also significant correlations at Vittinge between budset (with only three stages) and frost damage.

The broad sense heritabilities for frost damage varied between 0.08 and 0.18 and the narrow sense heritability between 0.15 and 0.32.

## Growth rhythm

Fig. 7 shows that there are 19 days between the earliest and the latest clone with respect to growth cessation during the second year. The hybrids do not seem to differ from the *P. trichocarpa* clones in any consistent way over the two years. Budset at October 22 1990 showed significant Pearson correlations with early growth, $r = 0.23***$, and growth cessation, $r = 0.20***$. Table 11 shows that almost 100% of the clones had one autumn flush or more and as many as 70% had two or more flushes after budset was recorded. The only clone at Vittinge having a bud at the end of September 1993 was the control clone 278, originating from Kenai Island, Alaska, at latitude 60°. All other 894 ramets had no apical buds at that time.

Table 5 Variance components in percent for parents and narrow sense heritability at Ultuna, 1989-90

| Character | Female | Male | Error | $H^2$ |
|---|---|---|---|---|
| **Plant heights** | | | | |
| Year 1 | 15* | 2 | 80 | 0.34 |
| Year 2 | 24*** | 2 | 71 | 0.51 |
| Year 3 | 6*** | 0 | 94 | 0.12 |
| **Growth rhythm** | | | | |
| Early growth spring 1990 | 16 | 14 | 70 | 0.59 |
| Date of growth cessation 1990 | 3** | 12*** | 86 | 0.29 |
| Budset, October 10, 1989 | 5* | 16*** | 56 | 0.34 |
| Budset October 22, 1990 | 0 | 17*** | 62 | 0.34 |
| Reflushing stage October 22, 1990 | 1 | 11*** | 77 | 0.23 |
| Number of reflushes autumn 1990 | 8*** | 13*** | 79 | 0.42 |
| Polycyclic growth autumn 1990 | 6* | 9*** | 83 | 0.29 |
| Bud burst, spring 1990 | 5* | 8* | 88 | 0.24 |
| **Morphological characters** | | | | |
| Straightness autumn 1989 | 0 | 11** | 89 | 0.22 |
| **Damage** | | | | |
| Rust damage, November 9, 1990 | 7*** | 6*** | 49 | 0.26 |
| Frost damage, October 12, 1989 | 0 | 14** | 84 | 0.32 |

Table 6 Variance components in per cent for clone and plot within species and broad sense heritability at Vittinge, 1993-1994, third and fourth growth period

| Character | Clone (spec) | Plot (spec) | Error | $H^2$ |
|---|---|---|---|---|
| Plant height, 1993 | 3 | 20*** | 72 | 0.03 |
| Plant height, 1994 | 6** | 20*** | 69 | 0.06 |
| Budset, November 17, 1994 | 24*** | 12*** | 55 | 0.24 |
| Several leaders, autumn 1993 | 0 | 7** | 83 | 0.00 |
| Frost damage, September 18, 1993 | 17*** | 6*** | 72 | 0.17 |
| Frost damage, October 23, 1994 | 9*** | 11*** | 69 | 0.09 |
| Frost damage, November 17, 1994 | 8*** | 6* | 85 | 0.08 |

Table 7 Significant differences according to the Duncan test between groups consisting of Belgian (B), Swedish (S), *P. trichocarpa* (t), and hybrid (h) poplars, and mean values of the traits at Vittinge, 1993-94, third and fourth growth period

| Characteristic | Result of the Duncan test and mean value of the traits |
|---|---|
| Plant height 1993, cm | NS |
| Plant height 1994, cm | Bth 170 / St 197 |
| Bud set November 17, 1994, scale 1-3 | Bth 2.0 / St 2.3 |
| Several leaders autumn 1993, scale 1-3 | Bt 0.87 / St 0.61 |
| Frost damage September 18, 1993, scale 1-4 | BSt 0.30 / Bh 0.74 |
| Frost damage October 23, 1993, cm | BSt 37 / Bh 45 |
| Frost damage November 17, 1994, cm | Bt 9 / St 4 |

