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MODELLING GROWTH AND ECOPHYSIOLOGICAL RESPONSES OF *EUCALYPTUS GRANDIS* CLONES IN MINAS GERAIS, BRAZIL

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BEVILACQUA, E., BLAKE, T.J. & SUITER FILHO, W. 1997. Modelling growth and ecophysiological responses of *Eucalyptus grandis* clones in Minas Gerais, Brazil. The relationships between environment, physiology and dry matter production were studied in rooted cuttings of 11 *Eucalyptus grandis* (W. Hill ex Maiden) clones after three months growth in the field in Minas Gerais, Brazil. A matrix of Spearman's rank correlation coefficients indicated that stomatal conductance was negatively correlated with leaf area and stem dry weight ($r = -0.68$ and $r = -0.66$ respectively, $p < 0.05$)). Stomatal conductance was also negatively correlated with leaf-, above-ground-, and total dry mass, ($r = - 0.55$ to $r = - 0.59$, $p< 0.1$). Because of their lower stomatal conductance, more vigorous clones were no more water stressed than slower-growing clones, despite their greater leaf area. Surface response curves showed that during the dry period of the year, air temperature and relative humidity were the main environmental variables controlling stomatal conductance. These two variables accounted for almost three quarters of the variation in stomatal conductance, whereas light intensity explained less than 4% of the variation in stomatal conductance. Although relative humidity had the greatest influence on stomatal conductance, air temperature was more important for photosynthesis. Xylem pressure potentials, net photosynthesis (P_n), transpiration (Tj) and water use efficiency (ratio of PyT^were poorly correlated with dry matter production.

Keywords: Drought - *Eucalyptus grandis* - growth models - vigour - environmental control

BEVILACQUA, E., BLAKE, T.J. & SUITER FILHO, W. 1997. Pembentukan model pertumbuhan dan model ekofisiologi Won *Eucalyptus grandis di* Minas Gerais, Brazil. Perkaitan antara persekitaran, fisiologi dan pengeluaran bahan kering dikaji pada keratan akar 11 klon *Eucalyptus grandis* (W. Hill *ex* Maiden), tiga bulan, selepas penanaman di lapangan di Minas Gerais, Brazil. Matriks koefisien korelasi tahap Spearman menunjukkan bahawa konduktans stomata mempunyai korelasi negatif

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dengan luas daun dan berat kering batang ($r = -0.68$ dan $r = -0.66$ masing-masing, $p<0.05$). Konduktans stomata mempunyai korelasi negatif denganjisim kering daun, jisim kering atas tanah dan jumlah jisim kering, tetapi pada tahap keyakinan yang lebih rendah ($r = -0.55$ hingga $r = -0.59$, $p<0.1$). Disebabkan konduktans stomatanya yang lebih rendah, lebih banyak klon yang kuat tidak lagi mengalami tekanan air berbanding klon yang lambat membesar, walaupun luas daunnya lebih besar. Graf gerak balas permukaan menunjukkan bahawa semasa musim kering, suhu udara dan kelembapan relatif merupakan pembolehubah sekitar utama yang mengawal konduktans stomata. Kedua-dua pembolehubah tersebut menyumbang hampir tiga suku daripada perubahan dalam konduktans stomata, manakala kekuatan cahaya menerangkan kurang daripada 4% perubahan dalam konduktans stomata. Walaupun kelembapan relatif mempunyai pengaruh vang paling kuat ke atas konduktans stomata, suhu angin lebih penting bagi fotosintesis. Potensi tekanan zilem, fotosintesis bersih (P_n), transpirasi (Tj) dan efisiensi penggunaan air (nisbah P/T,) mempunyai perkaitan yang lemah dengan pengeluaran bahan kering.

Introduction

More vigorous growth of some species and clones has been correlated with a range of morphological and physiological characteristics (Sinha & Khanna 1975), including net photosynthesis and higher water use efficiency (Blake & Yeatman 1989). Most of these correlations, however, were established in irrigated and fertilised field trials. It is usually difficult to correlate process variables with growth rates under the more stressful conditions that occur in forest plantations (Ceulemans *et al.* 1988, Blake *et al.* 1995). This could be because environmental stresses tend to limit growth more than process variables such as photosynthesis (Kramer 1986), especially since growth is a cumulative variable measured over a relatively long time period, whereas most process variables are measured on a much shorter time scale.

