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Original article

Photosynthesis, leaf area and productivity of 5 poplar clones during their establishment year

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Summary — The stem volume and biomass (stem + branches) production, net photosynthesis of mature leaves and leaf area production of 5 poplar *(Populus)* clones, *Populus trichocarpa* x *deltoides* (Raspalje and Beaupré), *Populus* x *euramericana* (Robusta) and *P trichocarpa* (Columbia River and Fritzi Pauley), were studied during the first year of growth in an experimental high density plantation (15 600 plants ha^{-1}). Significant differences were found in volume production, woody biomass production, total leaf area and net photosynthesis. Above-ground biomass production was 3.5 times higher in Raspalje than in Robusta. The best performing clones (Raspalje, Beaupré) were those with large leaves, high leaf area index and high photosynthetic rates. A positive relationship between leaf photosynthetic capacity and above-ground biomass production was also noted for 4 of the 5 clones. The euramerican clone Robusta was an exception, showing high photosynthetic rates, but low biomass production. This discrepancy was mainly due to the lower leaf area of this clone, and possibly also due to a larger carbon allocation to below-ground biomass (Barigah, 1991). The root/shoot ratios at the end of the first season in the clones Raspalje and Robusta were 1.23 and 1.79, respectively.

net photosynthesis / leaf area / biomass production / *Populus*

Résumé — Photosynthèse, surface foliaire et productivité de 5 clones de peuplier dans leur première année. *Des plants issus de boutures de 5 clones de peuplier (*Populus trichocarpa *x* deltoides *(Raspalje et Beaupré),* P *x* euramericana *(Robusta) et* P trichocarpa *(Columbia River et Fritzi Pauley) ont été cultivés en peuplement dense (15 600 tiges* ha^{-1}*). Des mesures d'assimilation de* CO_2 *et de croissance (surface foliaire, volume de tiges, biomasse aérienne) ont été réalisées sur les jeunes plants. L'accumulation de biomasse du clone le plus performant (Raspalje) représentait 3,5 fois celle observée dans le clone le moins performant (Robusta). Les clones les plus performants (Raspalje, Beaupré) étaient également caractérisés par une surface foliaire importante et une assimilation nette foliaire élevée. Les différences de surface foliaire entre clones étaient liées à des différences de surface individuelle des feuilles et non au nombre de feuilles par arbre, qui était quasi constant. La biomasse aérienne était posi-*

tivement corrélée à la capacité photosynthétique foliaire pour 4 clones. Cependant le clone Robusta, de capacité de production faible, présentait une photosynthèse foliaire élevée. Cette faible production de biomasse aérienne chez Robusta était due à un faible développement foliaire et probablement aussi à un investissement en biomasse racinaire important (Barigah, 1991) ; le rapport de la biomasse racinaire à la biomasse aérienne était respectivement de 1,23 et de 1,79 pour les clones Raspalje et Robusta.

***photosynthèse foliaire / surface foliaire / production de biomasse /* Populus**

INTRODUCTION

Plant productivity depends on the interaction of light intercepting the leaf area of a plant and the intensity of the CO_2 assimilation process taking place in those leaves. The production of forest stands has been shown to be strongly correlated with total annual intercepted irradiance (Linder, 1984; Beadle and Long, 1985). Differences in the amount of leaf area displayed or in the intensity of the photosynthetic rate will result in different biomass productivity rates.

Photosynthetic capacity is known to vary widely among tree species, usually being higher in deciduous than in coniferous trees (Ceulemans and Saugier, 1991). In several tree species, intensive selection for increased biomass productivity has resulted in hybrids demonstrating heterosis for photosynthetic performance (Isebrands *et al,* 1988). Moreover, a positive correlation between photosynthetic capacity and biomass productivity has already been demonstrated for poplar hybrids (Ceulemans and Impens, 1983; Michael *et al,* 1990), larch hybrids (Matyssek and Schulze, 1987) and different provenances of loblolly pine (Boltz *et al,* 1986).

However, in many other cases, net photosynthesis rate measurements have been found to be poorly correlated with growth rate and productivity, such as in the case of *Populus grandidentata*, *P tremuloides* and *P smithii* (Okafo and Hanover, 1978; Reighard and Hanover, 1990). These conflicting results are due to the difficulty of measuring the gas exchange rate on comparable leaves in different genotypes, to phenological and physiological changes during the growing season, and to the distribution of photosynthates within the tree. For example, some poplar clones retain green leaves late in the fall with a measurable photosynthetic production even after frosts, thus contributing significantly to a late season stem diameter increment (Nelson *et al,* 1982) and root growth (Isebrands and Nelson, 1983).

