# THE RELATIONSHIPS BETWEEN YIELD AND CARBON FIXATION IN SELECTED HYBRID FAMILIES AFTER CROSSING SELFED LINES OF *BETULA PENDULA* ROTH

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## ABSTRACT

$CO_2$ exchange parameters, leaf stomatal characters and stem volume, were observed in fast- and slow-growing hybrid families produced by crossing selfed lines of silver birch (*Betula pendula* Roth) in an eight-year-old field trial. Significant differences among families were found for net photosynthesis ($P_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), stomatal density and guard cell length and total guard cell length per unit leaf area. The proportions of total variance assigned to family were between 36 and 54% for $P_N$, $g_s$ and $C_i$ and between 75 and 83% for stomatal density, guard cell length and total guard cell length per unit area. Light response curves of $P_N$ of fast- and slow-growing families were also different over the whole range of photosynthetically active radiation (PAR). Net photosynthesis was positively correlated with yield, whereas stomatal density or total guard cell length per unit leaf area was positively correlated with $P_N$.

**Key words:** *Betula pendula*, hybrids, photosynthesis, stomata, stem volume.

## INTRODUCTION

The growth rate of a plant depends on many environmental and endogenous factors, but can ultimately be defined in terms of the carbon status by the balance between photosynthetic $CO_2$ assimilation and respiration costs, and also by a carbon partitioning factor as modeled by MASLE *et al.* (1990). Therefore, net photosynthesis ($P_N$) together with certain other $CO_2$ exchange parameters are important yield components. The stomata play an essential role in $CO_2$ exchange because they are the passages through which most of the carbon dioxide used in photosynthesis enters the leaves and also through which most water is lost as vapor from leaves.

Differences in net photosynthesis among families or clones have been found in several forest tree species, *e.g.* Douglas-fir (KRUEGER and FERRELL 1965), poplar (LUUKKANEN & KOZLOWSKI 1972; NELSON & EHLERS 1984), pitch pine (LEDIG & CLARK 1977), black locust (MEBRAHTU & HANOVER 1991), black spruce (JOHNSEN & MAJOR 1995) and silver birch (WANG *et al.* 1995). Higher net photosynthesis within a given species was not always associated with higher yield. Different patterns of correlation between net photosynthesis and growth of trees in different species have also been reported to be weakly to strongly positive (MAHON *et al.* 1977; CEULEMANS & IMPENS 1983; LAPIDO *et al.* 1984; CEULEMEMANS *et al.* 1987; WANG *et al.* 1995) or negative to non-existent (LAPIDO *et al.* 1984; MEBRAHTU & HANOVER 1991). Thus it seems that there is no single general trend existing between the photosynthetic rate per unit area and growth. The situation is similar in crop plants (AZCÓ-BIETO & CABALLERO 1993).

A wide variation in guard cell length and stomatal density among and within species has been noted. For example, guard cell length varied among 38 species of trees from 17 to 56 μm and stomatal density from 100 to 600 stomata.mm$^{-2}$ of leaf surface (DAVIES *et al.* 1973); stomatal density varied between 205 to 404 stomata·mm$^{-2}$ on the lower surface and between 42 and 187 stomata·mm$^{-2}$ on the upper surface among 5 *Populus* clones (SIWECKI & KOZLOWSKI 1973).

In silver birch observations have been made on a full- and half-sib progeny test. Significant differences among families and a positive correlation between net photosynthesis and growth were found as referred previously (WANG *et al.*, loc. cit.). In the present study the measurements were made on hybrid families after crossing selfed lines. These unique hybrid families in forest trees are characterized by small genetic variation among individuals within a family (WANG *et al.*, TAG in press), which can enhance the precision of the measurements. Meanwhile, the observations were extended from photosynthesis alone to some other $CO_2$ exchange parameters and leaf stomatal characters, and

also light response curves of $P_N$ were determined on some fast- and slow-growing families.

In this study, we have set out to specify precisely the photosynthetic components that form the basis of growth differences in genetically well defined and homogenous birch families. Differences in $CO_2$ exchange parameters and leaf stomatal characters among selected hybrid families were observed in a progeny test field trial of *Betula pendula*. The correlations among $CO_2$ exchange parameters, stomatal characters and growth rate were analyzed.

## MATERIALS AND METHODS

### Plant materials

The material used in this study was a progeny test of crosses between selfed individuals of silver birch established by the Foundation for Forest Tree Breeding (experiment No. 1253). The trial is located in Loppi (lat. 60° 42′, long. 24° 20′ and alt. 150 m) in southern Finland, and was planted with two-year-old seedlings in 1987. It contains 41 entries including 33 hybrid families derived from selfs and seven controls of standard seed origins. A randomized complete block design was used with 2 × 4 plants spaced at 2.5 × 2.5 m per plot and six blocks in the whole trial.

