EARLY SELECTION OF *EUCALYPTUS GRANDIS* CLONES IN CENTRAL BRAZIL

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BLAKE, T.J., BEVILACQUA, E. & SUITER FILHO, W. 1995. Early selection of *Eucalyptus grandis* clones in central Brazil. Genetic variation in productivity of nine *Eucalyptus grandis* clones was compared after 3 and 15 months of growth in the field in Minas Gerais, Brazil. Clones that were larger (i.e. heavier) after 3 months were still larger after 15 months of growth and had lower stomatal conductances. After 15 months, larger cultivars had a greater allocation of biomass towards stemwood production relative to leaves. Other physiological processes and leaf characteristics (e.g. net photosynthesis, average leaf area, stomatal size and density) were not related to productivity when analyzed by rank correlations. The results suggest that the greater productivity of some clones was associated with more efficient stemwood production, the ability to control relative leaf development and a lower stomatal conductance at an early age.

Keywords: *Eucalyptus grandis* - early selection - photosynthesis - stomatal conductance - water relations - productivity

BLAKE, T.J., BEVILACQUA, E. & SUITER FILHO, W. 1995. Pemilihan klon-klon *Eucalyptus grandis* di bahagian tengah Brazil. Variasi genetik di dalam produktiviti sembilan klon *Eucalyptus grandis* telah dibuat perbandingan selepas 3 dan 15 bulan pertumbuhannya di ladang Minas Gerais, Brazil. Klon yang lebih besar (iaitu lebih berat) selepas tiga bulan masih lagi lebih besar selepas 15 bulan pertumbuhannya dan mempunyai konduktans stomata yang lebih rendah. Selepas 15 bulan, kultivar-kultivar yang lebih besar mendapat peruntukan biojisim secara relatif lebih banyak bagi pengeluaran kayu batang berbanding dengan daun. Proses-proses fisiologi lain dan sifat-sifat daun (contohnya fotosintesis, purata kawasan daun, saiz dan ketumpatan stomata) adalah tidak berkaitan dengan produktiviti setelah dibuat analisis korelasi kesuburan. Keputusan kajian ini menunjukkan bahawa kelebihan produktiviti bagi sesetengah klon adalah berkaitan dengan pengeluaran kayu batang yang lebih efisien, keupayaan untuk mengawal pembesaran daun relatif dan konduktans stomata yang lebih rendah di peringkat awal.

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Introduction

Rooted cuttings offer many silvicultural advantages and are often preferred to seedlings as a method of regenerating fast-growing tree species (Klomp & Hong 1985). Cloning programmes produce many new cultivars which show contrasting growth rates when planted together on the same site (Blake & Suiter Filho 1988, Tschaplinski & Blake 1989). With the larger number of new clones, however, there is a need to identify and develop criteria for the early selection of superior genotypes.

There are presently no accepted criteria for the selection of superior genotypes at an early age. Usually the largest (tallest) plants are selected, or more often, smaller, diseased or deformed varieties are culled. Attempts have been made to correlate an assortment of morphological, physiological and enzymatic characteristics with growth. Many photosynthetic characteristics (e.g. photosynthetic efficiency and capacity, net assimilation rate, etc.) have been tested as early selection criteria. Net photosynthesis has been correlated with shoot weight growth in *Populus* spp. under more controlled conditions in a nursery (Ceulemans *et al.* 1987, Tschaplinski & Blake 1989). However, correlations between photosynthetic capacity and harvest yields are often poor (Ledig 1969, McDonald 1984).

A number of factors other than photosynthesis can influence growth and yield. In particular, the duration of the growing season, the distribution of photosynthate within the tree (Luukkanen & Kozlowski 1972) and variation in stomatal size, frequency and morphology (Pallardy & Kozlowski 1979a, Blake *et al.* 1984) are all reported as determinants of productivity.