In addition to photosynthetic rate, leaf area is also a very important determinant of biomass productivity. Comparing different spruce *(Picea abies)* provenances Gross and Hettesheimer (1983) found a negative correlation between leaf area and both biomass production of the trees and CO_2 assimilation rate. The relationship between biomass productivity and its determining factors may thus be complicated. Nevertheless, variability in plant genotypes according to plant branchiness and leaf distribution, position and orientation within the crown could strongly influence the efficiency of conversion of solar energy into biomass production (Isebrands and Nelson, 1982; Isebrands and Michael, 1986). However, direct linear relationships between biomass production and solar radiation intercepted by the foliage have been demonstrated in agricultural crops (Monteith, 1981) as well as in forest stands (Linder, 1984; Leverenz and Hinckley, 1990). Although this simple relationship appears robust in young plantations, its general and empirical approach have been criticized (Byrne *et al,* 1986; Agren *et al,* 1991).

In this study, photosynthetic capacity, leaf area development, and biomass production rates of different kinds of poplar *(Populus)* clones were compared during their first year of growth.

MATERIALS AND METHODS

Five poplar clones were used: 2 fast-growing and high-producing interamerican *P trichocarpa* x *P deltoides* hybrid clones (Raspalje and Beaupré); 2 native American clones *P trichocarpa* (Columbia River and Fritzi Pauley); and 1 *Populus* x *euramericana* clone (Robusta), which is often referred to as the reference clone. The latter is the result of a spontaneous hybridization between *P deltoides* and a European *P nigra*, presumably the poplar clone Italica. The origin, sex, parentage and provenances (table I) of these clones have previously been described (Ceulemans and Impens, 1983; Ceulemans, 1990).

Hardwood cuttings of each of the 5 clones were planted on 8 April, 1987 in Orsay (48°50'N, 2°20'E) near Paris, France, in monoclonal plots of 4 x 4 m on a 0.8 x 0.8 m planting pattern (*ie* a tree density of 1.56 plants per m^2). All plots were irrigated and fertilized. During the first growing season 4 trees per clone were monitored weekly for detailed measurements (height, diameter, leaf dimensions, number of leaves, photosynthesis, stem height and diameter at 22 cm above the ground). Measurements of young stem diameter at 22 cm above the ground was found to be a good compromise between the need for a measurement of the diameter close to the ground and the necessity to eliminate stem distorsion caused by the connection of the roots. These 4 trees were chosen from the 9 interior trees and had one border row around them. Stem volume index was calculated from height *(H)* and diameter *(D)* measurements as D^2H. To estimate total leaf area per tree (main stem), 80 leaves of surrounding trees were harvested at different heights to measure their leaf area, using a ΔT leaf area meter (Delta-T Devices, Burwell, Cambridge, UK), and their dimensions (length and width). The allometric relationship between leaf dimensions and leaf area (table II) was then applied to monitor leaf area development of the 4 trees per clone. At the end of the first growing season, all trees including the border ones were harvested, because no border effect was found between the plants in the first year for height or for volume index (Van Hecke *et al*, unpublished data). Leaf biomass and leaf area index *(LAI)* were estimated using leaf mass per area data collected during the growing season. Wood volume (stems and branches) was measured by immersion in water, and wood biomass was measured at harvest after oven-drying at

Table I. List of the clonal poplar materials used with clonal and scientific species name, parentage and hybrid combination, sex, section and place of origin.

Clonal names	*Parentage*	*Sex*	*Section of parents*	*Origin of parents*
Beaupré	*P trichocarpa* x *P deltoides*	F	Tacamahaca Aigeiros	Washington Iowa x Missouri
Raspalje	*P trichocarpa* x *P deltoides*	F	Tacamahaca Aigeiros	Washington Iowa x Missouri
Columbia River	*P trichocarpa*	M	Tacamahaca	Oregon
Fritzi Pauley	*P trichocarpa*	F	Tacamahaca	Washington
Robusta	*P deltoides* x *P nigra*	M	Aigeiros Aigeiros	Iowa x Missouri Europe

Abbreviations: F = female, M = male

Table II. List of the allometric relationships between leaf dimensions and leaf area used to monitor leaf area development of the trees.