**Table 8 Variance components in percent and genotype site interaction between heights at Ultuna (U) and Vittinge (V), log transformed values**

| Age U/Age V | No of obs | Site | Clone | Clone x site | Main plot effect | Error |
|---|---|---|---|---|---|---|
| 2/3 | 371 | 45* | 1 | 2 | 10*** | 37 |
| 2/4 | 346 | 32* | 0 | 0 | 13*** | 50 |
| 3/3 | 344 | 84*** | 1 | 0 | 3*** | 10 |
| 3/4 | 369 | 75*** | 0 | 0 | 4*** | 18 |

**Table 9 Pearson correlation coefficients between traits in the Ultuna trial 1989–1990, age 1–3**

| | Height | | Growth rhythm | | | | Morphological characters | |
|---|---|---|---|---|---|---|---|---|
| | Age 2 | Age 3 | Early growth | Date of growth cessation | Budset Oct. 22, 1990 | Polycyclic growth 1990 | Straightness autumn 1989 | Leaf size Sept 3, 1989 |
| | $x_2$ | $x_3$ | $x_4$ | $x_5$ | $x_6$ | $x_7$ | $x_8$ | $x_9$ |
| $x_1$ | 0.71*** | 0.42*** | 0.59*** | 0.19*** | 0.01 | 0.37 | −0.09 | 0.32*** |
| $x_2$ | | 0.60*** | 0.49*** | 0.28*** | −0.04 | 0.37 | −0.16* | 0.53*** |
| $x_3$ | | | 0.34*** | 0.18*** | −0.10 | 0.26 | −0.11 | 0.43*** |
| $x_4$ | | | | 0.09 | 0.23*** | 0.12 | −0.14* | 0.23** |
| $x_5$ | | | | | −0.20*** | 0.10 | 0.05 | 0.23*** |
| $x_6$ | | | | | | −0.17 | −0.12 | −0.15* |
| $x_7$ | | | | | | | 0.03 | −0.12 |
| $x_8$ | | | | | | | | −0.14* |

$x_1$ – Plant height, age 1

**Table 10 Person correlation coefficients between traits in the Vittinge trail 1993-94, age 3 and 4**

| Character | Height age 4 | Budset Nov. 17, 1994 | Frost damage Sept 18, 1993 | Frost damage Oct. 23, 1993 | Frost damage Nov. 17, 1994 |
|---|---|---|---|---|---|
| Height, age 3 | 0.69*** | −0.08* | −0.01 | 0.21*** | −0.13*** |
| Height, age 4 | | 0.04 | −0.10** | 0.00 | −0.14*** |
| Budset Nov. 17, 1994 | | | −0.29*** | −0.45*** | −0.46*** |
| Frost damage Sept 18, 1993 | | | | 0.30*** | 0.23*** |
| Frost damage Oct. 23, 1993 | | | | | 0.49*** |

On November 17th 1994 only 23% had a bud, 35% had a flushing bud, 18% had no apical bud and 24% a dead apical leader. For bud burst during spring 1990 only the effects of parents were significant.

In 1991 the height at Ultuna was measured once a month (Fig. 3). Most clones reached 50% growth at the very end of July, and 90% during the first third of September. Thus for most clones almost 40% of the annual growth occurred during the month of August.

### Several leaders and straightness

During autumn 1990, age two at Ultuna and autumn 1993, age three at Vittinge the trait 'several leaders'

was assessed; 13% and 43% of the plants at Ultuna and Vittinge, respectively, had several leaders. At neither site was there any significant genetic variation.

Straightness was assessed after the first growing season at Ultuna. The only significant effect in the ANOVAs was that of fathers. The Duncan test indicated a difference between *P. trichocarpa* and hybrids, the hybrids being somewhat straighter.