In this study, an array of physiological and morphological traits were studied on nine *Eucalyptus grandis* clones, 3 and 15 months after they were planted in the field. The aim was to determine which plant characteristics could be correlated with growth differences among clones and to determine which physiological parameters could be used for the selection of superior genotypes at an early age.

Materials and methods

Plant material

Nine *E. grandis* W. Hill ex Maiden clones were outplanted in a clonal bank 30 km east of Bom Despacho, Minas Gerais, Brazil in late June 1988. The cuttings were produced using current technology of the Cia. Agrícola E Florestal Santa Bárbara and were four months of age when they were planted at 3.0 × 1.5 m spacing. The clones were selected from closely related, high-yielding seedlings designated as 'plus trees' based on their field performance. Cuttings were rooted from stump sprouts of coppiced trees. The original seed source of the *E. grandis* material was from Atherton, Queensland, Australia. Propagation methods, soil, site and other conditions of the trials are as described previously (Blake & Suiter Filho 1988).

The nine clones measured were: 36502 (A), 25186 (B), 26746 (C), 37633 (D), 26894 (E), 26693 (F), 28684 (G), 25151 (H), and 37779 (I). The alphabetical ranking of cultivars (A to I) was based on the average total above-ground dry weight per tree measured 15 months after planting. Physiological and growth characteristics were measured in the field during the dry, rainless season in September 1988 and 1989, 3 and 15 months after planting respectively.

Morphological characteristics

Ten plants per clone were destructively sampled after 3 and 15 months of growth in the field for biomass determination. Stems, branches, leaves and roots were separated and biomass measured by weighing after drying at 70 °C for 48 h. Due to the size of the clones at 15 months, only above-ground components of the trees were sampled during the second harvest period. Total biomass was determined by the summation of the component parts.

Estimates of average leaf area, in terms of both oven-dried weight and surface area, and specific leaf area (SLA, leaf area per unit leaf weight) were obtained using independent samples collected from 2 trees per clone and by sampling groups of 10 leaves per branch, 2 branches from both the upper and lower crown. Surface area of leaf samples was determined using a LI-3000A Portable Area Meter (Li-Cor Inc., Lincoln, NE). Total leaf area per tree (LA) was calculated as the product of total leaf dry weight and the average SLA for each clone.

Physiological characteristics

Trees averaged 4.5 m in height and there were no obvious height differences among clones. Prior study had shown that photosynthesis in leaves from the middle to lower crown correlated better with growth differences than upper leaves (Tschaplinski & Blake 1989). Thus, leaves selected for gas-exchange measurements were sampled at 2 m above ground level, i.e. slightly below half tree height. After it was established that gas-exchange parameters measured immediately after detachment were similar to values in the intact plant, measurements were made on the fourth and fifth fully-expanded leaves from detached branches located in the middle crown. Samples were moved to an open area and measurements were made under full sunlight.

Measurements of stomatal conductance (C_s), H_2O transpiration (E_t) and net CO_2 assimilation (A) of leaves were collected using a LI-6200 Portable Photosynthesis System (Li-Cor Inc., Lincoln, NE), and xylem pressure potentials (ψ_x) were measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR).

Due to the diurnal variation in physiological processes, gas-exchange parameters for each plant had to be measured within a short, 2-h 'window'. Since it is only possible to measure about 40 - 45 samples in a 2-h period with the LI-6200, prior experience (Blake & Suiter Filho 1988, Blake *et al.* 1988) suggested that a smaller number of replicates on a larger number of clones would yield preferable results. A total of four trees per clone were measured five times over a two-day period, three times on the first day and twice on the second day. Daily CO_2 uptake (ΣA) and water loss (ΣE_l) were estimated by integrating diurnal trends for each plant. Environmental and gas exchange parameters were logged simultaneously on the LI-6200.

The environmental conditions were as follows: photosynthetically active radiation (PAR) was in the range of 300 to 2000 μmol m^{-2} s^{-1}; air temperature (t_a) varied from 29 to 42 °C; and relative humidity (RH) fluctuated from 17 to 47%. During any one measurement window, t_a varied no more than ± 2 °C, RH ± 4%, and PAR ± 150 μmol m^{-2} s^{-1}.