Clonal name	*Regression equation*
Beaupré	$0.606\ L \bullet w - 0.602$
Raspalje	$0.625\ L \bullet w - 1.732$
Robusta	$0.674\ L \bullet w - 0.288$
Columbia River	$0.648\ L \bullet w - 0.973$
Fritzi Pauley	$0.630\ L \bullet w - 0.791$

L and w are respectively the length and the width of the leaf blade.

80°C for 15 d. Since the dimensions of the plots were rather small, these biomass values were only used to compare the performance of the various clones and were not representative of the biomass production of real stands.

Leaf net photosynthetic rates and incident photosynthetic photon flux density (PPFD) were measured in the field using an ADC Parkinson leaf chamber connected to a portable CO_2 analyzer (ADC Company Ltd, Hoddedson, UK) in an open system arrangement. The leaf chamber was supplied with an air mixture of a known CO_2 concentration from a compressed air cylinder, and the CO_2 drop in the chamber was 79 ± 21 vpm. To avoid differences in photosynthetic rates due to the variation of the CO_2 concentration, which ranged from 360 to 385 vpm in the air contained in different gas cylinders, net photosynthesis at 350 vpm (A_{350}) was calculated using the formula:

$$A_{350} = A(350 - \Gamma) / (C - \Gamma)$$

This formula assumes a linear relationship between net photosynthesis *(A)* and CO_2 concentration *(C)* (Gaastra, 1959), and a constant CO_2 compensation point (Γ). This relationship was established in the laboratory at 22°C and is rather insensitive to variations in Γ, since a difference of 20 vpm in Γ only caused a 2% variation in A_{350} using Γ equal to 60 vpm.

Only fully expanded leaves having maximum photosynthetic rates (Barigah, 1991) were used for gas exchange measurements and all experiments were performed on single attached leaves. Measurements were made on several sunny days throughout the growing season. The data were plotted in a CO_2 assimilation *(A) versus* PPFD graph and were fitted using rectangular hyperbola equation ($A = \{\alpha \bullet \text{PPFD} \bullet A_{max} / (\alpha \bullet \text{PPFD} + A_{max})\}$; where α is the photochemical efficiency, and A_{max} is the asymptotic value of A at saturating irradiance. Leaf photosynthetic capacity was defined here as the PPFD-saturated net photosynthesis at an atmospheric CO_2 concentration of 350 vpm. Differences among clones in photosynthetic capacity were assessed using a *t*-test after comparing confidence intervals at the 95% level.

RESULTS

Growth patterns

The total tree height after the first growing season ranged from 1.8 m for clone Robusta to 3.5 m for clone Beaupré (table III). The 2 *P trichocarpa* x *P deltoides* clones (Beaupré and Raspajle) were superior to the other clones with regard to tree height, while clones Columbia River, Fritzi Pauley and Robusta had similar heights around 2.0 m. Stem volume index values (fig 1) increased for all clones from the beginning of the growing season until mid-October (day 288), except for clone Robusta (Barigah, 1991) which ended extension growth early in September (day 259). At the end of the first growing season, the ranking of the clones in terms of stem volume index was in agreement with that observed in height growth except for clones Columbia River and Fritzi Pauley.

Clone Beaupré had the highest wood volume production (732 cm^3, table III), but the highest biomass (stem + branches) was produced at the end of the first season by clone Raspalje, a branchy clone (table III). The fasted growing clone Raspalje produced 3.5 times more woody biomass than the slowest growing clone Robusta.

Table III. Leaf photosynthetic parameters, leaf area and productivity characteristics of 5 poplar clones under field conditions.