**Table 1 Families chosen for observing stem volume, $CO_2$ exchange parameters and stomatal characters**

| Family No | Parents | | Group |
|---|---|---|---|
| | Mother | Father | |
| F19 | V5360 | V5377 | Fast |
| F24 | V5379 | V5359 | |
| F34 | V5370 | V5762 | |
| F37 | V5755 | V5762 | |
| F39 | V5767 | V5778 | |
| S27 | V5454 | V5515 | Slow |
| S29 | V5516 | V5690 | |
| S42 | V5481 | V5619 | |
| S46 | V5769 | V5348 | |
| C49 | E1970 | E1980 | Control |

The families chosen for observing net photosynthesis and $CO_2$ exchange parameters comprised five fast- and four slow-growing hybrid families, regardless of parental origins, and one commercial full-sib family as control (Table 1). In each plot four trees were mechani cally sampled. For each tree four leaves from the upper layer of the crown and oriented towards the same compass direction were measured. Measurements were repeated in three blocks.

### Measurement of photosynthesis

$CO_2$ exchange parameters including net photosynthesis ($P_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$), $CO_2$ resistance ($R_s$) and water transpiration (E) of the leaf were measured with the LI-6200 Portable Photosynthesis System in the beginning of July 1994. For technical details we refer to WANG, *et al.* (1995). The measurements were made in 1,000–2,400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR), a temperature of 21.5–36.5 °C (Temp), 21–39% relative humidity (RH) and over a period from 10:00–18:40 (Time).

### Analysis of the data

The data were analyzed with REG, ANOVA and VARCOMP procedures in the SAS system. The block effect was considered fixed.

Since $CO_2$ exchange parameters were measured under variable environmental conditions and some of the environmental factors significantly affect measurements, the data, including $P_N$, $g_s$, $R_s$ and E, were corrected by modeling the theoretical values on the basis of measured values and the environmental factors.

Models were built based on a stepwise regression method involving environmental variables as follows:

$$tP_N = -37.8295 - 7.4149\ Time^2 + 227.7903\ Temp^{-1} + 2.8371\ RH - 0.04134\ RH^2$$

$$tg_s = -0.4445 + 0.01992\ Time^{-2} + 0.0001729\ Temp^2 + 162.3973\ Temp^{-2} + 0.0004991\ RH^2$$

$$tR_s = 1.2557 + 0.6083\ Time^2 - 0.0008839\ Temp^2 - 741.2154\ Temp^{-2} + 1068.0708\ RH^{-2}$$

$$tE = 0.02466 - 0.003071\ Time^2 - 0.0009064\ Temp + 0.00002411\ Temp^2 - 5.8460\ RH^{-2}.$$

Where symbols preceded by 't' represent theoretical expectations of the measured variables. The parameters used in the modeling are shown in Table 2. Then, under given environmental conditions, *e.g.*, Time = 12:00, Temp = 25°C and RH = 27%, the $CO_2$ exchange parameters of each measurement were estimated by:
$P_N = 15.87\ mP_N / tP_N$,
$g_s = 0.3669\ mg_s / tg_s$,
$R_s = 1.1345\ mR_s / tR_s$,
and $E = 0.008282\ mE / tE$.

The symbols preceded by 'm' represent measured values. The constants in the above models are theoreti-

**Table 2 Parameters used in stepwise regression for modelling the theoretical valueas of net photosynthesis ($tP_N$), stomatal conductance ($tg_s$), $CO_2$ resistance ($tR_s$), and water transpiration. The variables kept inthe model were significant at 0.05 level**

| Dependent variable | Step | Variable entered | Partial $R^2$ | Model $R^2$ | F | Prob>F |
|---|---|---|---|---|---|---|
| $tP_N$ | 1 | $RH^2$ | 0.2901 | 0.2901 | 287.73 | 0.0001 |
| | 2 | $Temp^{-1}$ | 0.0955 | 0.3857 | 109.32 | 0.0001 |
| | 3 | $Time^2$ | 0.0424 | 0.4280 | 52.01 | 0.0001 |
| | 4 | RH | 0.0032 | 0.4312 | 3.91 | 0.0483 |
| $tg_s$ | 1 | $RH^2$ | 0.4163 | 0.4163 | 502.09 | 0.0001 |
| | 2 | $Time^{-2}$ | 0.0296 | 0.4459 | 367.55 | 0.0001 |
| | 3 | $Temp^{-2}$ | 0.0087 | 0.4546 | 11.25 | 0.0008 |
| | 4 | $Temp^2$ | 0.0049 | 0.4595 | 6.37 | 0.0118 |
| $tR_s$ | 1 | $RH^{-2}$ | 0.4274 | 0.4274 | 525.45 | 0.0001 |
| | 2 | $Time^2$ | 0.0203 | 0.4477 | 25.90 | 0.0001 |
| | 3 | $Temp^{-2}$ | 0.0048 | 0.4526 | 6.21 | 0.0129 |
| | 4 | $Temp^2$ | 0.0099 | 0.4625 | 12.91 | 0.0003 |
| tE | 1 | Temp | 0.3263 | 0.3263 | 340.98 | 0.0001 |
| | 2 | $RH^{-2}$ | 0.2421 | 0.5684 | 394.38 | 0.0001 |
| | 3 | $Time^2$ | 0.0077 | 0.5761 | 12.72 | 0.0004 |
| | 4 | $Temp^2$ | 0.0085 | 0.5846 | 14.41 | 0.0002 |

cal values of the observed parameters under given environmental conditions. However, $C_i$ was kept uncorrected because the general correlation between $C_i$ and environmental factors was low (R = 0.1171).