### Leaf rust

The only pathogen discovered was leaf rust, *Melampsora sp.* In 1990 rust was abundant. In this year the two *P. trichocarpa* × *P. deltoides* hybrid families were free
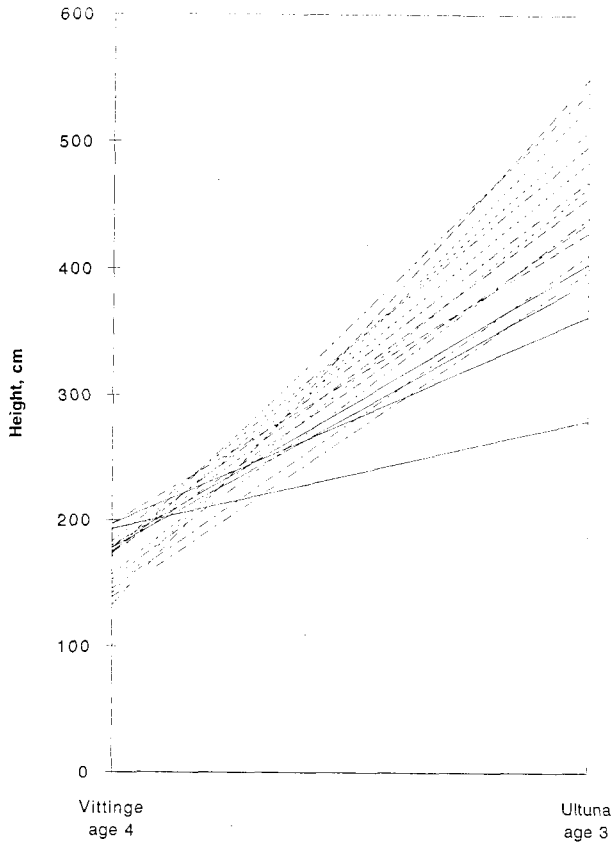
Figure 5 Heights of the clones common to the Vittinge and Ultuna trials after four and three growing seasons respectively

from rust, and the other hybrids had limited traces of rust. Of the *P. trichocarpa* families family II had no rust. The others had moderate numbers of spots on less than 50% of the crown and no necrosis. Families IV and VI had moderate attacks on 70 and 80% of the crown, respectively. The genetic variance was among species rather than within species and the block effect was important.

## DISCUSSION

### Height development

The high narrow sense heritabilities (0.34 and 0.51) at the Ultuna trial in the two first years were striking considering that the material is selected and the parents are few (Table 2). The amount of genetic variance and heritability are in agreement with that of RAJORA (1994) and DUNLAP *et al.* (1994). DUNLAP *et al.* (1994) still obtained a high mean production. In a trial near Seattle the mean height two years after establishment (with cuttings) was 457 cm and the mean diameter 40 mm. WU *et al.* (1992) and WU & STETTLER (1995) reported essentially higher broad sense heritabilities in interspecific hybrid populations and in hybrid second and backcross generations, respectively.

The reason for the drop of the narrow sense heritability to 0.12 in year 3 at Ultuna, as well as the
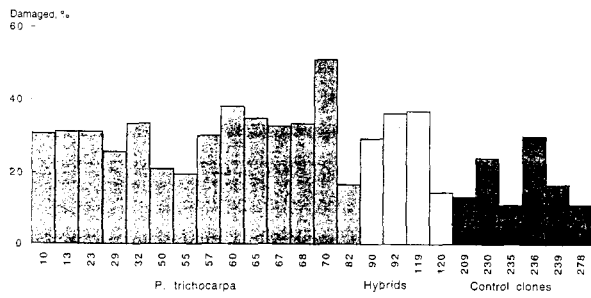


Figure 6 Frost damage at Vittinge. a) After winter 1992/93, percent severely damaged clones. Severe damage means that the apical bud is dead
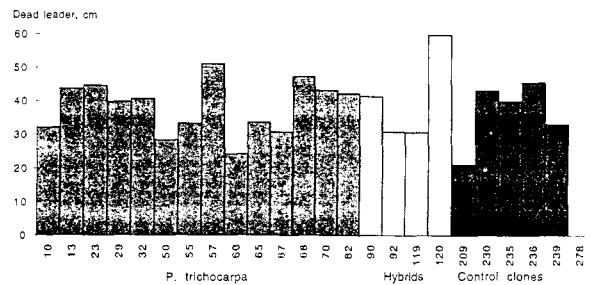