	BPR *	*RAS* *	*ROB* *	*COR* *	*FRP* *
Photosynthetic characteristics					
Maximum photosynthesis (µmol m^{-2} s^{-1}) at 350 vpm	27.2^a	25.8^a	25.0^a	17.5^b	19.2^b
Maximum photosynthetic capacity (µmol s^{-1} $leaf^{-1}$)	0.69^a	0.52^b	0.17^d	0.19^c	0.22^c
Leaf characteristics					
Average leaf area (cm^2 $leaf^{-1}$)	254^a	201^b	66^d	107^c	112^c
No of leaves (main stem only)	54^b	57^b	64^a	54^b	48^c
Leaf area per tree (m^2 $tree^{-1}$) (main stem only)	1.26^a	1.23^a	0.42^d	0.68^b	0.57^c
Leaf area index (m^2 m^{-2})					
Stem leaves	1.97^a	1.92^a	0.66^d	1.06^b	0.89^c
Branch leaves	0.78^b	1.03^a	0.16^d	0.64^c	0.60^c
Total	2.75^b	2.95^a	0.82^e	1.70^c	1.49^d
Productivity					
Height (m)	3.5^a	3.2^b	1.8^d	2.0^c	2.1^c
Actual woody volume (cm^3/tree) *(a)*	732^a	703^b	198^e	381^c	293^d
Stem volume index (HD^2) *(b)*	$1\,764^a$	$1\,675^b$	457^e	956^c	728^d
a/b	0.42	0.42	0.43	0.40	0.40
Biomass (g/tree)**					
Stem	242^a (63%)	233^b (57%)	62^e (56%)	135^c (63%)	114^d (57%)
Branches	36^b (9%)	50^a (12%)	9^d (8%)	20^c (9%)	20^c (10%)
Stem + branches	278^b (72%)	283^a (69%)	71^e (64%)	155^c (72%)	134^d (67%)
Leaves	107^b (28%)	125^a (31%)	40^e (36%)	61^c (28%)	67^c (33%)
Above-ground biomass	385^b	408^a	111^e	216^c	201^d
Above-ground biomass per area (g m^{-2})	601^b	637^a	173^e	338^c	315^d

* BPR = Beaupré; RAS = Raspalje; ROB = Robusta; COR = Columbia River; FRP = Fritzi Pauley; means within columns not followed by the same letter are significantly different ($p = 0.05$) using *t*-test). ** Numbers in parentheses correspond to the proportion of the plant part to the total above-ground biomass.

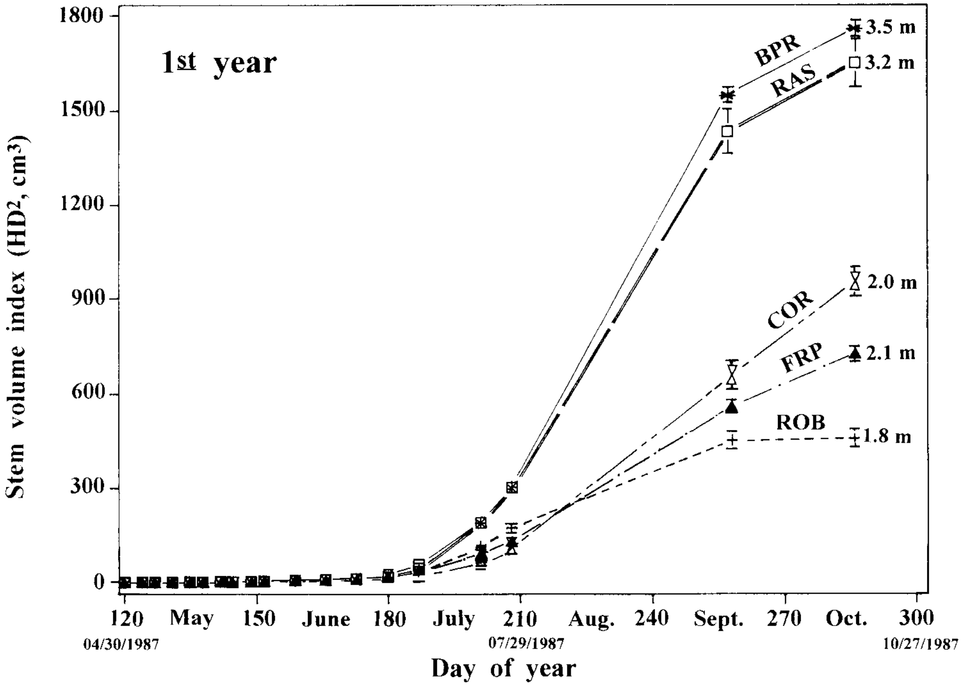

Fig 1. Development of stem volume (D^2H) of 5 poplar clones during their first growing season. Numbers on the right-hand side indicate the mean tree height (in m) at the end of the growing season. BPR = Beaupré (✳), RAS = Raspalje (□), COR = Columbia River (X), FRP = Fritzi Pauley (▲), ROB = Robusta (+).

The proportion of biomass allocation to the leaves was nearly the same for all clones, ranging from 28% of total biomass for clone Beaupré to 36% in clone Robusta (table III). The ratio stem volume index/actual wood volume almost constant (0.41) among genotypes, which confirms the relevance of using D^2H as an index of wood production.