### Observations of the $P_N$ light response curve

To minimize the variation caused by environment, the light response curve of $P_N$ for each family was measured on the basis of only one average leaf from the upper crown layer of a tree of average growth in one block. The intensity of PAR was controlled by changing the number of layers of transparent polyethylene, and total darkness was obtained by wrapping the chamber with dark clothe.

### Observations of guard cell length and stomatal density

The samples used for the observation of stomatal characters were the same as for the measurements of $CO_2$ exchange parameters, but only one of the leaves from each individual was observed. Leaves were kept fresh before the observation. Stomatal density (no./$mm^2$) and guard cell length (μm) of fresh leaves were observed with a JSM–840 Electronic Scanning Microscope. A piece of leaf about 0.5 $cm^2$ in area was cut from the middle of the leaf close to the main vein between two sub-veins. The leaf specimen was coated with gold for 5 min, and then observed under 300× magnification. Eleven fields were observed for stomatal density and one field was transferred to the computer as an image for the measurement of guard cell length. The total guard cell length per unit area ($\mu m \cdot mm^{-2}$) was calculated by the mean guard cell length multiplied by stomatal density. Plot means of the observations were used in data analysis.

## RESULTS

### Differences in stem volume and $CO_2$ exchange parameters among families and groups

The family and group means of stem volume, net photosynthesis ($P_N$) and other $CO_2$ exchange parameters are listed in Table 3. The differences in stem volume among families and among groups were significant (P<0.0001). The stem volume of the best family (F37) was 112% higher than the poorest one (S46) and 31% higher than the control.

The differences in $P_N$ among families were significant (P<0.005), ranging from 14.25–19.18 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The highest family mean of $P_N$ (F34) was 35% higher than the lowest one (S46). The proportion of the total variance explained by family was 54%, indicating a strong genetic control for this character.

There were significant differences in $P_N$ among groups (P<0.01). The mean of the fast group was

**Table 3 Family means of stem volume $CO_2$ exchange parameters and leaf stomatal characters[a]**

| Group | Family No | Stem volume ($dm^3$) | $P_N$ ($\mu mol.\ M^{-2}.s^{-1}$) | $g_s$ ($mol\ m^{-2}.s^{-1}$) | $C_i$ (ppm) | $R_s$ ($s.cm^{-1}$) | E ($mmol\ .m^{-2}.s^{-2}$) | Stomatal density ($No.mm^2$) | Guard cell length ($\mu m$) | Total guard cell length ($\mu m$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Fast | F19 | 6.62 | 16.73 | 0.381 | 247.4 | 1.081 | 8.38 | 161 | 26.8 | 4319.4 |
| | F24 | 6.39 | 15.20 | 0.331 | 241.1 | 1.262 | 7.70 | 138 | 28.8 | 3981.8 |
| | F34 | 7.15 | 19.18 | 0.441 | 245.2 | 0.934 | 9.31 | 212 | 26.9 | 5697.5 |
| | F37 | 7.67 | 17.33 | 0.377 | 240.7 | 1.164 | 8.08 | 199 | 24.8 | 4976.2 |
| | F39 | 6.04 | 16.09 | 0.388 | 248.5 | 1.065 | 8.77 | 188 | 25.2 | 4613.5 |
| | **Mean** | **6.77a*** | **16.91a** | **0.384** | **244.6a** | **1.101** | **8.44** | **180a** | **26.5a** | **4717.7a** |
| Slow | S27 | 4.50 | 15.00 | 0.363 | 250.0 | 1.146 | 8.15 | 128 | 34.3 | 4400.0 |
| | S29 | 5.31 | 16.84 | 0.373 | 244.1 | 1.106 | 8.42 | 143 | 27.7 | 3851.8 |
| | S42 | 4.64 | 14.96 | 0.349 | 247.9 | 1.147 | 8.38 | 94 | 33.9 | 3168.4 |
| | S46 | 3.62 | 14.25 | 0.356 | 252.5 | 1.197 | 8.08 | 96 | 32.7 | 3103.5 |
| | **Mean** | **4.52c** | **15.27b** | **0.360** | **248.6ab** | **1.153** | **8.26** | **115b** | **32.2b** | **3630.1b** |
| **Control** | **C49** | **5.86b** | **15.53ab** | **0.340** | **242.6c** | **1.241** | **7.91** | **166c** | **25.3c** | **4205.1c** |
| Family | P>F | 0.0001 | 0.0032 | 0.0355 | 0.0115 | – | – | 0.0001 | 0.0001 | 0.0001 |
| | $\sigma^2$(%) | – | 53.90 | 36.54 | 45.33 | – | – | 82.43 | 74.41 | 75.10 |
| Group | P>F | 0.0001 | 0.0094 | – | 0.0129 | – | – | 0.0001 | 0.0001 | 0.0001 |

* Means with the same letters are not significantly different ($\alpha = 0.05$)

a) $P_N$ – net photosynthesis; $g_s$ – stomatal conductance; $C_i$ – intercellular $CO_2$ concentration; R – $CO_2$ resistance; E – water trnaspration.

significantly higher than that of the slow group, while the differences between the fast group and control and between the slow group and control were not significant. The mean $P_N$ of the fast group was 10% higher than that of the slow group (Table 3).