Gas exchange rates and other physiological process variables were poorly correlated with dry matter production after 15 months growth in a plantation in Minas Gerais, Brazil (Blake *et al.* 1995). Early rankings in dry mass of *E. grandis* clones after 3 months of field growth, however, were correlated with growth after 15 months. This study, therefore, investigated correlations between early growth performance and physiological characteristics after 3 months in a plantation. It is thought that such correlations may exist at an early age, before competition for light and water complicate the modelling of relationships in older and larger trees. Such correlations may provide insight into early selection criteria based on physiological processes.

Materials and methods

Four-month-old rooted cuttings of *Eucalyptus grandis* W. Hill *ex* Maiden, 300 per clone, were planted at a 3.0 X 1.5 m spacing by Compagnia Agricola E Florestal Santa Barbara, 30 km east of Bom Despacho, Minas Gerais, Brazil. Propagation techniques, site conditions and plant specifications were as described previously (Blake & Suiter Filho 1988, Blake *et al.* 1995).

The present study was designed to observe correlations between physiological and growth characteristics of 11 *E. grandis* clones 3 months after they were transplanted to the field. The clones were: 36502 (A), 25186 (B), 26746 (C), 37633 (D), 26894 (E), 26693 (F), 28684 (G), 25151 (H), 37779 (I), 20092 (J), and 27003 (K). Clones A -1 were remeasured 12 months later, i.e. after 15 months growth in the field. Total above-ground biomass ranking (largest to smallest) of the 9 clones was: A > B > C > D > E > F > G > H > I . After 3 months growth, ranking of the 11 clones was in the following order (highest to lowest) : C > H > A > B > F > E > D > I > G >J > K.

Physiology and growth were measured in mid-September 1988, as follows: stomatal conductance (C.), transpiration (T,) and net photosynthesis (P_n) were measured on leaves in the mid-, to upper one-third of the crown, using a Li-6200 portable photosynthesis system (Li-Cor Inc., Lincoln, Nebraska). Sensors on the Li-6200 portable photosynthesis system logged leaf and air temperatures, relative humidity (R.H.) and photosynthetically active radiation (PAR) at the time of gas exchange measurements. A shoot in the same part of the crown was then detached and xylem pressure potential (\|/$_x$) was measured with a Scholander-Hammel pressure chamber (PMS Instruments, Corvallis, Oregon), using the precautions of Ritchie and Hinckley (1975).

Physiological measurements, at each sampling time, were confined to a 1.5 hour window, to reduce diurnal variation. Measurements started at 1000 h on 15 September 1988 and were repeated at 1300 h and at 1600 h. The diurnal sampling of all 11 clones (3 cuttings per clone for physiological readings) was repeated the following day. At the end of the measurement period, cuttings were selected for the determination of growth parameters.

Ten cuttings per clone were harvested and total leaf area of each plant was determined using a Li-Cor LI-3000 Portable Area Meter (Li-Cor Inc., Lincoln, NE). Cuttings were then oven-dried (70 °C for 48 h) and dry weights of leaf, stem and roots were determined separately.

Total H,,O transpiration and CO,$_2$ gain per plant were calculated by multiplying the average, instantaneous unit rates of T, and P_n by the average leaf area per plant for each clone.

Light, temperature and other ambient conditions were relatively consistent during each 1.5 h measurement period. Ambient conditions were in the ranges: air temperature, 30-40 °C; R.H., 10-30%; PAR 1000-2000 (Irnol nr* s$^{'1}$. Maximum, minimum and mean' temperatures (measured at 0900 and 2100 h) during September 1988 were 33.2, 12.0 and 22.3 °C respectively. A single rain day provided only 43.6mm of rainfall for the month of September, and soil surface was relatively dry. Soil moistures at 5 and 10 cm depths were 23% and 36% respectively.

Comparisons of physiological variation among clones were conducted using a blocked analysis-of-covariance with the General Linear Model Procedure (PROC GLM) from SAS/PC (SAS Institute Inc. 1987). Observations were blocked for each sampling date and time period, with environmental parameters (i.e. air temperature, relative humidity and PAR) being used as covariates.

