Selection for biomass production based on respiration parameters in eucalypts: effects of origin and growth climates on growth rates

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Abstract: Seventeen *Eucalyptus* species and 30 rapid-growing *Eucalyptus camaldulensis* trees (referred to as plus trees), growing in a plantation were studied to examine relationships among measured plant growth and respiratory parameters, geographical origins, and growth climate. The respiratory parameters measured at two different temperatures by isothermal calorimetry were metabolic heat rate, rate of CO_2 production, and the ratio of heat rate to CO_2 rate. Metabolic heat rate was also measured as a continuous function of temperature by differential scanning calorimetry in the range of 10 to 40°C. Tree growth was measured as rates of height and stem volume growth. The values of respiratory and growth variables of *Eucalyptus* species are significantly correlated with latitude and altitude of origin of their seed sources. The maximum metabolic heat rate, the temperature of the maximum heat rate, the temperature coefficients of metabolic rate, and the temperatures at which the slopes of Arrhenius plots change are all genetically determined parameters that vary both within and among species. Measurement of growth rate – respiration rate – temperature relationships guide understanding of why relative growth rates of *Eucalyptus* species and individual genotypes differ with climate, making it possible to identify genotypes best suited for rapid growth in different climates. The temperature dependence of respiration rates is an important factor determining relative growth rates of eucalypts in different climates. To achieve optimum biomass production the temperature dependence of individual plants must be matched to growth climate.

Résumé : Nous avons étudié les relations entre la croissance et les paramètres liés à la respiration, les origines géographiques et le climat, chez 17 espèces d'*Eucalyptus* et 30 *Eucalyptus camaldulensis* à croissance rapide (appelés ici « arbres plus ») croissant en plantation. Les paramètres liés à la respiration étaient le taux de production de chaleur métabolique, le taux de production de CO_2 et le rapport entre ces deux taux. Ces paramètres ont été mesurés à deux températures par calorimétrie isothermale. Le taux de production de chaleur métabolique a aussi été mesuré en continu entre 10 et 40°C par balayage calorimétrique différentiel. Les taux de croissance en hauteur et en volume de la tige ont servi de mesure de croissance des arbres. Les valeurs des variables respiratoires et de croissance des espèces d'*Eucalyptus* sont corrélées significativement avec la latitude et l'altitude du lieu d'origine de leurs semences. Le taux maximal de production de chaleur métabolique, la température à laquelle ce taux est atteint, les coefficients thermiques du taux métabolique, et les températures auxquelles les pentes des graphiques d'Arrhénius changent, sont des paramètres contrôlés génétiquement qui varient entre et à l'intérieur des espèces. Les relations entre le taux de croissance, le taux de respiration et la température nous aident à comprendre le pourquoi des variations de croissance parmi les espèces d'*Eucalyptus* et parmi les génotypes individuels dans des conditions climatiques différentes. Cette compréhension accrue rend possible l'identification des génotypes les plus aptes à fournir des croissances rapides dans différentes conditions climatiques. Les taux relatifs de croissance des *Eucalyptus* dans différentes conditions climatiques sont fortement assujettis à la dépendance des taux de respiration envers la température. Pour obtenir une production optimale de biomasse, il faut coordonner la dépendance thermique des plantes individuelles avec le climat.

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Introduction

Current tree selection procedures commonly include (*i*) initial collection of diverse, potentially fast-growing genotypes from various geographical regions, (*ii*) an attempt to identify trees within the selected populations that are capable of rapid growth at a given location, (*iii*) identification of trees, both within and among species, that produce the best chemical form of biomass to meet specific commercial needs for pulp, fiber, and lumber, and (*iv*) identification of

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trees with superior characteristics to include in a breeding (or molecular genetics) program. Selection of genotypes (clones) for biomass production is commonly done by a combination of empirical means and quantitative genetic theory (Namkoong et al. 1988). A collection of trees is planted at one or several sites, and their growth characteristics are measured over several years. Phenotypically superior trees are carried through advanced generations in breeding programs to develop improved varieties or clones for commercial use (Ahuja and Libby 1993*a*, 1993*b*).

Two major questions are encountered in these procedures: (1) Which trees should be included in the base population or initial collection (Zobel and Talbert 1984)? (2) What are the most appropriate procedures for selecting superior trees from the base population for clonal propagation or inclusion in breeding programs (Ledig 1989)?

In attempting to answer question 1, the dominant early consideration has been geographical origin, i.e., altitude and latitude, as an indication of suitability. It is a common first assumption that genotypes originating from native latitudes and altitudes similar to the planting site will be the most productive (Eldridge et al. 1993). However, matching origin and growth sites by latitude and altitude is only a reasonable starting place for selection; other factors must be considered to match trees with growth climate (Hackett 1988). Moreover, a wide range of differences in range of adaptation and patterns of growth rate responses to temperature may exist among trees from any given geographical origin (Booth 1991; Booth and Pryor 1991). Consequently, initial collections based on location routinely require extensive on-site screening and development of land races on the new site. This process, though effective, requires a generation or more for selection (Zobel and Talbert 1984). Identification of traits during early growth that identify plants for early selection could greatly reduce the time and resources required for selection of superior trees.