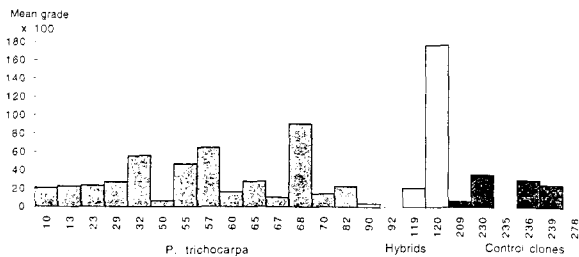Figure 6c Late frost damage October 23, 1993, cm of the leader dead



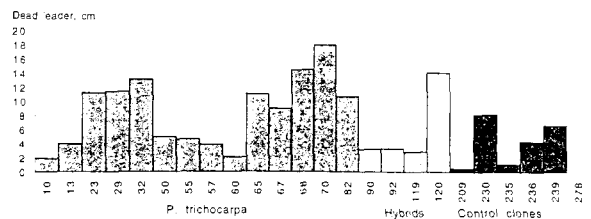Figure 6b Early frost damage September 29, 1993, graded 0-3



Figure 6d Frost damage November 17, 1994, cm of the leader dead
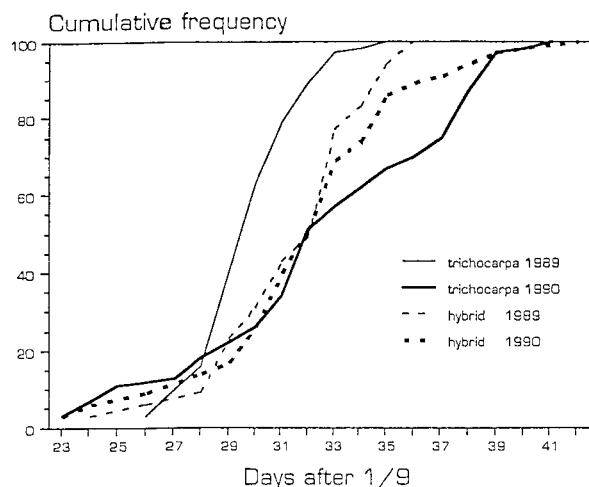
Cumulative frequency



Figure 7 Cumulative percentage showing time growth cessation in the first and second growth periods of the 62 *P. trichocarpa* clones and the 35 *Populus* hybrids

drop in broad sense heritability year 2, might be attributed to soil compaction in certain parts of the trial. If the family effect in Table 4 is neglected, the clone effect for year 2 becomes more similar to the two other years, as is indicated by the figures within brackets. The pronounced within-family variation is evident from Table 4, Fig. 3 and 4. This is in good agreement with ROGERS *et al.* (1989).

Pearson correlations between the heights for the different years vary between 0.42 and 0.71, indicating that there are great changes between the growth in different years (Table 9–10). There are significant correlations between the final heights on the one hand and early growth, growth cessation and leaf area on the other hand. The correlations with early growth and leaf area are especially strong. This difference is however considered insufficient for judging the relative importance of early and late growth.

The height development and survival at Vittinge were strongly affected by frost damage and drought. The broad sense heritabilities are thus several times lower than that at Ultuna. The three selected clones at Ultuna that had the lowest production escaped frost damage comparatively better and were the best producing Belgian clones at Vittinge, while two of the best producing clones at Ultuna were among the lowest producing clones at Vittinge. In spite of this, as well as the large difference in genetic effects at the two sites, there was no significant clone × site interaction (Table 8). This is promising for future poplar breeding in southern Sweden since the number of breeding zones can be kept at a minimum.

A comparison of heights at age 2 of the clones in common with the Finnish trial showed that the mean

height in Finland was only 54% of that at Ultuna (STEENACKERS & SMETS 1990 b).

In contrast to the work of CEULEMANS (1990) and CEULEMANS *et al.* (1992), carried out under different climatic and photoperiodic conditions, there was no superiority of the hybrids either in this investigation or in the Finnish (Table 6, Fig. 1, 2 and 4).

RAJORA *et al.* (1994) investigated the sources of variance for growth traits and rust resistance and found that the genetic effect for males was much higher than for females. In our investigation the male effect is most often dominating, but not for height at Ultuna, where the female effect is dominating.