During the time of both measurement periods, it had not rained at the study area for the preceding 100 days. Soil water potentials were less the -1.5 MPa.

Stomatal characteristics

Stomatal density and length were estimated for each clone by sampling leaves after 15 months of field growth. Leaf impressions were made by applying flexible Collodium (Fisher Scientific Ltd.) immediately adjacent to and on either side of the leaf midrib on the abaxial (lower) surface of the leaf. Stomata are located exclusively on the abaxial surface of *E. grandis* leaves. For sampling, two trees per clone were randomly selected, from which two branches from the middle crown were chosen. Four leaf impressions were obtained from each of two fully expanded leaves selected from the middle of each branch for a total of 32 impressions per clone.

Impressions were viewed under a 160X microscope. Guard cell length, measured with an ocular micrometer, was used as a measure of stomatal length. Stomatal density was estimated by recording the number of stomata within the viewing area from four random-located regions within each impression. A total of 128 measurements of stomatal length and density were made per clone. Techniques for measuring stomatal dimensions are in Blake (1980) and Blake *et al.* (1984).

Statistical analysis

Clonal comparisons of biomass components were analyzed using a conventional one-way analysis of variance (ANOVA), and gas-exchange characteristics of clones were compared using a blocked analysis of covariance. Observations were blocked for each sampling data using environmental parameters (i.e. t_a, PAR, RH) as covariates. Leaf and stomatal characteristics were analyzed using a nested, hierarchical design and Duncan's multiple comparison test was used to calculate significant differences between clonal means. Allometric relationships between biomass components within trees were studied by regression analysis.

Clones were ranked from 1 (highest) to 9 (lowest) for each of the measured parameters, 3 and 15 months after planting, and the rankings were compared using Spearman's Rank Correlation Coefficient.

Results

Biomass and its partitioning

Stem and total above-ground dry weights of the smallest clone (I) were 42% and 57% respectively, of those of the largest clone (A) (Table 1). Total above-ground dry weight, leaf dry weight and leaf area after 15 months of growth were less variable than stem dry weight and specific leaf area.

Table 1. Average biomass components and leaf area per tree of nine *Eucalyptus grandis* clones after 15 months of field growth. Clones were ranked in order of total above-ground productivity. Means with the same letters in each column do not differ significantly when compared using Duncan's multiple comparison test ($p<0.05$, $n=10$).

Clone	Above-ground dry weight (kg) Total	Stem	Branch	Leaf	Total leaf area (m^2)	NAR ($g\ m^{-2}$)	Biomass ranking at 3 months
A	4.72a	1.98bc	1.21a	1.53a	10.80ab	436.8b	3
B	4.54ab	2.75a	0.89bc	0.90c	8.50b	578.8a	4
C	4.16ab	2.12b	0.87bc	1.18bc	10.11ab	413.6b	1
D	4.03ab	1.66bc	1.18a	1.18bc	12.08a	345.4cd	7
E	3.93ab	1.82bc	1.03abc	1.09bc	8.74b	460.9b	6
F	3.90ab	1.68bc	1.10ab	1.12bc	8.70b	450.1b	5
G	3.72b	1.55c	0.87bc	1.30ab	10.80ab	339.1d	9
H	3.55b	1.58bc	0.78c	1.19bc	8.45b	430.0b	2
I	2.68c	0.83d	0.78c	1.07bc	8.56b	314.9d	8

There was a positive correlation between clonal rankings in productivity after 3 and 15 months in the field. Clones that were larger (i.e. heavier) at 3 months were also larger after 15 months. Clones A and C, which were two of the three heaviest clones at 3 months, ranked first and third in total plant dry weight after 15 months (Table 1). By contrast, clones G and I, which ranked as the two smallest clones at 3 months, were still well below average in most dry weight parameters at 15 months (Table 1).