To answer question 2, procedures for rapidly measuring physiological parameters that reflect growth performance of genotypes within a given climate are needed. Under many growth conditions, respiratory reactions involved in energy metabolism and biomass production have been correlated with plant growth (Amthor 1989; Hansen et al. 1989, 1994; Anekonda et al. 1993, 1994*a*, 1994*b*; Criddle et al. 1994, 1995, 1996). Thus, respiratory rates, when properly measured and interpreted, may be an appropriate measure of potential growth properties of plants in a given environment.

Two recent studies have described the relation of respiration rate to growth rate (Hansen et al. 1994) and the relation of the temperature dependence of respiration rate to the latitude and altitude of origin of woody plants (Criddle et al. 1994). A brief presentation of key equations of the model and definition of terms employed is therefore presented here for reference.

The specific growth rate (R_{SG}), in moles of carbon per mass of tissue is related to the specific metabolic heat rate ($\dot{q}$) and the specific rate of CO_2 production (R_{CO_2}) by eq. 1 (Hansen et al. 1994):

$$[1] \quad R_{SG} = \frac{-\dot{q} - R_{CO_2}\,(1 - \gamma_p/4)\,\Delta H_{O_2}}{\Delta H_B}$$

where γ_p is the average oxidation state of carbon in respiratory substrate; ΔH_{O_2} is the enthalpy change for combustion of substrate per mole of oxygen consumed, and ΔH_B is the enthalpy of biosynthesis per mole of carbon. ΔH_{O_2} is a constant with a value of -455 ± 15 kJ/mol. Values for γ_p and ΔH_B are not available, but treating them as constants is the first step in an iterative process that evaluates measurements of $\dot{q}$, R_{CO_2}, and uses these values to determine the variability of γ_p and ΔH_B (for details refer to Hansen et al. 1994, 1995). Equation 1 states that growth rates equals the total rate of energy available from combustion of substrate, i.e., $R_{CO_2}\,(1 - \gamma_p/4)\,\Delta H_{O_2}$, minus energy lost to the surroundings ($\dot{q}$), divided by the energy per unit carbon incorporated in new growth (ΔH_B).

Though not immediately apparent without further development of the equations, growth rate is proportional to the metabolic heat rate times a function of the efficiency (Hansen et al. 1995). Metabolic heat rate ($\dot{q}$) and R_{CO_2} vary with temperature. The temperature dependences of $\dot{q}$ and R_{CO_2} in the range where the Arrhenius relation holds are described by eqs. 2 and 3, respectively:

$$[2] \quad \dot{q} = A_q\, e^{-\mu_q/T}$$

$$[3] \quad R_{CO_2} = A_{CO_2}\, e^{-\mu_{CO_2}/T}$$

where μ_q and μ_{CO_2} are the Arrhenius coefficients of temperature dependence of the metabolic heat rate and R_{CO_2}, respectively, and A_q and A_{CO_2} are constants.

The temperature dependence of respiratory rate, μ_q, is related to a linear sum of latitude and altitude of origin of woody plants (Criddle et al. 1994). As latitude and altitude of origin increase, μ_q decreases.

Because of the functional relation between respiratory rate parameters and growth rate, respiratory rate measured as a function of temperature may be used to define the effects of temperature on growth rate (Anekonda et al. 1995; Criddle et al. 1996).

This paper therefore addresses the influence of temperature on growth performance and metabolic rate parameters of several *Eucalyptus* species and of different genotypes within a species, and attempts to define the relation between laboratory measurements of metabolic rate parameters at various temperatures and growth rates in the field. Metabolic parameters are then related to growth climate differences and the latitude and altitude of seed source origin.

Materials and methods

Plant materials and site preparation for species trial

The collection of plant material used for species trials consists of 17 *Eucalyptus* species grown from individual seed collections obtained by the Simpson Tehama Fiber Farm, primarily from CSIRO (Commonwealth Scientific and Industrial Research Organization) Division of Forestry, Australian Tree Seed Center (Table 1). Some additional collections were from other seed collectors in Australia and from the USDA *Eucalyptus* program in Florida. Trees from these *Eucalyptus* species were planted on May 22, 1992, in a plantation at Corning, Calif.

Planting sites were prepared by ripping to 1 m in late summer, followed by disking in early spring. Soil for species studies was ripped in August 1991 and disked in March 1992. The soil in the plantation is Corning–Newville gravelly loam (Soil

Table 1. Seed source information for the provenances or clones of the 17 *Eucalyptus* species studied.