## Survival and frost damage

There are three types of damage behind the mortality in these trials:
1. Poor condition of cuttings or plants at establishment.
2. Drought after establishment.
3. Frost damage.

The loss at Ultuna was of the first type. At Vittinge all types of losses occurred. The calculated mortality at Vittinge refers to losses owing to frost damage only. In spite of the serious frost damage at Vittinge the survival after three and four years was approximately the same as in U.K. and Finland after one and two growing seasons. The survival of 44 clones that were shared between U.K. and Finland was in U.K. 70% after the first growing season, 1989, and in Finland 80% after the second growing season, 1990 (STEENACKERS & SMETS 1990 b). The reasons for the losses in U. K. and Finland were not reported.

At Ultuna there was little severe frost damage and when it occurred, plants soon recovered. The 5% severely frost-damaged trees at October 24 1990 could be compared with the percentage of trees having more than one leader during autumn 1990, amounting to 13%. The explanation for this difference is clearly that the frost damage is a single event, while 'several leaders' is an effect of repeated frost events.

Fig. 1 shows a higher mean growth for the hybrids than for *P. trichocarpa* in 1989. For the next two years the order is different, which must be attributed to the lower frost hardiness of the hybrids. The differences are however not significant. As seen from Fig. 3 there was a pronounced drop in height of clones 26 and 33 depending on frost damage. Evidently such a set-back is harmful for the long-term growth of a clone.

At Vittinge the frost damage became more and more limiting for the height development and growth. The frost damage of the different clones varied between the recordings at different occasions. If also the damage recorded October 24 1990 is taken into consideration,

none of the Belgian clones were consistently good or poor. At Vittinge, however, the control clone number 278, originating from Kenai Island, always had less or no damage and clone 120 was always more severely damaged than the mean (Fig. 6). One possible reason for the inconsistency in frost hardiness can be different rhythms of inwintering. Another reason can be that the varying frost hardiness is also an effect of drought.

One explanation why these vigorous but not very hardy clones were selected, may be that they were more suited to stand less severe frosts, like that at Ultuna (cf Fig. 6a).

A reason for the descending figures for heritability over time in the assessments of frost damage at Vittinge may be 'hang over' effects of earlier frost damage events.

## Growth rhythm

In contrast to many other hardwoods in which growth cessation, once triggered by long nights, is stable (JONSSON & ERIKSSON 1989), the poplar clones in this study frequently had one or more flushes (Table 10). The repeated flushes after the first budset indicates that the weather conditions exert a strong influence on growth cessation. When warmer periods reappeared, few or no clones proved to be stable. HOWE et al. (1995) found that this was typical for genotypes moved long distances to the north. In their study long nights induced terminal buds in both northern and southern genotypes, but only temporarily in the latter.

The late budset at Vittinge recorded November 17 1994 was approximately eight weeks later than the first growth cessation according to the assessments in 1989 and 1990 (Fig. 7) and what is normal in Belgium. As a consequence both early and late frost damage occurred. This late budset had a significant relationship with frost damage (Table 10).

As is shown for the clones in Fig. 3 half the annual growth occurs in August and September. MONTEIRO (1988) tested more than 200 poplar clones in Portugal. Most of them had a similar growth rhythm to the Belgian clones, but some 30 of them had most of their growth essentially earlier, i. e. in July and little or nothing in September.

## Weather characteristics and their impact on the results

The weather conditions obviously play a significant rôle for the large difference in growth and frost damage between the Ultuna and the Vittinge trials. Two tendencies of possible importance for the frost damage seem perceptible during these years: warm early autumns,

suddenly interrupted by periods with unusually low temperatures and several weeks of intensive drought almost every growing season.

The weather observations at Ultuna, Uppsala, recorded –10 °C the 13th of October and –14 °C at the end of the month in the year 1992. Such a low October temperature did not occur during the previous 30 years. The next autumn, 1993, there was –4.5 °C on September 18th and –5.5 °C on 15–16th of October. Of these events only the first is rare, occurring twice during the last 30 years.