The more productive clones allocated a greater percentage of biomass to stem dry weight relative to leaves. Their lower relative leafiness is shown by the negative correlation between stemwood biomass and leaf area ratio (LAR, i.e. the ratio of leaf area/total above-ground biomass) (Figure 1).

The strong, linear relationship ($r^2 > 0.90$) between LA and stem dry weight is shown for six representative clones in Figure 2. Clone B, the second heaviest, had the steepest slope and higher rates of stemwood dry weight per unit leaf area. The least productive clone in terms of total dry weight (I) had the lowest stem dry weight and slope.

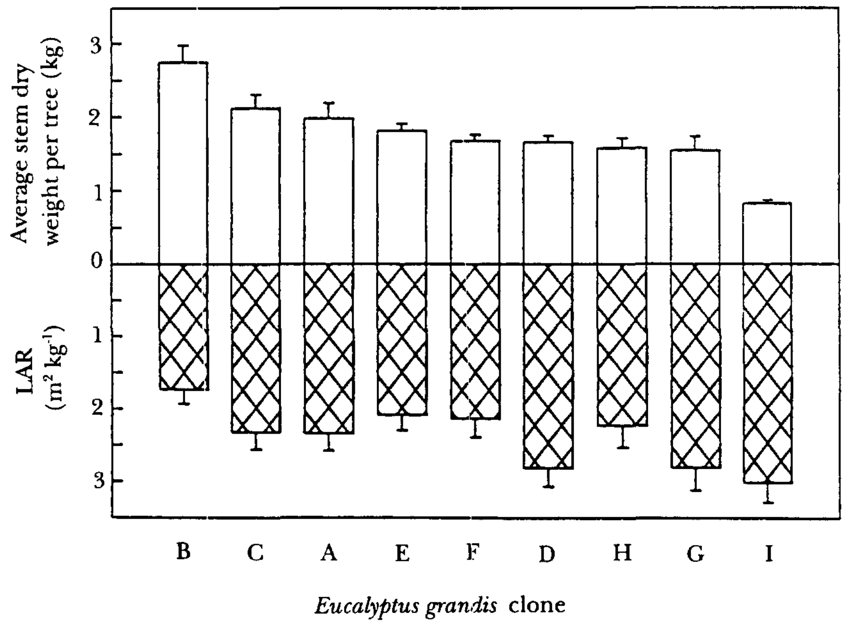

Figure 1. Average stem dry weight per tree and leaf area ratio (LAR, total leaf area: total above ground dry weight) for nine *Eucalyptus grandis* clones after 15 months of field growth. Clones are listed in order of average stem dry weight. Vertical lines represent standard error of means (n=10).