Name of species (code)	Provenance[a] or clone	Seed source locality	Seed source origin factors[b] Lat. (°S)	Long. (°E)	Alt. (m)	$F_{(A+L)}$
1 Brooker's gum (A)	17947	Otway State Forest, Vic, Australia	38.60	143.83	500	606
E. brookerana	16865	North of Triabunna, Tas, Australia	42.27	147.85	440	378
2 Mountain grey gum (C) *E. cypellocarpa*	12655	Bonang, Vic, Australia	37.20	148.70	860	847
3 Mountain gum (D) *E. dalrympleana*	15530	South of Batlow, NSW, Australia	35.62	148.15	1028	881
4 Alpine ash (E) *E. delegatensis*	16954	Matlock, Vic, Australia	37.58	146.18	1100	1119
5 Brown barrel (F) *E. fastigata*	16306	Brown Mtn Nimmitabel, NSW, Australia	36.53	149.40	1090	1020
6 White ash (G)	12164	Badja Mtn East Cooma, NSW	36.50	149.40	1750	1678
E. fraxinoides	15526	Nimmitabel, NSW, Australia	36.48	149.32	1100	1025
7 Maiden's gum (H) *E. globulus* ssp. *maidenii*	91/342	Batemans Bay, NSW, Australia	35.74	150.26	540	299
8 Tingaringy gum (I) *E. glaucescens*	17829	Mt. Erica, Vic, Australia	38.00	146.37	1235	1305
9 Shining gum (J) *E. nitens*	C2	Los Angeles, Chile; originally from Mt. Useful, Vic, Australia	37.40	146.31	1200	1204
10 Messmate stringy gum (K)	15910	Gibraltar Range, NSW, Australia	29.63	152.13	1000	344
E. obliqua	15913	Powelltown, Vic, Australia	37.88	145.85	370	415
11 Swamp gum (L) *E. ovata*	17285	21 km South of Bombala, NSW, Australia	37.10	149.30	750	689
12 Narrow-leaved Peppermint (M) *E. radiata* ssp. *radiata*	17312	Riddels Creek, Vic, Australia	37.45	144.67	350	363
13 Mountain ash (N)	16953	Healsville, Vic, Australia	37.57	145.53	900	918
E. regnans	15191	Swan Port, Tas, Australia	42.40	147.85	450	839
14 Candlebark (O) *E. rubida*	17287	South of Captains Flat, NSW, Australia	35.87	149.33	1100	968
15 Gully gum (P) *E. smithii*	16373	20 km WNW Braidwood, NSW, Australia	35.37	149.60	850	684
16 Forest red gum (Q) *E. tereticornis*	351	Florida, U.S.A.				
17 Manna gum (R) *E. viminalis*	91/338	Tallaganda State Forest, NSW, Australia	35.98	149.87	500	683

[a]Provenance name of each species. The second provenance was chosen for species A, G, K, and N for the purpose of canonical correlation analysis.

[b]The altitude plus latitude function is $(F_{A+L}) = (85\text{ m})(L - 35°) + (A - 200\text{ m})$, where L is the absolute value of latitude in degrees and A is altitude in metres. The constants 35°C and 200 m arise as the northern-most latitude and lowest altitude for the species included in this study. This equation assumes that the climatic change resulting from a 1° change in latitude is equivalent to that from an 85-m change in altitude at origin (Criddle et al. 1994).

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Survey Tehama County, California, May 1967) with north aspect and a 3% slope. Forty-nine 3-month-old seedlings of each species were planted in square plots with a between-tree spacing of 3 × 3 m. The trees were drip irrigated at the rate of 0.244 ha·m/ha in 1992 and fertilized at irrigation with urea (UN32) at a rate of 2.39 kg/ha. Irrigation of 0.31 ha·m/ha and 1.84 kg/ha urea were used in 1993. Trees were protected from insect and rodent pests with standard agricultural management practices.

Among the available provenances for each species in the field (one to three), the best was selected based on its 1st-year height. In the selected provenance, the five tallest trees were chosen, labeled individually, and used for measurement of respiratory traits. An additional provenance was included for a subset of four selected species, i.e., *E. brookerana*, *E. fraxinoides*, *E. obliqua*, and *E. regnans* (Table 1). Two criteria for selecting these four species were (*i*) presence of large, between-species differences in measured respiration parameters and (*ii*) large, between-seed source and between-species variation for origin factors. Because respiration parameters were measured on two provenances only for these four species, a canonical correlation analysis was possible using only these four species (see below).

Tree height, basal diameter, and stem volume growth were measured on 7-month-old trees during December 1992 and on 15-month-old trees during August 1993. Specific height growth and stem volumes were calculated as indicated in the footnote of Table 2.