Significant differences were found among families for $g_s$ and $C_i$, but not for $R_s$ and E. The proportions of the total variances of $g_s$ and $C_i$ explained by family were 37% and 45%, respectively. The differences among groups were significant for $C_i$, but not for $g_s$, $R_s$ or E. The mean of $C_i$ for the fast group was significantly lower than that for the slow group (Table 3).

## Comparisons of light response curves of $P_N$ among different families

To compare $P_N$ in the whole range of PAR among the fast- and slow-growing families, the light response curves of the fast- and slow-growing families were observed. To minimise the effect of changing environments, only four families were measured within one hour, including two fast (F34 and F39) and two slow ones (S42 and S46). The results are shown in Fig. 1. For the material in the present study net photosynthesis started with PAR around 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and the light saturation point was around 950 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The

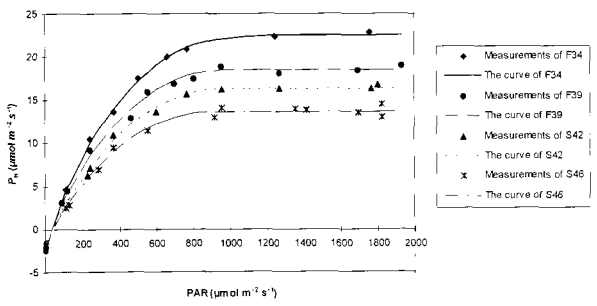


**Figure 1** Light response curves of net photosynthesis ($P_N$) of different families

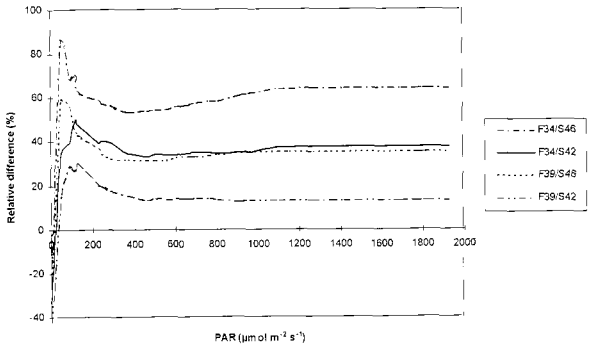


**Figure 2** Relative differences in dark respiration and net photosynthesis ($P_N$) between fast- and slow-growing families