Photosynthetic characteristics

The relationships between CO_2 assimilation rate *(A)* and PPFD did not show a very clear saturation level, even at PPFD values of 2 000 μmol m^{-2} s^{-1} (fig 2). However, since *A* increased only slightly between 1 300 and 2 000 μmol m^{-2} s^{-1}, the values recorded over this range were considered as the maximum net photosynthesis by taking mean value of individual photosynthesis rate of several leaves.

The highest values of photosynthetic capacity (defined as *A* at saturating PPFD and 350 vpm CO_2) were observed for clones Beaupré, Raspalje and Robusta (between 25.0 and 27.2 μmol m^{-2} s^{-1}). Significantly lower values of *A* were found in the 2 *P trichocarpa* clones, Columbia River and Fritzi Pauley (17.5 and 19.2 μmol m^{-2} s^{-1}, respectively). Differences among clones Beaupré, Raspalje and Robusta were not significant at the $p = 0.05$ level.

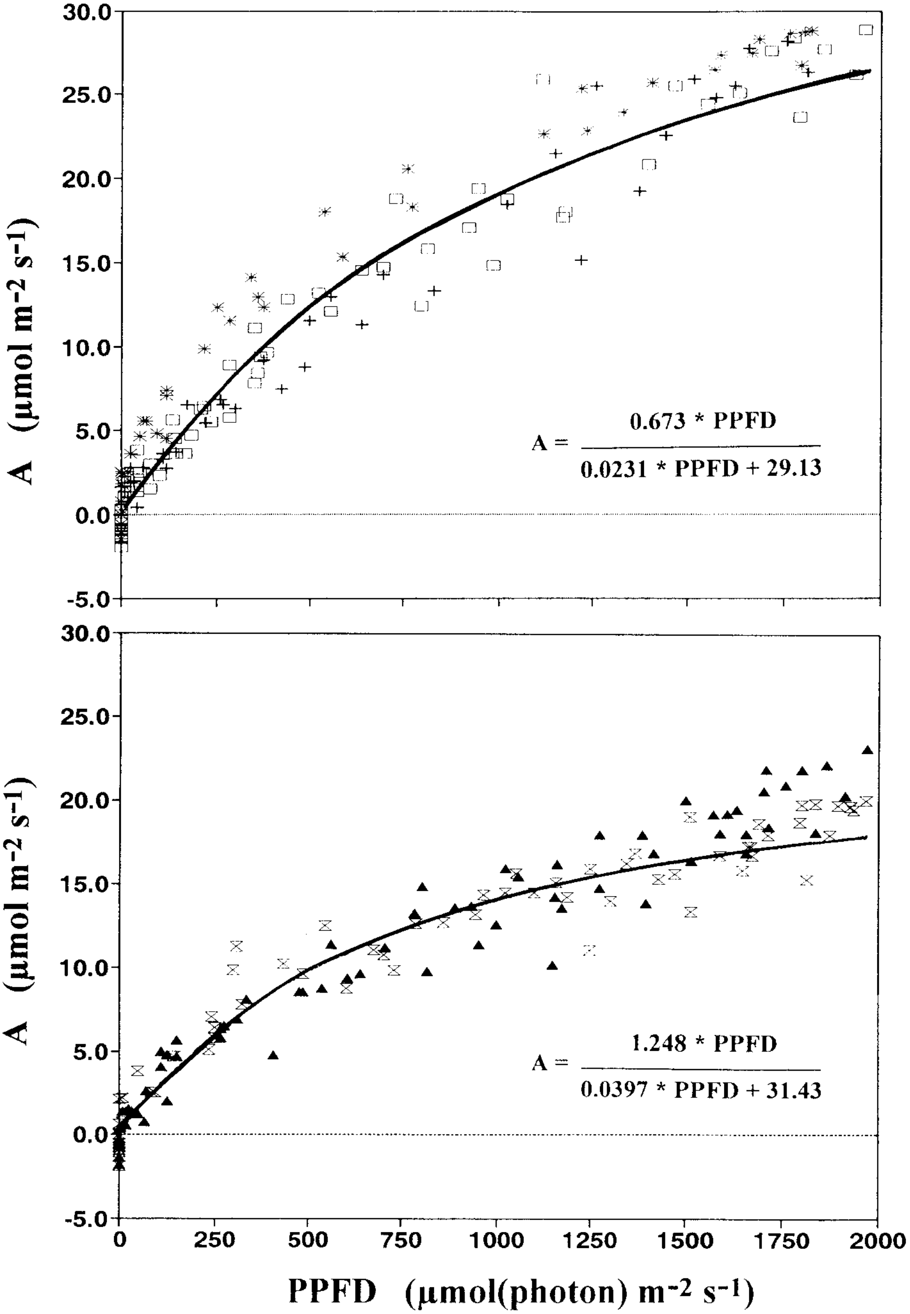

Fig 2. Relationships between CO_2 assimilation *(A)* and photosynthetic photon flux density (PPFD) for (top) 3 poplar clones (Beaupré (✳), Raspalje (□) and Robusta (+)) and (bottom) the Trichocarpa poplar clones (Columbia River (⧖) and Fritzi Pauley (▲)), measured under field conditions on clear, sunny days.

Leaf area characteristics

Clones Raspalje and Beaupré had the highest leaf area values per tree at the end of the growing season (table III); the lowest values were observed in Robusta and the values in Columbia River and Fritzi Pauley were intermediate. At mid-August of the first year *LAI* values were 2.75 and 2.95 in clones Beaupré and Raspalje, respectively, and only 0.8 for clone Robusta. Significant differences in the leaf area distribution over main stem and branches (table III) were observed for the studied clones.

The results (table III) showed that in all clones more than half of the total leaf area was produced on the main stem (the branch leaves were not numerous and were smaller than the main stem ones). However Barigah (1991) observed early in September 1989 that the branch leaf area was 3 times higher than the main stem leaf area in clone Raspalje and 1.4 times in clone Robusta.

Clone Robusta had the largest number of leaves on the main stem after the first growing season (64 leaves), and clone Fritzi Pauley the smallest (48 leaves), but clone Robusta had the smallest average individual leaf area with 66 cm^2 *versus* 201 cm^2 for clone Raspalje and 254 cm^2 for clone Beaupré (table III).