Since growth is cumulative, while process variables are measured instantaneously, a matrix of Spearman's rank correlation coefficients and their statistical significance were used to model the relationships between growth and physiology. *Eucalyptus grandis* clones were ranked (highest to lowest) by assigning a rank from 1 to 11.

To gain a better understanding of how gas exchange in *E. grandis* responds to variation in temperature, relative humidity and light intensity over the course of the day during the dry period of the year, second-order polynomial regression equations were developed. Data from all clones were pooled for the model development. These equations generated response surface models used to predict the response of physiological processes to diurnal variation in environmental variables.

Results

A matrix of Spearman's rank correlation coefficients was used to compare growth and physiology (Table 1). Leaf area showed significant ($p < 0.01$) positive correlations with above-ground dry matter ($r = + 0.95$), total plant dry weight ($r = + 0.89$), and stem dry weight ($r = +0.81$). Leaf weight showed similar, strong ($r = + 0.92$ to $r = + 0.61$) correlations to these dry weight parameters. More vigorous clones had larger, deeper root systems, and root dry weight showed significant ($p < 0.05$) positive correlations with leaf weight ($r = + 0.65$) and total plant dry weight ($r = + 0.64$).

Stomatal conductance (C_s) showed significant negative correlations with stem dry weight ($r = - 0.66$), leaf area ($r = - 0.68$) and leaf dry weight ($r = - 0.55$), indicating that larger clones had a lower C_s than smaller, less vigorous clones, despite their greater leaf area. Positive correlations were observed between C_s and other gas exchange variables, i.e. T, ($r = + 0.82$), P_n ($r = + 0.71$) and WUE ($r = + 0.68$), indicating that due to their higher stomatal conductances smaller clones gained more carbon dioxide and lost more water in transpiration per unit leaf area.

Xylem pressure potential (V_x), a measure of plant water stress, was positively correlated with water use efficiency (WUE) ($r = + 0.78$), and negatively correlated with C_s ($r = - 0.54$), but was not significantly correlated with any measured growth parameter (Table 1). Despite their greater leaf areas, larger clones were no more water stressed. ψ_x values reached a minimum in the early afternoon (from -2.2 to -2.7 MPa) and values were similar in larger and smaller clones. At these xylem pressure potentials, *E. grandis* *would* have started to lose turgor. However, measurement of predawn ψ_x revealed that leaves were rehydrated overnight. Other process variables (e.g. P_n,T, and WUE) were not significantly correlated with any measured growth parameter (Table 1).

Total water loss per plant was positively correlated with above-ground dry weight ($r = + 0.61$), indicating that larger plants lost more water because of their greater leaf area. Total carbon gain per plant was not significantly correlated ($p > 0.10$) with any measured growth variable (Table 1).

Relative humidity explained more (43.6%) of the variation in stomatal conductance than air temperature (26.3%). However, photosynthetically active radiation

Table 1. Spearman's correlation coefficients using the ranking of *Eucalyptus* clones to determine correlations between physiological and biomass components at three months of age

	Physiological parameters								Morphological parameters Dry weights (g)			
	P_n	T_l	C_s	WUE	ψ_x	CO_2 gain	H_2O loss	Stem	Leaf	Above	Below	Total
T_l	+0.85***											
C_s	+0.71 **	+0.82***	-									
WUE	+0.79***	+0.62**	+0.68**	-								
ψ_x	+0.38	+0.25	- 0.54*	+0.78***	-							
CO_2 gain	+0.64	+0.57	+0.34	+0.49	- 0.25	-						
H_2O loss	+0.05	+0.46	+0.17	+0.30	- 0. 10	+0.72**						
Stem	- 0.33	+0.41	- 0.66**	+0.47	+0.35	+0.24	+0.42	-				
Leaf	- 0.33	- 0.30	- 0.55*	+0.18	+0.07	+0.38	+0.46	+0.61**	-			
Above	- 0.26	- 0.27	- 0.57 *	- 0.33	+0.28	+0.49	+0.61**	+0.85***	+0.88***	-		
Below	+0.05	- 0.03	- 0.08	+0.22	- 0.29	+0.36	+0.25	+0.26	+0.65**	+0.50	-	
Total	- 0.26	- 0.29	- 0.59*	- 0.27	+0.19	+0.43	+0.52	+0.84***	+0.92***	+0.97***	+0.64**	-
Leaf area (cm^2)	- 0.49	- 0.48	- 0.68**	- 0.46	+0.32	+0.31	+0.46	+0.81***	+0.85***	+0.95***	+0.33	+0.89***