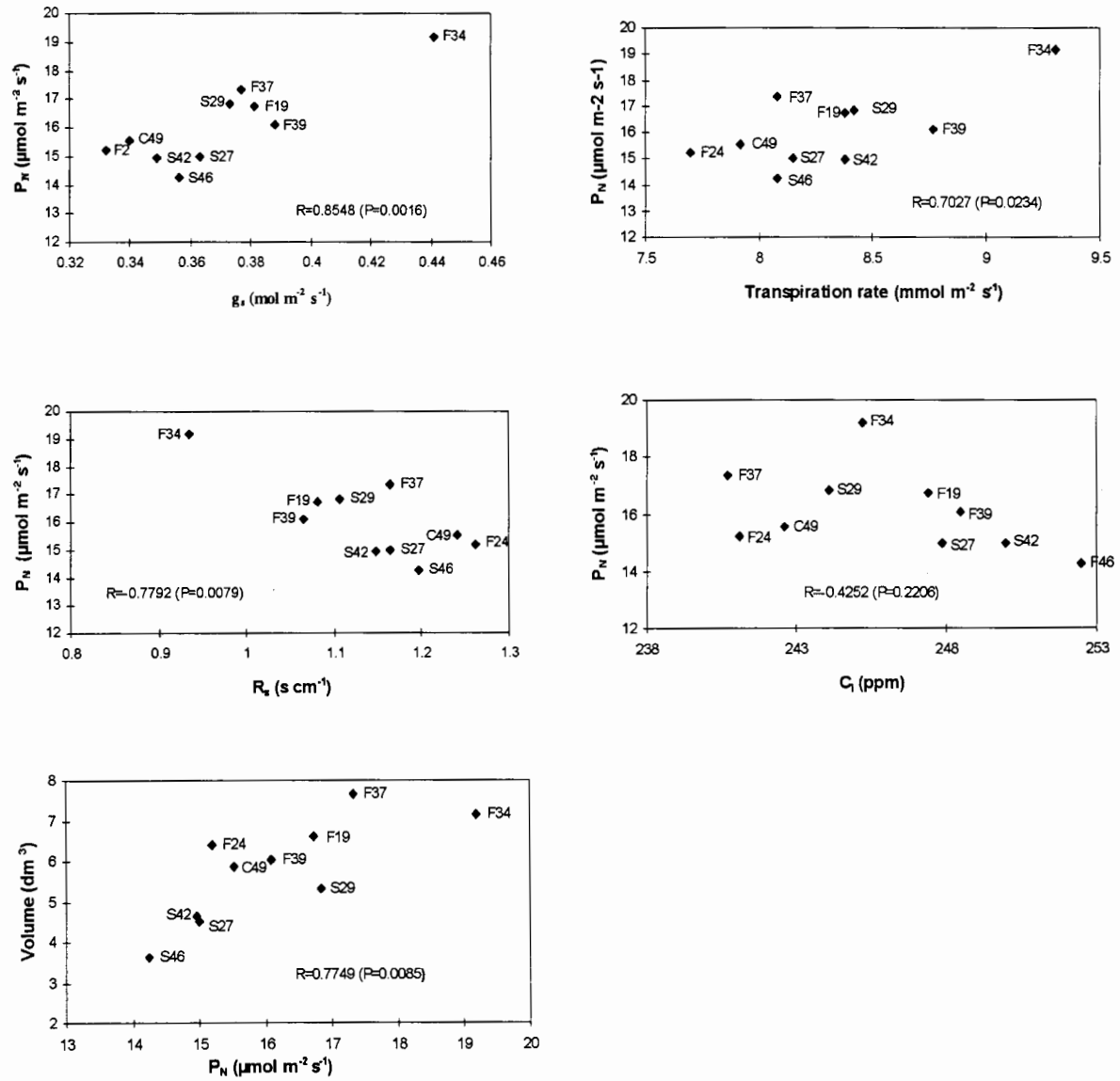


**Figure 3** Correlations between $P_N$ and other $CO_2$ exchange parameters / growth rate

differences in $P_N$ among the families occur at the starting point of $P_N$. The families F34 and F39 with higher $P_N$ values at PAR's above saturation point had higher $P_N$ values in the whole range of PAR. There were clear differences in dark respiration among the families, ranging from 1.72–2.50 µmol·m–2·s$^{-1}$. The fast families F34 and F39 with higher $P_N$ had higher dark respiration than the two slow families, by 29% on average. Although the absolute differences among the families were very small at low PAR levels, the relative differences between the fast- and slow-growing families were relatively constant at PAR levels above about 120 µmol·m$^{-2}$· s$^{-1}$ (Fig. 2).

## Differences in guard cell length and stomatal density

Stomata occur only on the lower surface of the leaf of *Betula pendula* (Figure 4). The grand mean stomatal density was 152 stomata·mm$^{-2}$. The grand mean guard cell length, measured as average length of guard cells, was 28.6 µm. The differences in these two characters among the families were significant ($P<0.0001$), ranging from 94 – 211 stomata·mm$^{-2}$ for stomatal density and from 24.8 – 34.2 µm for guard cell length. The proportions of the total variances assigned to family for stomatal density and guard cell length were 82% and