Although the clones were selected for hardiness, around 25% of the plants were severely damaged by frost after the otherwise very mild winter 1992/93 (Fig. 6a). In the autumn of 1993 an assessment was done on October 23th. At that time every individual, except for clone 278, had between 20–60 cm of the leader destroyed by frost (Fig. 6c).

It can also be mentioned that the mean of the monthly minimum temperatures for the period November–April was –14.0 and –12.2 °C for the winter 1989/90 and 1990/91, respectively, and –10.8 and –15.5°C for the winter 1992/93 and 1993/94, respectively, thus around the same mean for the two periods.

Obviously the most important differences in the weather conditions between the two periods 1989–91 and 1992–94, responsible for the frost damage the last period are the early, sudden and unusually strong frost spells in October 1992 and in September 1993. Another key question for the successful cultivation of these poplars in southern Sweden then is if these early and strong frost spells will occur more often in the future.

## Rust resistance

The rust resistance is the only trait with a highly significant difference between species. In spite of the fact that only one autumn with abundant rust is recorded, we may point to the similarity of the results with those of LEFÈVRE et al (1994) and HSIANG et al (1993). Thus the rust incidences and their severity vary among the P. trichocarpa clones, the hybrids with P. maximowiczii and P. nigra having significantly fewer infestations while the hybrids with P. deltoides are free from rust. LEFÈVRE et al (1994) interpret the inheritance within the pure P. trichocarpa as polygenic and that in the hybrid with P. deltoides as a major gene effect. HSIANG et al. (1992) also studied rust resistance in P. maximowiczii and its hybrids with P. trichocarpa and with the hybrids between P. trichocarpa and P. deltoides. The crosses in which P. maximowiczii was involved had fewer rust attacks and they were less severe than in pure P. trichocarpa.

Table 11 Percentage of plants flushing during the autumns of 1989 and 1990

| Clones | One single flush | | Two or more flushes | |
|---|---|---|---|---|
| | 1989 | 1990 | 1989 | 1990 |
| P. trichocarpa | 28 | 30 | 20 | 70 |
| hybrids | 15 | 25 | 28 | 73 |

## Morphological and special traits

The morphological traits have rather weak genetic components. The cases of several leaders may be attributed to an effect of a series of frost events. The Pearson correlations between leaf size on the one hand and heights, early growth and growth cessation on the other hand may indicate that the leaves grow during the entire period of height development.

## Differences between species

The analysis of variance with the species considered as a random factor indicates small and insignificant effects for species, rust infestations being the only exceptions. The results of the Duncan tests of the Vittinge trial are shown in Table 7. The Duncan tests of different species in the Ultuna trial showed very few significant differences. Except for a frequent negative deviation for the single P. maximowiczii and the difference in height between the two hybrids, mentioned before, there is only a difference in leaf size between the P. nigra hybrid and the rest of the clones, P. nigra having somewhat smaller leaves.

## CONCLUSION

In spite of the good narrow sense heritabilities, especially for height but also for growth rhythm, none of the investigated clones have satisfactory hardiness. The repeated flushes in the autumn of 1989 and 1990 (Table 11), the poor budset in 1993 and 1994, and the frost damage, indicate that budset and inwintering are too unstable or too late. The instability of the budset and the fact that their inwintering is too dependent on temperature, means that the plants are insufficiently prepared for sudden drops in temperature during autumn. The possibility that the destructive early frost spells may be as rare in the future as they have been earlier, cannot change that conclusion. Inwintering is unstable and does not lead to stable dormancy. If the winter comes slowly and steadily, without considerable fluctuations in temperature, the plants may build up enough hardiness to pass both the autumn and the

winter without severe damage. Fluctuations in temperature, both downwards and upwards may, however, disturb or destroy the process of inwintering and the plants may be damaged.

We need a more hardy material, inwintering according to daylength, rather than temperature, so that it is well prepared for early autumn frosts and the winter conditions. To get this material we have to make crosses. In these breeding efforts we can make use of the Belgian clones, which are very promising in several respects. Establishing this was a principle aim of the investigation.

## ACKNOWLEDGEMENTS

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