DISCUSSION

In terms of woody biomass and stem volume productivity, the 2 *P trichocarpa* x *P deltoides* clones Beaupré and Raspalje, were clearly superior to the other 3 clones. The higher productivity of these 2 clones can be explained by both their significantly larger leaf area production (thus, higher *LAI*) and their higher photosynthetic performance. Indeed by ranking the different parameters reported in table III, the correlation between net photosynthesis, leaf area and biomass production becomes evident. The *P trichocarpa* clones, Columbia River and Fritzi Pauley, had the lowest photosynthetic rates as well as a low leaf area production (thus, low *LAI*), resulting in a low biomass productivity (fig 3, table III).

For 4 out of the 5 poplar clones the maximum net photosynthesis was significantly correlated with above-ground biomass production (fig 3). Net photosynthetic rate has often been reported not to be correlated with yield (Ledig, 1969; Gifford and Evans, 1981); the reasons for these weak correlations seems to be inadequate or varying nitrogen and water supply, lack of standardisation of photosynthetic measurements (*eg,* leaf age), plant density, and number of comparable replications. The high maximum net photosynthesis values of the *P trichocarpa* x *P deltoides* clones were of a comparable order of magnitude to those previously reported for similar poplar hybrids (Isebrands *et al,* 1988; Ceulemans, 1990), while the low photosynthetic performance of the 2 *P trichocarpa* clones (Columbia River and Fritzi Pauley) is also in agreement with previous observations (Ceulemans, 1990).

Clone Robusta was the only clone that combined a rather high photosynthetic rate (comparable to clones Beaupré and Raspalje) with a low volume and a low above-ground biomass production (fig 3). This can be mainly explained by its low leaf area production and low *LAI*, but also by the fact that the clone Robusta had a proportionally larger allocation to below-ground biomass. For example, at the end of the first growing season the root/shoot ratio was 1.23 for clone Raspalje and 1.79 for Robusta (Barigah, 1991). Similar observations (weak correlation between net photosynthetic rate and wood biomass productivity, and significant differences in root/shoot ratio) have already been made for the same clones (Impens, 1988) as well as for other poplar clones and species (Okafo and Hanover, 1978; Reighard and Hanover, 1990). The