Plant materials and site preparation for open-pollinated, half-sib family trial

The second collection of material used in this study consists of 30 phenotypically superior plus trees of *E. camaldulensis*. The Simpson Tehama Fiber Farm obtained open-pollinated (OP), half-sib families primarily from Australia and Florida. Specific identity of seed sources is not clear because of lack of pedigree. Lake Albacutya provenance may have been over-represented in these families. All OP families were planted in two seasons: once during the Spring of 1989 with spacing of 2.1 × 3 m and once during the Spring of 1990 with a spacing of 2.4 × 3 m. This study includes plus trees that belong to both 3- and 4-year age groups. Each OP seed lot was planted in closely located fields 8–40 ha in size. Planting site preparation, irrigation, fertilizer schedule, and plant protection measures applied to these plots were similar to those in the species trial above.

Sixteen of the of 30 plus trees (SC8–SC24, Table 3) were selected during July and august 1992, and the remaining 14 (SC26–SC40, Table 3) were selected during July 1993 using standard criteria defined by the Simpson Tree Improvement program that follow the procedures for selecting from even-aged stands (Zobel and Talbert 1984). Therefore, all 30 trees were selected at age 3 in the field.

Besides various other parameters, height and diameter at breast height were measured at the time of selection. Stem volume index was estimated as indicated in footnote *c* of Table 3. Because metabolic properties of these trees were measured during Summer 1993, they provided measurements at age 4 for trees SC8–SC24 and at age 3 for trees SC26–SC40.

Sample collection for calorespirometric experiments

Shoot apices, including terminal buds and subapical portions, were collected near 07:00–10:00 in the field and placed in small vials with cold, half-strength Hoagland's solution containing 1% sucrose. The vials were maintained near 5°C during transport and during the period of storage prior to calorespirometric measurements. Shoot apices were collected from the two most recent primary branches in species studies and from the two most recent secondary branches of the two topmost primary branches of the plus trees.

A single sample was examined from each of 5 trees from the 17 species for measurement in the isothermal mode of calorimetry, while single samples of only 3 tallest trees were used in the scanning-mode measurements. Species samples were collected on June 2, 7, 9, 14, and 16, 1993. Sample collection order and the order of measurements of all samples and replicates were randomized.

Plus tree samples SC8–SC24 were collected on May 18, 24, 26, 31, and June 23, 1993. Samples of SC26–SC40 were collected on August 10, 12, and 16, 1993. Initial plans called for calorimetric measurements on six tissue samples per plus tree in the isothermal mode and two in the scanning mode. Limits on equipment availability, field sampling convenience, and some procedural difficulties resulted in some changes in these numbers so that plus tree sampling was not as uniform as species sampling, contributing to some degree of confounding of tree age with seasonal differences in the values for metabolic parameters.

Calorespirometric methods

Calorimetric measurements were all made using a Hart Scientific model 7707, heat-conduction, differential, scanning calorimeter (Criddle et al. 1991*b*). Approximately 1 cm long sections, including the apical meristem with subtending developing stem and leaves, were placed in the 1-cm^3 calorimeter ampules along with a 50-mL vial. Isothermal metabolic heat rates, $\dot{q}$, were measured with 40 μL of H_2O in the vial. Then, the H_2O was removed from the vial and replaced with 40 μL of 0.4 M NaOH. CO_2 produced by the respiring tissues was absorbed by the NaOH, to produce carbonate ion and additional heat at a rate proportional to the CO_2 production rate, R_{CO_2}. Metabolic heat rates were measured at 15 and 25°C for the field samples. CO_2 rates were measured at 25°C except in the selected species for which CO_2 rates were also measured at 15°C to determine the temperature dependence of CO_2 production rates. Respiratory rates of the samples declined during the first 0.5 h and then remained constant for 2–3 days at 5°C. The field to laboratory transport time was about 2 h; hence, measurement of field samples began immediately following transport. All isothermal measurements were made on the day of collection or the following day.

Throughout this report, subscripts are used to identify the temperature of measurement of respiratory parameters when measurements are at other than 25°C. For example, metabolic heat rate measured at 15°C is denoted as $\dot{q}_{15}$.

Scanning calorimetric measurements on tissue samples employed the procedures of Hansen and Criddle (1990). Samples were scanned over the temperature range from 10 to 40°C at a rate of about 7°C. All scanning measurements were made overnight on the day of, or on the day following sample collection. Three samples were measured simultaneously in about 8 h. The data collected from these experiments are metabolic heat rates as a continuous function of temperature (Hansen and Criddle 1990). The rates of heat production were measured using approximately 15 mg dry weight of shoot sections for each sample. The head space in the ampule was charged with oxygen to ensure adequate O_2 throughout each experiment.

Data analyses

Linear and quadratic regression analyses were performed using isothermal data to quantify correlations among respiration rate and growth rate parameters for all 17 species (Table 4) (SAS Institute Inc. 1992).

Canonical correlation analysis was performed between respiration measurements and origin factors using isothermal data for the selected four species. This analysis estimates the strength

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Table 2. Growth and curve-shape parameters for 17 *Eucalyptus* species.