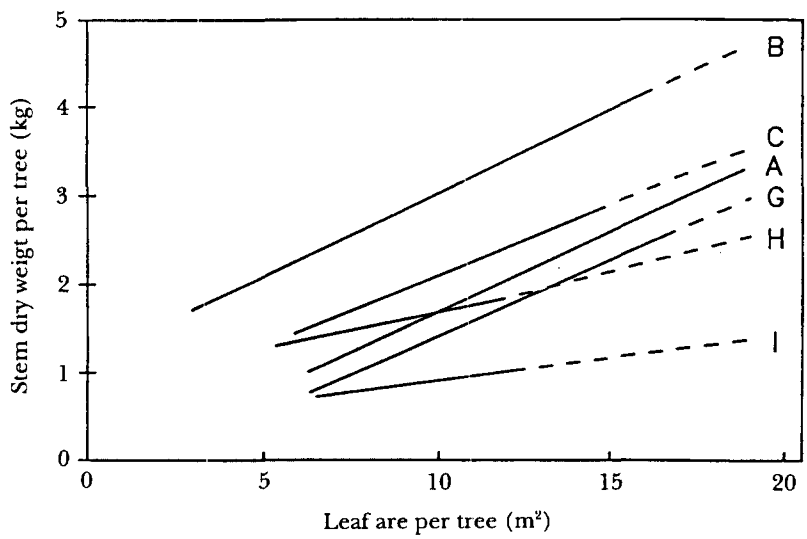

Figure 2. Linear regression equations describing the relationship between leaf area and stem dry weight per tree after 15 months of field growth for the three largest (i.e. clones A, B and C) and the three smallest (i.e. G, H and I) *Eucalyptus grandis* clones. Equations were developed based on 10 trees per clone. Dotted lines are extrapolations of regression equations beyond range of observed data for each clone.

There was statistically significant clonal variation in net assimilation rate (NAR, i.e. total above-ground biomass per unit LA) (Table 1). Two of the three smallest clones (i.e. G & I) had significantly lower NAR's as compared to most of the faster growing, heavier clones. As with stem dry weight, regression analysis showed that heavier clones accumulated more above-ground biomass per unit LA than smaller clones.

Leaf morphology

About two thirds (68%) of the variation in average leaf area was explained by clonal differences. A much smaller proportion of the variation (32%) was attributable to within-tree variation. Clones can be grouped into three distinct classes based on average leaf area. Clones C, F and H had the largest leaves, averaging over 43 cm^2 in size, while the leaves of B, D and E were all smaller than 26 cm^2 (Table 2). The remaining three clones (i.e. A, G and I) had leaves of intermediate size. Leaf area was not correlated with total above-ground biomass. Clone D, with the smallest leaves, had the highest SLA and the highest daily CO_2 uptake.

Stomatal characteristics

Stomatal size varied less among clones than stomatal density. The number of stomata per unit area was negatively correlated with average stomatal length. Clone D, with the longest stomata, had the fewest number per unit area (Table 2). There were no significant correlations between stomatal characteristics and either biomass or leaf area differences among clones.

Table 2. Morphological and stomatal leaf traits of nine *Eucalyptus grandis* clones measured after 15 months of field growth. Clones were ranked in order of total above-ground productivity. Means with the same letters in each column do not differ significantly when compared using Duncan's multiple comparison test ($p<0.05$, $n=128$).

Clone	Stomatal density (mm^{-2})	Stomatal length (μm)	Average leaf area (cm^2)	Specific leaf area ($cm^2 g^{-1}$)
A	164.1b	28.12c	36.79b	70.61d
B	164.9b	28.93c	25.42c	94.18ab
C	168.9b	25.93d	43.41a	86.11bc
D	151.2bc	25.79d	21.91c	102.22a
E	151.2bc	28.86c	23.94c	80.55c
F	194.4a	28.58c	43.89a	77.44cd
G	158.6b	31.15b	35.29b	83.09c
H	132.1c	33.20a	43.34a	70.81d
I	171.3b	25.74d	33.05b	80.22c

Physiological characteristics

Clones varied significantly in gas-exchange parameters. Total daily assimilation per unit leaf area, obtained by integrating diurnal patterns of A over the course of the day, showed a maximum variation of 109% in daily CO_2 uptake among clones. Clone D, an intermediate sized clone with large, thin leaves (i.e. high SLA), had significantly higher daily rates of net assimilation, transpiration and stomatal conductance, relative to the other clones (Table 3), whereas clone B combined the highest stemwood productivity with the lowest gas-exchange capabilities, including the lowest average C_s, lowest ΣA and the second lowest ΣE_t.

Table 3. Gas-exchange characteristics of nine *Eucalyptus grandis* clones after 15 months of field growth. Clones were ranked in order of total above-ground productivity. ΣA represents the daily net assimilation rate (mg CO_2 m^{-2} d^{-1}), ΣE_t represents the daily transpiration rate (mg H_2O m^{-2} d^{-1}), C_s represents the daily average stomatal conductance (cm s^{-1}), and WUE represents the water use efficiency (mg CO_2 mg^{-1} H_2O). Means with the same letters in each column do not differ significantly when compared using Duncan's multiple comparison test ($p<0.05$, n=4).