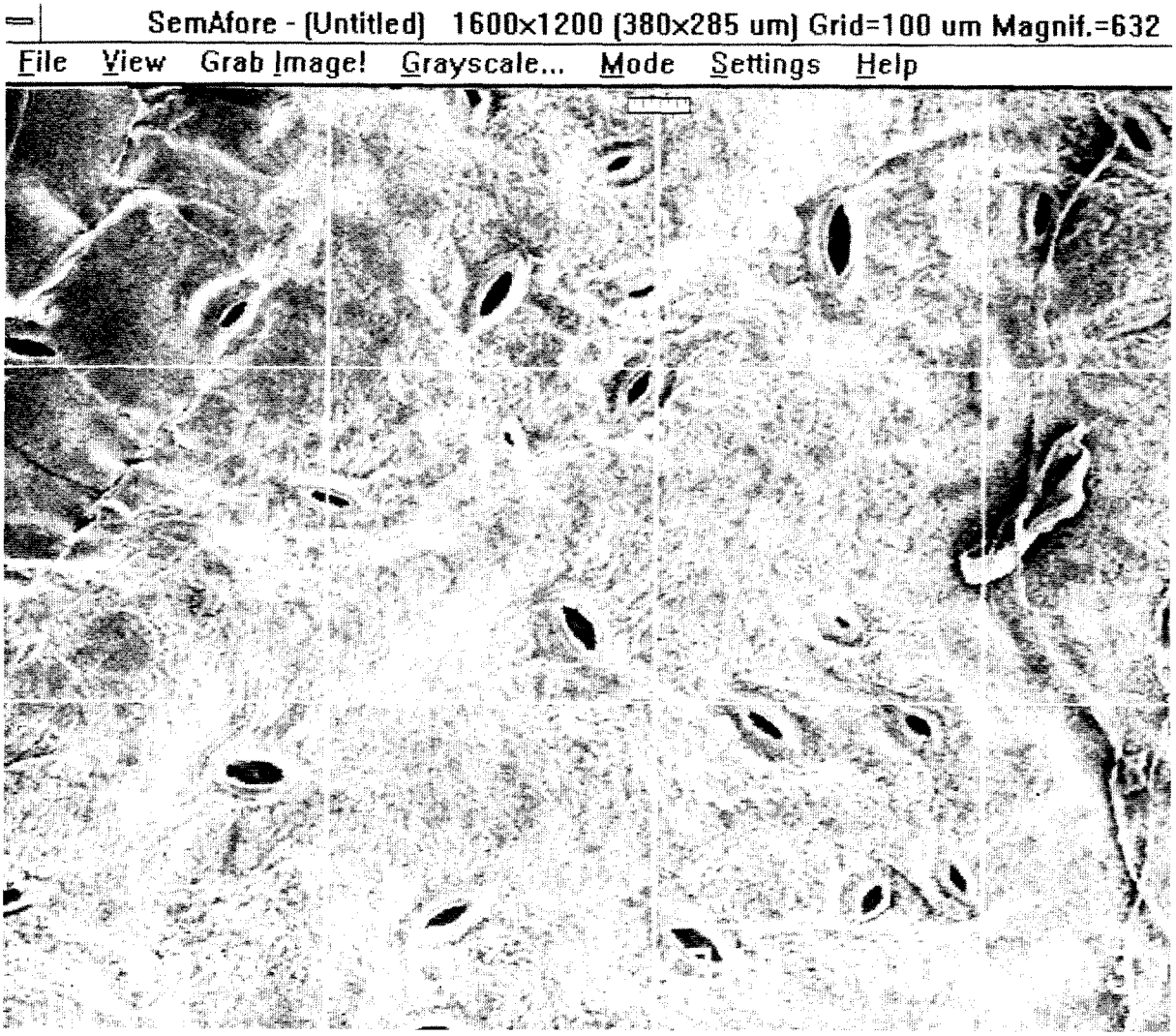


**Figure 4a** Leaf stomata of *Betula pendula* fast-growing family F34

74%, respectively. There was a negative relationship between stomatal density and guard cell length (R = –0.8513, P<0.005). However, the total guard cell length per unit leaf area, differed significantly among families (P<0.0001), ranging from 3103.5 – 5697.5 $\mu m \cdot mm^{-2}$. The variance assigned to family was 75% of the total variance (Table 3).

The differences between the groups and the control were significant for stomatal density and guard cell length and for the total guard cell length per unit leaf area (Table 3). Stomatal density of the fast-growing family group was 57% higher, whereas its guard cell length was 22% lower than those of the slow-growing family group. Also, the differences in the total guard cell length per unit leaf area among the groups were significant. The fast-growing family group was 30% higher in guard cell length than the slow-growing family group, the control being intermediate.

**Correlations between $P_N$ and other $CO_2$ exchange parameters and stem volume**

Net photosynthetic rate was positively correlated with $g_s$ (R = 0.8548, P<0.005) and E (R = 0.7027, P<0.05), negatively correlated with $R_s$ (R = –0.7792, P<0.01) but not correlated with $C_i$ at the level of family means. The correlation between $P_N$ and stem volume was positive and significant (R = 0.7749, P<0.01), although the slow-growing family No. S29 had a higher $P_N$ than the three fast-growing families F24, F39 and F19 (Fig. 3).

**Correlations between stomatal characters and $CO_2$ exchange parameters**

The correlations between stomatal characters and $CO_2$ exchange parameters are shown in Fig. 5. Stomatal density was positively correlated with $g_s$ (R = 0.6754 ,