				Scanning mode measurements					Isothermal mode measurements		
Species (code)	N^a	Height^b ($m \cdot m^{-1} \cdot a^{-1}$)	Volume^c ($m^3 \cdot m^{-3} \cdot a^{-1}$)	T_{ls} (°C)	T_{max} (°C)	T_{hs} (°C)	$\dot{q}_{max}$ ($\mu W \cdot g^{-1}$)^d	μ_q (kK)	$\dot{q}$ ($\mu W \cdot g^{-1}$)^d	R_{CO_2} ($pmol \cdot g^{-1} \cdot s^{-1}$)^d	$\dot{q}/R_{CO_2}$ ($kJ \cdot mol^{-1}$)
E. brookerana (A)	1	1.32	4.75	26.0	30.1	32.7	18.8×10^3	7.9	25×10^3	54×10^3	459
E. cypellocarpa (C)	3	1.00	2.67	27.7	31.9	35.2	12.1×10^3	7.1	11×10^3	22×10^3	495
E. dalrympleana (D)	2	1.20	3.96	26.6	31.8	35.7	15.1×10^3	7.6	20×10^3	44×10^3	458
E. delegatensis (E)	2	1.36	4.59	26.1	30.5	33.5	12.6×10^3	8.6	14×10^3	26×10^3	550
E. fastigata (F)	3	0.92	2.36	35.6	38.4	40.2	15.5×10^3	9.7	11×10^3	18×10^3	618
E. fraxinoides (G)	2	1.35	7.58	26.9	30.2	33.1	08.1×10^3	8.2	12×10^3	62×10^3	697
E. globulus (H)	3	1.11	3.06	31.8	36.2	37.4	18.1×10^3	7.1	17×10^3	32×10^3	532
E. glaucescens (I)	3	1.11	2.71	30.7	35.1	38.0	16.3×10^3	6.8	17×10^3	37×10^3	464
E. nitens (J)	3	1.41	6.69	29.3	32.4	34.7	12.6×10^3	8.4	20×10^3	40×10^3	508
E. obliqua (K)	3	0.90	3.90	29.2	32.5	34.7	10.2×10^3	8.4	10×10^3	18×10^3	571
E. ovata (L)	3	1.00	3.24	28.0	32.3	35.2	11.3×10^3	6.4	17×10^3	38×10^3	441
E. radiata (M)	3	0.51	3.65	30.1	33.1	36.2	12.3×10^3	8.7	17×10^3	38×10^3	524
E. regnans (N)	3	0.94	2.63	30.9	34.3	37.2	12.1×10^3	8.9	11×10^3	19×10^3	582
E. rubida (O)	3	0.75	4.57	29.1	33.1	35.9	16.5×10^3	8.6	19×10^3	40×10^3	472
E. smithii (P)	3	0.85	2.27	29.2	33.0	35.4	13.9×10^3	5.5	19×10^3	39×10^3	492
E. tereticornis (Q)	2	0.87	1.99	32.0	37.6	—	18.6×10^3	8.6	14×10^3	29×10^3	489
E. viminalis (R)	3	0.59	2.22	31.3	35.4	37.9	11.3×10^3	9.6	18×10^3	43×10^3	421
SE		0.05–0.29	0.27–5.5	0.4–2.7	0.6–3.7	0.7–4.8	0×10^3 to 4.7×10^3	0.1–0.8	0.5×10^3 to 1.6×10^3	1×10^3 to 7×10^3	15–105

[a]The number of trees measured in scanning experiments. Single samples were measured in isothermal mode from each of the five tallest trees from the 17 species.

[b]Height is the average specific height growth of the five tallest trees in the field using the following equation: height = (August 1993 height − December 1992 height)/December 1992 height.

[c]Volume is the average specific stem volume growth of the five tallest trees in the field using the equation, volume = (August 1993 volume − December 1992 volume)/December 1992 volume. Where, stem volume = (basal diameter)^2 × tree height.

[d]Mass was determined on a dry-weight basis.

Table 3. Growth and curve-shape parameters for 30 plus trees.