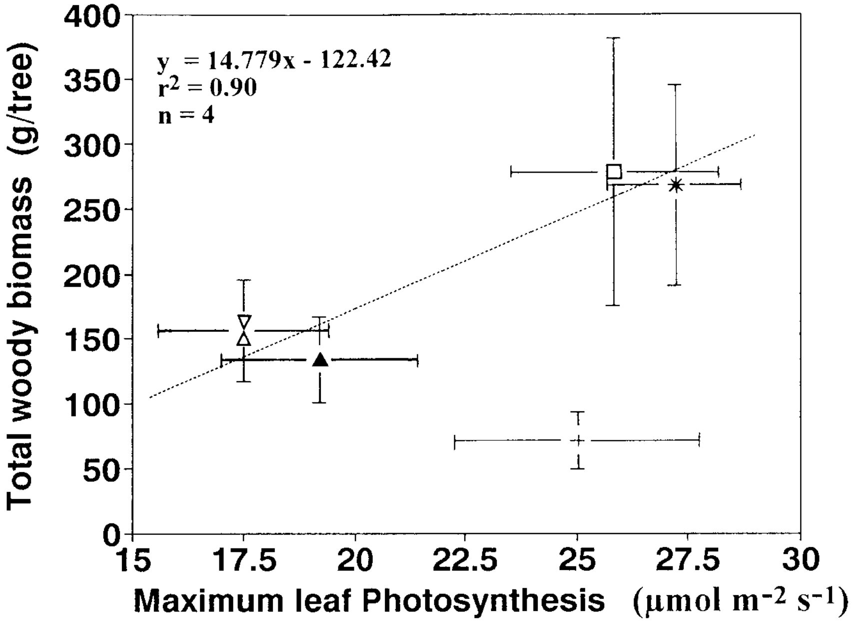

Fig 3. Relationship between total woody biomass per tree and maximum net photosynthesis. Mean values of minimum 15–25 trees per clone are shown. The linear regression has been calculated for the 4 clones (without Robusta). Beaupré (✳), Raspalje (□), Columbia River (⧖), Fritzi Pauley (▲) and Robusta (+).

ecological significance of the difference in the root/shoot ratio is still uncertain as there is very little knowledge about the specific roles root compounds play in tree survival, growth and development (Loescher *et al*, 1990). Cannell *et al* (1988) found that, compared to willow trees *(Salix viminalis)*, balsam poplar *(P trichocarpa)* stored much more biomass in their roots than above ground (the above-ground biomass and below-ground biomass were respectively 14 t ha^{-1} and 3 t ha^{-1} for the willow, and 8 t ha^{-1} and 4 t ha^{-1} for the poplar). Cannell *et al* (1988) stated that the abundance of biomass found in the roots of the balsam poplar was a clonal characteristic, but in fact this characteristic is also very common in the *Populus* genus (Isebrands, 1982; Reighard and Hanover, 1990) and in other genera like *Malus*, *Prunus*, *Acer* and *Pinus* (Heim *et al*, 1979; Kramer, 1986; Loescher *et al*, 1990). Furthermore, Blake and Raitanen (1981) and Afocel (1983) considered the first growth cycle for cuttings to be poorly productive due to greater biomass allocation to root establishment than to above-ground biomass structures.

As the high root/shoot ratio observed in clone Robusta was not directly reflected in its above-ground growth, the abundant reserves stored in the root system of Robusta might be the support for the high root respiration rate observed in this clone (Barigah, 1991) and/or for drought adaptation or resistance to diseases. However, these factors were not monitored in this study.