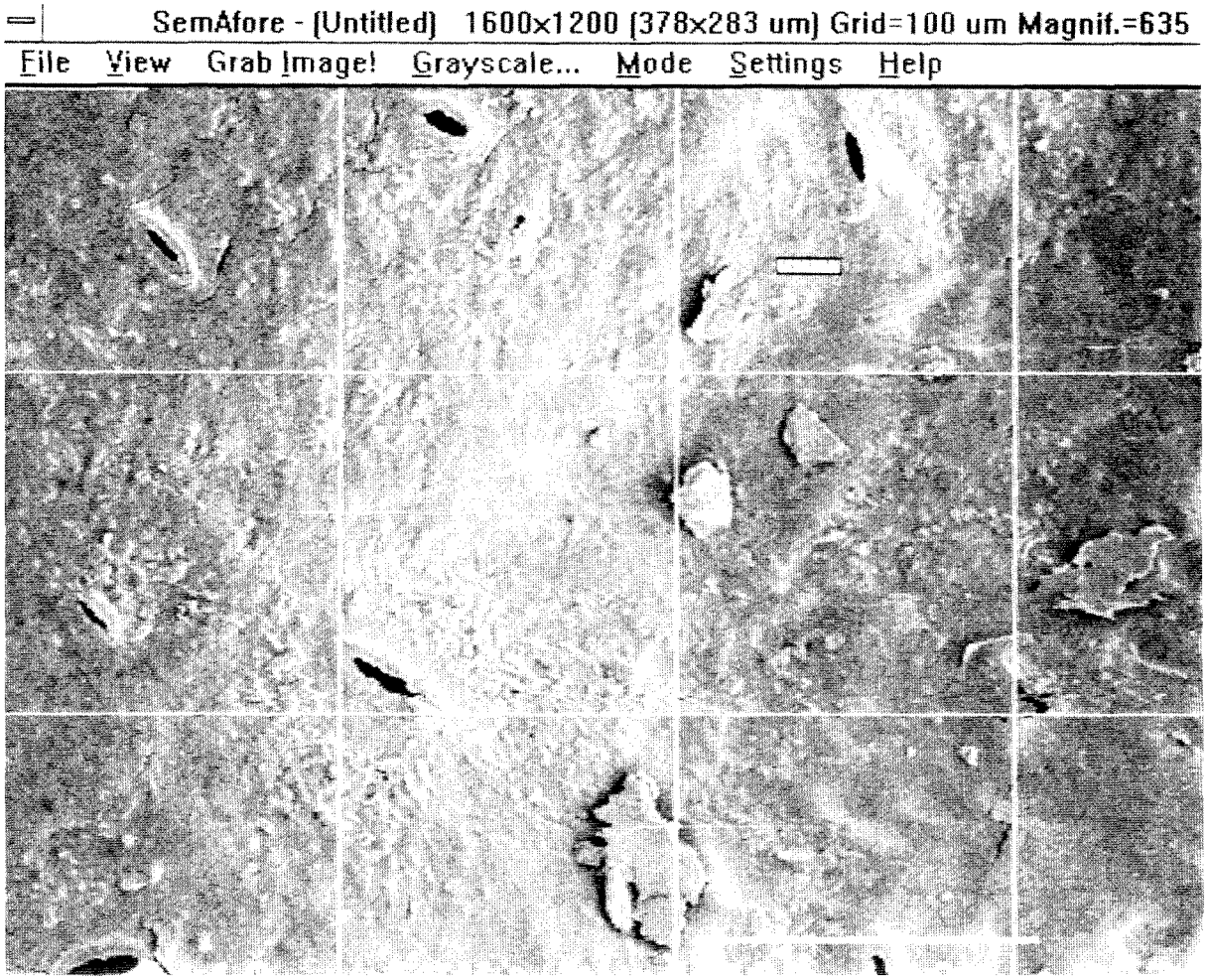


**Figure 4b** Leaf stomata of *Betula pendula* slow-growing family S 42

P<0.05) and $P_N$ (R = 0.8351, P<0.005), but not correlated with $R_s$. However, guard cell length was not correlated with $g_s$, $P_N$ or $R_s$. Nevertheless, the total guard cell length per unit leaf area was positively correlated with $g_s$ (R = 0.7712, P<0.01) and $P_N$ (R = 0.8443, P<0.005) and negatively correlated with $R_s$ (R = –0.6325, P<0.05).

## DISCUSSION

We found significant differences in $P_N$ among families and between fast- and slow-growing family groups as we did in our previous study (WANG *et al.* 1995) in concordance with other studies (LEDIG & CLARK 1977, MEBRAHTU & HANOVER 1991). However, the differences in this study were more significant and the genetic variance components were higher than in our previous study. The enhanced differences can probably be attributed to the high genetic uniformity of the families resulting from crosses between selfed individuals compared to the lower uniformity of normal half- and full-sib families.

Comparisons of the light response curves among the families confirmed the variation in $P_N$ and also demonstrated the differences in $P_N$ over the whole range of PAR. We found that $P_N$ started to positively respond when PAR reached about 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and the relative differences in $P_N$ among the families were about constant when PAR was higher than 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The families with high $P_N$ also had a high dark respiration rate in this study. The comparisons of $P_N$ among families by $P_N$ light response curves are informative, but the work involved will normally lead to considerable reduction of sample size or a much longer measuring time, both of which compromises can contribute to errors in the measurements.

In many studies photosynthetic capacity (PSC), the maximum rate of net photosynthesis under natural conditions of atmospheric $CO_2$ content and optimal conditions with respect to all other external factors, is used to characterize certain physiological types of plants as well as plant species, ecotypes and breeding materials (LARCHER 1975). In the present study net pho-