				Scanning mode measurements					Isothermal mode measurements		
Plus tree	N^a	Height[b] (m)	Volume[c] (m^3)	T_{ls} (°C)	T_{max} (°C)	T_{hs} (°C)	$\dot{q}_{max}$ ($\mu W \cdot g^{-1}$)[d]	μ_q (kK)	$\dot{q}$ ($\mu W \cdot g^{-1}$)[d]	R_{CO_2} ($pmol \cdot g^{-1} \cdot s^{-1}$)[d]	$\dot{q}/R_{CO_2}$ ($kJ \cdot mol^{-1}$)
SC8	2	10.2	13.9	29.2	34.1	33.9	14.7×10^3	6.2	15×10^3	133×10^3	404
SC9	2	11.1	25.5	27.1	31.5	34.4	11.6×10^3	5.1	16×10^3	142×10^3	402
SC10	2	09.6	09.9	29.8	35.0	35.5	15.1×10^3	6.1	20×10^3	152×10^3	473
SC11	5	11.1	19.4	30.9	35.0	32.1	13.9×10^3	6.0	19×10^3	150×10^3	447
SC12	2	10.2	19.2	31.8	36.5	39.0	10.5×10^3	6.3	11×10^3	115×10^3	351
SC13	2	09.6	10.4	33.3	37.3	39.5	26.4×10^3	8.0	19×10^3	172×10^3	422
SC14	1	10.8	18.1	30.7	32.7	35.7	7.7×10^3	8.2	16×10^3	140×10^3	413
SC15	1	10.8	18.1	31.5	35.4	37.7	12.8×10^3	7.5	21×10^3	166×10^3	451
SC16	1	10.2	12.2	28.6	35.4	39.6	16.8×10^3	7.6	23×10^3	180×10^3	464
SC17	1	10.2	17.8	32.0	33.1	38.9	8.9×10^3	5.7	16×10^3	119×10^3	478
SC18	2	09.6	18.1	31.4	34.6	34.0	20.2×10^3	7.4	21×10^3	161×10^3	481
SC19	2	08.7	12.9	30.0	34.7	38.2	14.2×10^3	7.4	14×10^3	118×10^3	446
SC20	2	09.6	19.4	30.8	34.6	33.1	15.5×10^3	6.0	18×10^3	145×10^3	443
SC21	2	09.3	10.6	27.9	30.4	34.2	10.4×10^3	5.6	14×10^3	135×10^3	391
SC22	2	08.7	14.0	29.5	31.9	35.3	10.1×10^3	6.7	12×10^3	113×10^3	395
SC23	2	08.4	14.7	35.3	39.3	—	17.8×10^3	7.4	12×10^3	140×10^3	335
SC24	2	09.9	19.3	25.9	30.0	32.8	14.7×10^3	6.8	26×10^3	204×10^3	459
SC26	2	11.7	32.9	33.3	39.5	—	16.1×10^3	7.2	16×10^3	120×10^3	464
SC27	2	11.1	32.2	29.2	33.8	37.9	11.4×10^3	6.0	13×10^3	099×10^3	478
SC28	2	11.4	34.0	32.9	36.8	41.8	14.7×10^3	7.5	16×10^3	159×10^3	363
SC29	2	12.0	27.0	34.5	40.4	—	14.4×10^3	5.3	10×10^3	089×10^3	421
SC31	2	11.1	30.3	32.7	36.7	40.3	14.5×10^3	7.7	13×10^3	097×10^3	508
SC32	2	10.5	23.6	35.6	42.0	42.4	16.9×10^3	9.7	11×10^3	136×10^3	286
SC33	3	09.9	17.3	35.3	39.5	44.5	14.4×10^3	7.3	8×10^3	060×10^3	482
SC34	3	10.5	26.0	33.3	39.5	42.9	19.2×10^3	8.0	9×10^3	101×10^3	345
SC35	2	10.5	22.6	35.7	39.5	41.7	13.1×10^3	7.8	10×10^3	095×10^3	420
SC36	2	11.1	23.3	37.2	42.5	45.4	23.1×10^3	8.6	11×10^3	112×10^3	359
SC37	3	09.9	20.0	35.0	41.0	44.8	22.9×10^3	9.2	10×10^3	066×10^3	556
SC38	3	11.4	25.6	31.7	38.0	41.1	13.5×10^3	6.9	12×10^3	116×10^3	409
SC39	3	09.3	20.2	30.7	35.6	39.6	15.2×10^3	6.4	12×10^3	108×10^3	412
SC40	2	10.8	25.9	33.2	37.0	40.5	13.6×10^3	7.1	14×10^3	138×10^3	399
SE				0–4.9	0–4.5	0–4.5	0×10^3 to 9×10^3	0.1–2.3	0.2×10^3 to 3.8×10^3	2×10^3 to 21×10^3	11–96

[a]The number of tissue samples measured in scanning experiments on each of the plus trees.
[b]Height was measured in metres.
[c]Volume was in cubic metres of the plus trees at the time of selection. Volume was estimated using the following equation: volume = (diameter at breast height)^2 × tree height.
[d]Mass was determined on a dry-weight basis.

of correlation between combined origin and combined respiration parameters (Manly 1986; SAS Institute Inc. 1992). Similar analysis on the remaining 13 species was not possible because of lack of respiration measurements on more than one seed source.

Isothermal heat rate values were collected directly as microwatts after approximately 30 min of thermal equilibration, then simply corrected for base-line values. Scanning calorimetric data were plotted on Arrhenius axes using eq. 4:

$$[4] \quad \ln \dot{q} = \ln A - \frac{\mu_q}{T}$$

where $\dot{q}$ is the metabolic heat rate in microwatts and T is the kelvin temperature. A_q is a constant, preexponential term, and μ_q is the temperature coefficient of heat rate with units of kelvins (K, or more conveniently kilokelvins, kK) (Johnson et al. 1974). Ln A_q and μ_q values were determined by linear least squares regression of segments of the curve that appear linear. Similarly, μ_{CO_2} is the Arrhenius coefficient for temperature dependence of the rate of CO_2 production on temperature.