Clone	ΣA	ΣE_t	C_s	WUE
A	130.91bc	50.29b	0.0110b	2.60c
B	91.67e	25.47ef	0.0049e	3.60b
C	94.76e	33.18d	0.0069cd	2.86c
D	171.56a	68.38a	0.0173a	2.51c
E	115.12cd	33.90d	0.0070cd	3.40b
F	139.47b	49.12b	0.0108b	2.84c
G	100.27de	29.22de	0.0055de	3.43b
H	119.08cd	40.45c	0.0846c	2.94c
I	93.36e	22.49f	0.0048e	4.15a

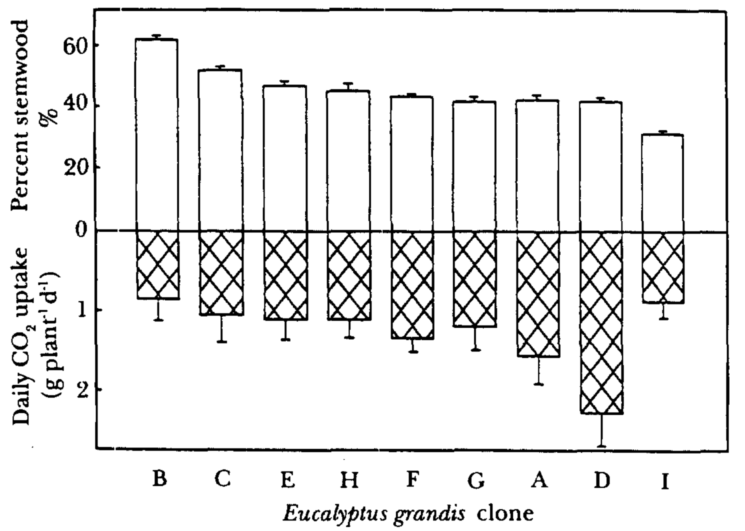

Figure 3. The proportional allocation of above-ground biomass to stemwood production and the daily rates of CO_2 uptake for nine *Eucalyptus grandis* clones after 15 months of field growth. Daily CO_2 uptake per plant for each clone was estimated by the product of average leaf area per plant and daily unit CO_2 uptake (i.e. ΣA). Clones are listed in order of daily net assimilation. Vertical lines represent standard error of means (n=10).

Stomatal conductance at 3 months was correlated with stem weight after 15 months ($r = -0.65$, $p = 0.058$). Water use efficiency (WUE, i.e. CO_2 assimilation per unit H_2O transpiration) showed a strong negative correlation with C_s, but was not correlated with productivity. Daily CO_2 uptake and H_2O loss per plant were not significantly correlated with above-ground productivity. Total daily CO_2 assimilated per plant was negatively correlated with the biomass percentage in the stem (Figure 3).

Discussion

Distinct clonal differences were observed in the allocation of biomass within a tree (Table 1). Clones which developed higher LAR invested less carbon in the stem. This is to be expected since leaves compete with stems for available carbon. However, some clones were also more efficient at producing stemwood per unit carbon absorbed.

Control of relative leaf development was found to correlate with faster growth rates in *E. grandis* just prior to outplanting (Blake & Suiter Filho 1988) and also in *Populus* cultivars (Tschaplinski & Blake 1989). Many studies showing a greater partitioning of carbon towards leaves in faster-growing trees were conducted using very young trees grown under non-limiting conditions, e.g. in an irrigated, fertilized nursery. However, a greater relative allocation to leaf area production would be less desirable in the seasonally-dry, sub-tropical savanna regions of Brazil, an area where trees are droughted for at least six months each year. Despite the long dry period, eucalypts grow very rapidly in Brazil, and genetically improved clones of *E. grandis* achieve up to 70 $m^3\ ha^{-1}\ y^{1}$ when grown on a 5-y rotation (Brandão 1984).