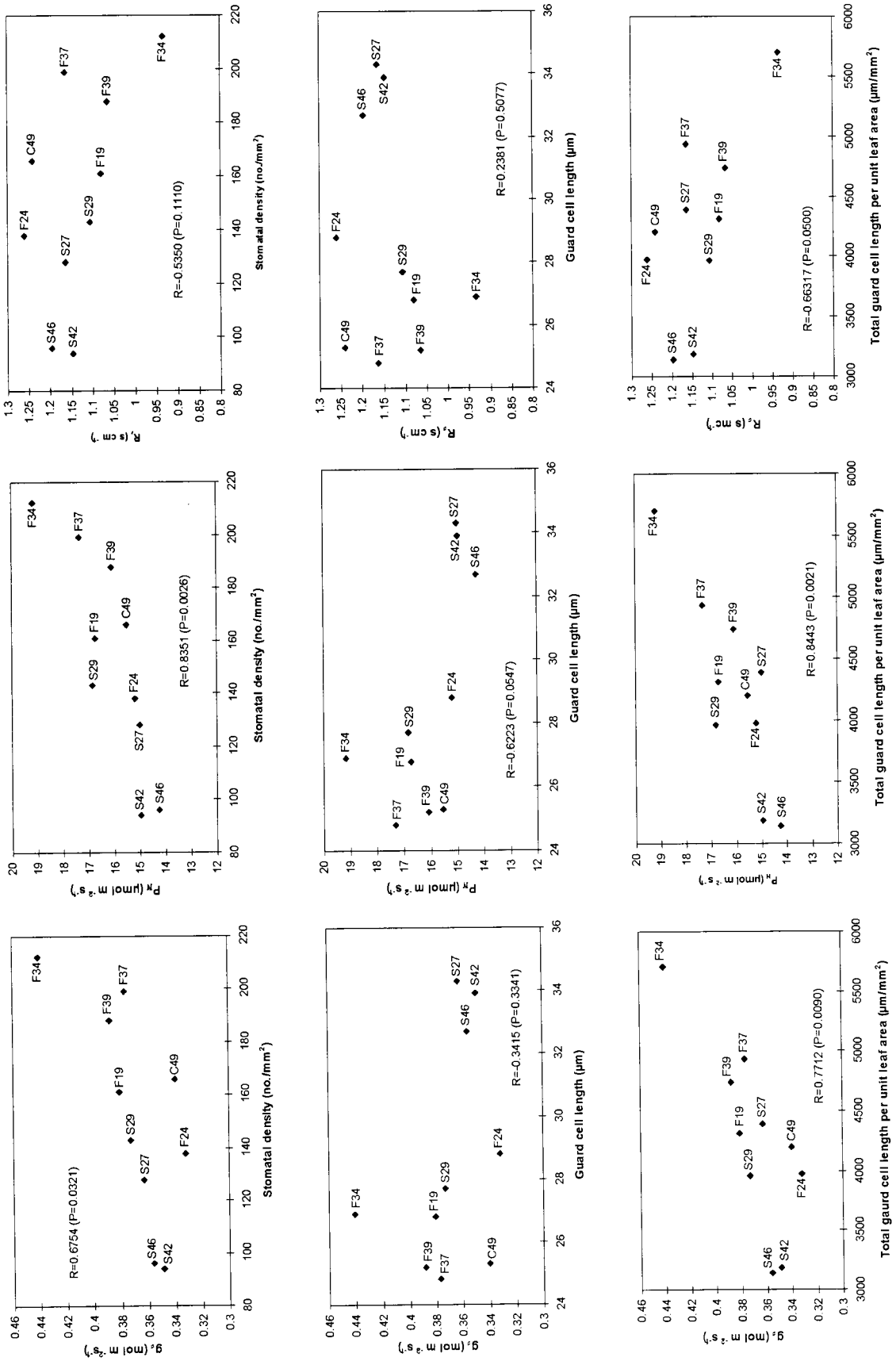


Figure 5 Correlations between stomatal characters and $CO_2$ exchange parameters

tosynthesis ($P_N$), observed after the correction by modeling the environmental conditions, can be very close to photosynthetic capacity. The modeling, however, was based on the real environmental conditions during the measurement rather than on optimal conditions for maximum rate of net photosynthesis. Thus $P_N$ was used for the comparisons instead of observing photosynthetic capacity.

In this study we also found that stomatal conductance ($g_s$) differed significantly among families, and correlated positively with $P_N$, which can be explained by a high $P_N$ requiring a high $g_s$ to secure an sufficient $CO_2$ supply for $P_N$. However, high $P_N$ values are associated with high water losses demonstrated by the positive correlation between $P_N$ and transpiration.

SIWECKI and KOZLOWSKI (1973) suggested that the resistance offered by stomata to $CO_2$ uptake by leaves often provides a major limitation for photosynthesis. Therefore, variations in guard cell length and stomatal density, or control of stomatal aperture may account for differences in stomatal resistance and hence in photosynthesis. In our study, significant differences in stomatal characters among families, and positive relationships between stomatal density or the total guard cell length per unit leaf area on the one hand and $g_s$ or $P_N$ on the other explained the physical basis of the families with high $g_s$ and hence high $P_N$. The wider the passage for carrying on $CO_2$ exchange, the higher the efficiency of $g_s$ and $P_N$. Unfortunately, we did not observe differences in the sensitivity of stomatal control among families.

Variations in stomatal characters and in some important $CO_2$ exchange parameters among families and groups appear to be under strong genetic control. This can partly explain the genetic and physiological reasons for superior yield in selected *Betula pendula* families. The access to hybrids crossed between selfed parents in this study has eliminated much of the disturbing genetic variation within families, thus giving us a sharper focus. The next step is to look for the molecular basis of fast growth. We conclude that fast-growing families generally have a higher stomatal density or higher total guard cell length per unit leaf area, higher stomatal conductance or lower $CO_2$ resistance and higher net photosynthetic rate, as well as a higher transpiration. These results also indicate the possibility of selecting and breeding for high yield at an early plant stage using $CO_2$ exchange parameters.

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