The observed Arrhenius plots are complex. A typical plot is shown in Fig. 1 to illustrate analysis methods. Four curve-shape parameters (Fig. 1) were used to compare thermal responses of eucalypts. These parameters have been previously discussed by Anekonda et al. (1994*b*), though terminology is changed somewhat in this discussion for consistency with the literature related to Arrhenius plots. The maximum metabolic heat rate per milligram of tissue ($\dot{q}_{max}$) and the temperature of that maximum activity (T_{max}) were determined from the Arrhenius plots and the dry weight of the sample. Two additional

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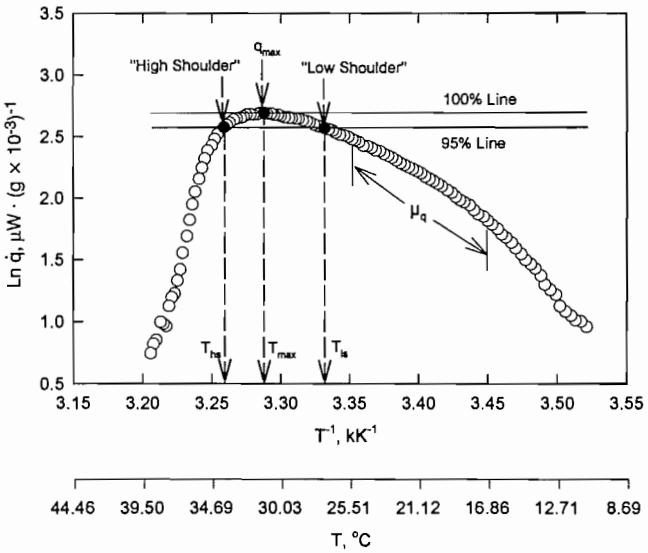
Table 4. Linear and quadratic regression of respiration parameters of 17 *Eucalyptus* species at Corning on latitude and altitude of their origin.

Trait	Intercept	Lat. (°S)	Elev. (m)	Lat.^{2}	Alt.^{2}	Lat.×alt.	R^2	F-test
Linear fit								
μg	26.2	−0.49	—	na	na	na	0.11	6.9***
Quadratic fit								
$\dot{q}$	6257	−338	—	4.60	12.1	—	0.61	42****
R_{CO_2}	57	−3	—	0.04	—	—	0.58	37****
$\dot{q}/R_{CO_2}$	−63150	3462	—	−47	254	−12	0.31	6***

Note: ***, $0.001 \geq p > 0.001$; and ****, $p \geq 0.0001$. na, not applicable.

Fig. 1. A typical Arrhenius plot for metabolic heat rate data obtained by scanning calorimetry. Mass measurements were on a dry-weight basis.



parameters are defined relative to a horizontal line (100% line) drawn through $\dot{q}_{max}$ (Fig. 1). This line passes above a rounded plateau of $\dot{q}$ values near the maximum heat rate. The heat rate changes more rapidly with increasing temperature beyond the ends of the plateau, producing shoulders. We define two shoulders, at the low (T_{ls} = low shoulder) and high (T_{hs} = high shoulder) temperature ends of the plateau, at the points where the heat rates are near 95% of the maximum value (95% line).

Results

Major differences exist in metabolic rate responses of *Eucalyptus* species to changes in temperature. Figure 2*a* graphically illustrates these differences with the results of scanning calorimetric determinations on five *Eucalyptus* species. A similar range of temperature responses exists among the species not shown. The overall shapes of the curves are similar, but differences exist in the temperatures of key features of curve shape, i.e., T_{ls}, T_{max}, and T_{hs}. These temperatures are indicators of the onset temperatures for high-temperature stress.

To illustrate the range of responses within a species, Fig. 2*b* presents scanning calorimetry results for 5 of the 30 *E. camaldulensis* plus trees studied. The native habitat of *E. camaldulensis* is broadly distributed over regions of Australia so that plants with an equally broad range of temperature responses may be expected. This figure shows that within the species *E. camaldulensis*, considerable variability exists in temperature responses of individual genotypes. Figure 2 makes it clear that inter- and intra-species variability in responses to temperature results in changes in relative metabolic rates of trees at different temperatures. We have established elsewhere by isothermal calorimetry that growth rates of eucalypts, redwoods, and poplars are correlated (r = 0.3–0.7) with their metabolic rates (Anekonda et al. 1993, 1994*b*; Criddle et al. 1996). Thus, these patterns of metabolic rate responses to temperature can be inferred as initial indicators of growth rate responses of these trees to growth temperatures.