Individual *E. grandis* clones showed strong ($r > 0.9$) linear correlations between LA and stemwood production at 15 months (Figure 3). Clones with high total above-ground dry weight (e.g. B) were more efficient at producing stem biomass than slower-growing ones. These clones produced more stem biomass per unit leaf area throughout the range of observed LA values and also had a greater (i.e. steeper) slope than less vigorous cultivars (e.g. clone I). Such distinct differences among clones suggests that selection of faster-growing clones based on allocation of biomass may be possible.

Clonal variation in leaf morphology (e.g. average leaf size, stomatal density, stomatal length, and specific leaf area) was observed, but these parameters had no consistent correlation with productivity. Although leaf traits may be important for survival, their use as a selection criteria for maximum growth is not justified.

Plant size, however, may be useful as a selection criterion. Clones with greater shoot dry weight after 3 months were larger (i.e. heavier) after 15 months (Table 1). The smallest clone after 3 months (I) still ranked last after 15 months. This agrees with earlier results for hybrid *Populus* cultivars, where the largest (i.e. heaviest) rooted cuttings grew more rapidly than those that were smaller (i.e. lighter) at the time of planting (Tschaplinski & Blake 1989).

In contrast to growth, which is a cumulative measurement, physiological parameters are process variables which can only be measured at discrete intervals. With the exception of stomatal conductance, none of the measured gas-exchange parameters measured at 15 months correlated with yield. There was no consistent relationship between a high daily CO_2 uptake and total shoot dry matter production. Clone B, one of the largest, had the lowest daily assimilation rates, whereas the opposite was true for clone A, which combined high total biomass productivity with high daily assimilation (Tables 1 and 2). The proportional allocation between stem and leaves, however, appears to have been influenced by $\sum A$. This is suggested by the higher proportion of stem dry weight in cultivars with lower assimilation rates (Figure 3). However, no direct cause and effect is apparent since one clone (i.e. I) appears to be a distinct exception to this rule.

Dehydration avoidance adaptations are often observed in either the root or leaf (Pallardy & Kozlowski 1979a, Blake & Suiter Filho 1998). In agreement with our present results, slower growth of some *E. grandis* clones before transplanting was associated with slow root growth combined with high stomatal conductance, suggesting that smaller rooted cuttings were unable to avoid dehydration (Blake & Suiter Filho 1988). In the present study, stomatal conductance at 3 months was negatively correlated with stem dry weight at 3 months ($r = -0.66$; $p = 0.026$) and at 15 months ($r = -0.65$; $p = 0.058$). Due to their lower stomatal conductances, faster-growing clones were able to develop a high leaf area without increasing plant moisture stress, as observed by similar xylem pressure potentials in larger and smaller clones.

The lower stomatal conductance in clones with higher stemwood production suggests that they are better able to avoid dehydration, which agrees with earlier results (Pallardy & Kozlowski 1979b, Blake & Suiter Filho 1988). Early and more complete stomatal closure and the ability to shed leaves when droughted appear to be more important in dehydration avoidance than differences in stomatal size and number.

In conclusion, major differences in partitioning of dry matter were observed among *E. grandis* clones. Early selection of clonal material that exhibits a greater size (weight) and a lower stomatal conductance under drought could lead to major gains in stemwood production. Major differences in partitioning of dry matter between stem and leaves observed 15 months after outplanting in the field could be expected to persist, since the trees were already 4 - 5 m in height and had grown for one-quarter of their 5-y rotation length.

Although we are still largely ignorant of the factors that determine the yield of forest crops, the mechanisms controlling carbon partitioning within a tree need to be understood for effective modelling of growth (Landsberg 1986). Assimilation rates appeared poorly correlated with biomass production in this seasonally dry environment. Clones which were more efficient at producing stemwood were observed to have a lower relative leafiness, had greater dehydration avoidance capability, and were more efficient at relocating carbon away from the leaf and towards the stem.

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