P_n = photosynthetic rate (|imol nv^f s"); Tj = transpiration rate ((imol m"^{2} s^{-1}); C$_($ = stomatal conductance (cm s'^{1}); WUE = water use efficiency (mol H_2O mol^1 CO_2); \|/$_x$ = xylem pressure potential (MPa); CO_2gain = P_n* leaf area (fimol s'^{1}); H_2O loss = T,*leaf area (nmols-'); * significant at p = 0.10; ** = significantatp = 0.05; *** = significant at p = 0.01.

(PAR) had only a slight influence on gas exchange, explaining less than 4% of the observed variation (Table 2). Temperature explained much more (52.9%) of the variation in P_n than relative humidity (13.8%); hence, it also had a greater influence (61.6%) on WUE (Table 2). Taken together, these three environmental parameters explained most of the variation in P_n, T, and WUE (viz. 53.3%, 68.9% and 76.2% respectively).

Surface response models (Figure 1) showed that increasing temperature and decreasing relative humidity caused a steady decline in C_s and P_n. Net photosynthesis and stomatal conductance declined to zero at temperatures ranging from 33 °C to 35 °C, but this occurred only at very low R.H. As air became hotter and drier, ^declined less than P causing WUE to decline markedly.

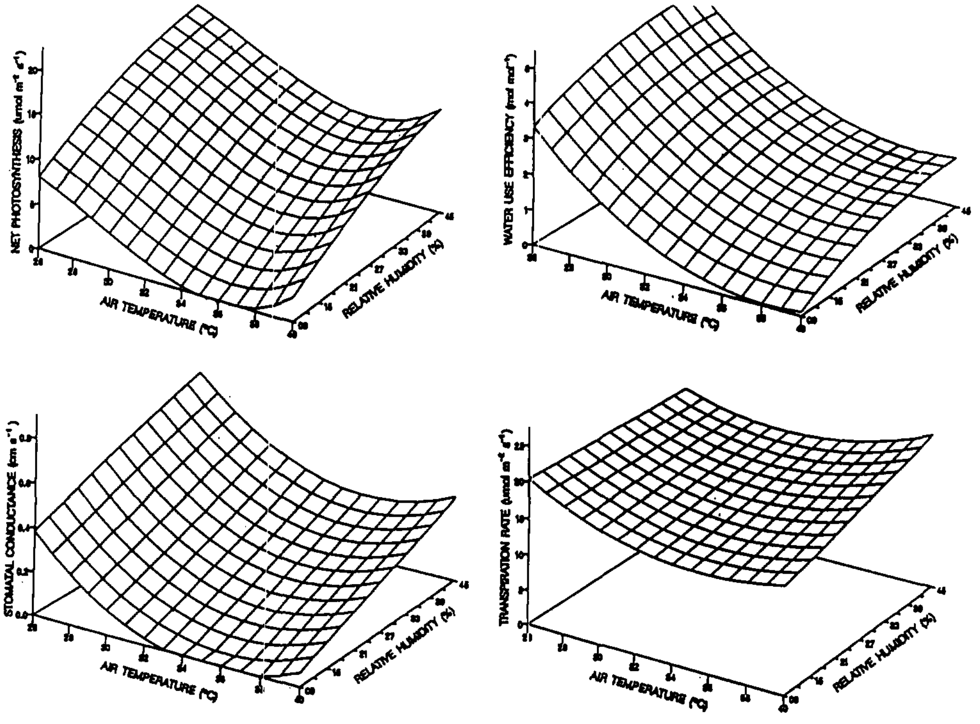

Figure 1. Multiple regression models demonstrating the predicted responses of net photosynthesis, stomatal conductance, transpiration and water use efficiency in *Eucalyptus* clones to increasing air temperature and relative humidity, while holding PAR constant

Discussion

Unit rates of net photosynthesis indicated that photosynthetic efficiency was no greater in fast-growing clones, which agrees with results obtained after 15 months growth (Blake *et al.* 1995). However, due to its greater leaf area, the fastest-growing clone fixed one third more carbon per plant than the least vigorous clone (1651 versus 1247 u,mol s'^{1}).