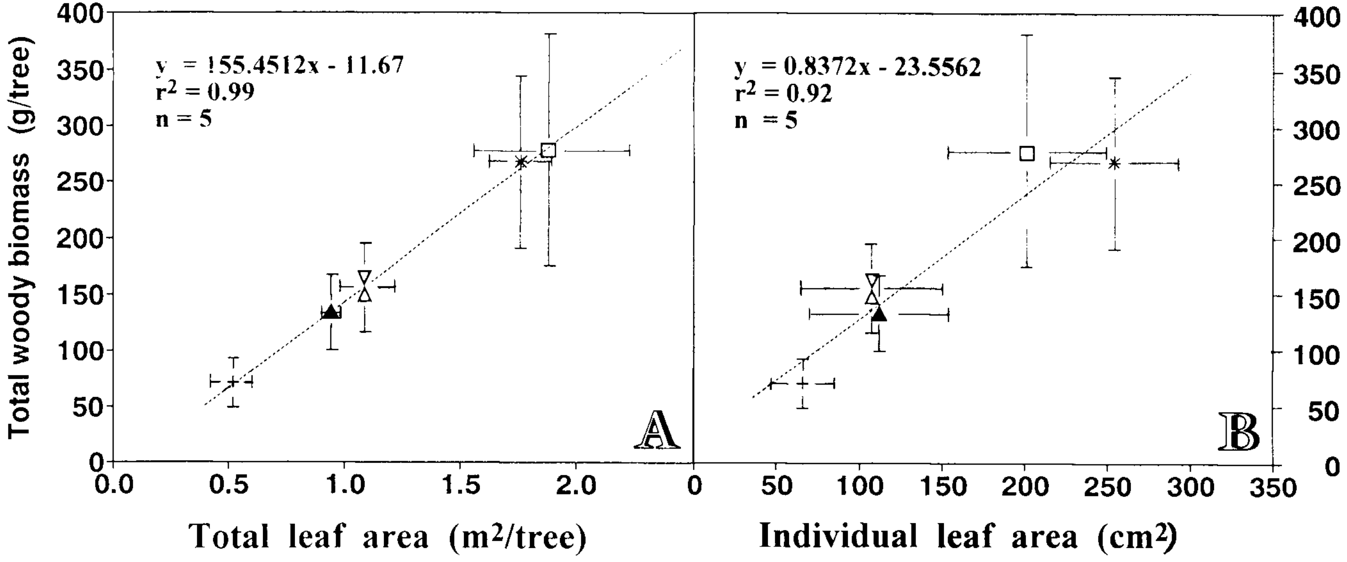

Fig 4. Relationships between total leaf area per tree **(A)** and mean individual leaf area **(B)** and total woody biomass per tree for the 5 poplar clones. For the total leaf area per tree **(A)** mean values of minimum 2–4 trees per clone are shown. For the individual leaf area **(B)** the mean values of the 5 largest leaves of minimum 15–25 trees per clone were used. Beaupré (✳), Raspalje (☐), Columbia River (☒), Fritzi Pauley (▲) and Robusta (+).

The best performing clones (Beaupré and Raspalje) seem to be those which not only develop the largest leaf area and have the largest *LAI*, but also those with the highest individual leaf size (fig 4). The high total biomass production of clone Raspalje might thus mainly be due to its large total and individual leaf area (Ridge *et al,* 1986). Clone Raspalje produced not only slightly more branches and leaves than clone Beaupré, but also a much higher leaf area per tree. However, individual leaf size of clone Beaupré was slightly larger than that of Raspalje (table III, fig 4). The larger number of branches in clone Raspalje seemed to result in a larger biomass production, although its main stem volume production was slightly inferior to that of clone Beaupré. It thus seems that poplar clones with a larger individual leaf area and a high number of leaves on their branches might have considerable advantages in developing a high total leaf area per tree early and rapidly during their first growing season, and consequently a high *LAI*.

A striking feature of the fast-growing *P trichocarpa* x *P deltoides* hybrids remains their large individual leaf size (fig 4B). Earlier experiments with a variety of these hybrids have already shown that stem volume and stem biomass production were more closely related to individual leaf size than to the number of leaves produced per tree (Ridge *et al,* 1986). The correlation between woody biomass and individual leaf size (fig 4B) might suggest that the inheritance of fast-growing, large leaves cause the observed increase in stem biomass (and stem volume) of the *P trichocarpa* x *P deltoides* hybrids. However, this relationship needs to be examined over a wide range of F_1, F_2 and backcross material so that the mechanisms associated with it can be understood.

The positive correlation between net photosynthesis and first year (above-ground) biomass production for 4 of the 5 study clones, as well as the extended leaf area duration of some clones due to late leaf senescence, guarantee high above-ground growth in poplar. A significant difference in leaf area duration between the clones Robusta (568 m^2 d m^{-2}) and Beaupré (927 m^2 d m^{-2}) during their second growing season has been reported previously (Nelson and Isebrands, 1983; Mau and Impens, 1989; Ceulemans *et al,* 1993).

In breeding and selection programmes for fast-growing and highly productive poplar clones, attention should be paid to a number of physiological, morphological and environmental factors (Magnussen, 1985; Ceulemans *et al,* 1987), to soil water regime and nutrient availability (Garbaye, 1979; Garbaye, 1980; Hinckley *et al,* 1990) as well as to the inheritance of late retention of green leaves in the fall with a measurable photosynthetic production even after frosts (Nelson *et al,* 1982).

In conclusion, we believe that high net photosynthetic rates, in combination with large leaf area production and duration, led to the high biomass production of fast-growing clones Beaupré and Raspalje during their establishment year.

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