Drought tolerance adaptations have been classified into dehydration postponement or avoidance adaptations and those that allow plants to tolerate dehydration (Kramer 1980). This study confirmed that the ability to postpone dehydration was more important for growth of *E. grandis* than the ability to tolerate dehydration. This was deduced by a number of lines of evidence.

Firstly, a negative correlation was observed between stomatal conductance and growth of stems, leaves and total dry weight, as observed after 15 months (Blake *et al.* 1995). A lower C. in more vigorous *E. grandis* clones would tend to compensate for their greater leaf area by reducing water loss. This would explain why faster-growing clones were no more water-stressed than slower-growing clones, despite their greater leaf area.

Secondly, the larger and deeper root systems of the more vigorous clones were better able to tap moisture at greater depths. The faster-growing clones had a greater root dry weight, as shown by a significant, positive correlation ($r = + 0.64$) between root and total dry matter production.

Thirdly, drought-induced leaf senescence was observed to be greater in less vigorous clones, which could at least partly explain their reduced growth rates. However, since fast-growing clones survived as well, or better, than less vigorous clones, the enhanced growth rate of fast-growing clones was not achieved at the expense of survival.

Despite its ability to avoid dehydration, *E. grandis* was less tolerant of dehydration than conifers such as jack pine (Blake & Tschaplinski 1992). *Eucalyptus grandis* lost turgor at 85% relative water content, compared with 65% in jack pine and osmotic adjustment was comparatively small (0.10 to 0.25 MPa) in *E. grandis* (Blake & Tschaplinski 1992). Fast- and slow-growing clones had very similar TLP, confirming earlier work that suggested *E. grandis* had a relatively low ability to tolerate dehydration (Blake & Suiter Filho 1988). *Eucalyptus grandis* had a relatively high cell wall elasticity, which increased by 1.76 MPa following a drought treatment, which would help this species to postpone dehydration (Blake & Tschaplinski 1992). A low C_s under drought and adaptations that help to postpone dehydration were therefore more important for growth rate of *E. grandis*, than dehydration tolerance. Drought postponement would allow more vigorous clones to continue growth longer during a drought, and recommence growth sooner after drought, compared with less vigorous clones.

Surface response models showed that C_s and WUE declined mainly in response to increasing temperature and vapour pressure deficit (Figure 1). P_n declined more than T, in hot, dry air, causing a rapid decline in WUE with increase in temperature. The decline in C_s at high temperatures increased substantially as humidity declined. Relative humidity explained more (43.6%) of the variation in C_s than air temperature (26.3%). However, air temperature explained more (53%) of the variation in P_n and WUE (76%).

Stomata closed in hot, dry air (Figure 1), causing P_n and WUE to both decline. Stomatal closure in response to declining humidity was previously observed in northern, boreal conifers (Grossnickle & Blake 1987). The ability of low humidity to inhibit growth could be, in part, explained by an increase in resistance to water movement through the soil-plant-air continuum. This was found to slow growth of northern conifer seedlings, even when seedlings were planted in moist soil (Grossnickle & Blake 1987).

Despite some changes in rank, most of the heavier clones after 3 months growth (e.g. clones A, B and C) were still larger after 15 months and the 3-month clonal ranking was highly correlated with that observed after 15 months growth in the field (Blake *et al.* 1995). Two of the three slowest-growing clones after 3 months (G and I) were among the three smallest clones after 15 months (Blake *et al.* 1995). Since clones averaged 4-5 m in height, had achieved canopy closure and were one quarter of their rotation age (5 y in Minas Gerais), many of the faster-growing clones should maintain their relative superiority to rotation age.

Comparison of clonal rankings under a controlled environment (Inoue, unpublished data; Inoue & Ribeiro 1988) and in the nursery (Blake *et al.* 1988) showed they were poorly correlated with field rankings after 3 and 15 months. This suggests measurements prior to transplanting are poor predictors of later field growth.

In conclusion, C_s, when measured in the field, was the gas exchange variable most correlated with field growth based on clonal rankings. Measurements made on the clones prior to outplanting were poorly correlated with field growth, which suggests the need to include dehydration avoidance ability in growth simulations of *E. grandis.* Air temperature and relative humidity were the main environmental variables controlling the diurnal variation in stomatal conductance during the dry period of the year.

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