Table 2 summarizes the metabolic heat rate versus temperature curve parameters, growth rates, and also the isothermally measured values of respiratory rates at 25°C for all 17 species examined in this part of the study. Table 3 presents a similar summary of metabolic heat rate versus temperature and growth rate data for all 30 plus trees.

Table 4 summarizes linear and quadratic regression of respiration parameters of 17 *Eucalyptus* species on latitude and altitude of their origin. μ_q alone has a linear, but inverse relation (11%) with origin latitude. In a quadratic fit, other respiration parameters are significantly related to origin factors in a complex fashion.

In general, values of T_{max}, T_{ls}, and T_{hs} for eucalypts change in a parallel fashion from species to species (Figs. 3*a*, 3*b*, 3*c*), indicating that the overall shapes of the temperature response curves are not greatly different. The values of T_{ls}, T_{max}, and T_{hs} fall in the range from about 25 to 40°C. Summer temperatures in this range are common at the growth site in Corning, Calif. Thus, the differences in species responses to high temperature are in a temperature range that can significantly influence relative growth of the different species in the Corning plantation.

The values of μ_q and $\dot{q}_{max}$ for each species are plotted in Figs. 3*d* and 3*e*. Both μ_q and $\dot{q}_{max}$ vary among species. However, the patterns of change of $\dot{q}_{max}$ and μ_q values from species to species do not parallel each other and do not parallel the changes noted in the shoulder and peak

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Fig. 2. (*a*) Arrhenius plots for five *Eucalyptus* species. (*b*) Arrhenius plots for five *Eucalyptus camaldulensis* plus trees. Mass measurements were on a dry-weight basis.

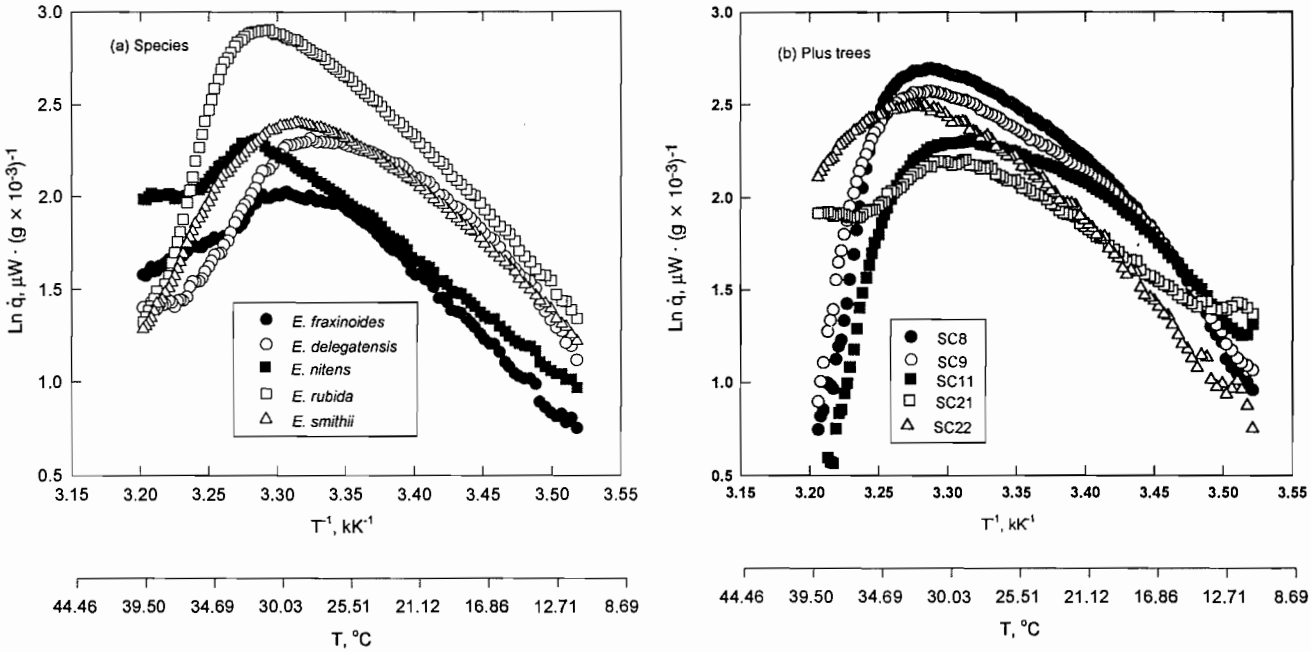

Fig. 3. Variation in values of (*a*) T_{ls}, (*b*) T_{max}, (*c*) T_{hs}, (*d*) μ_q, and (*e*) $\dot{q}_{max}$ among 17 species of *Eucalyptus*. Error bars are standard errors. The letters indicate species as listed in Table 1. Mass measurements were on a dry-weight basis.

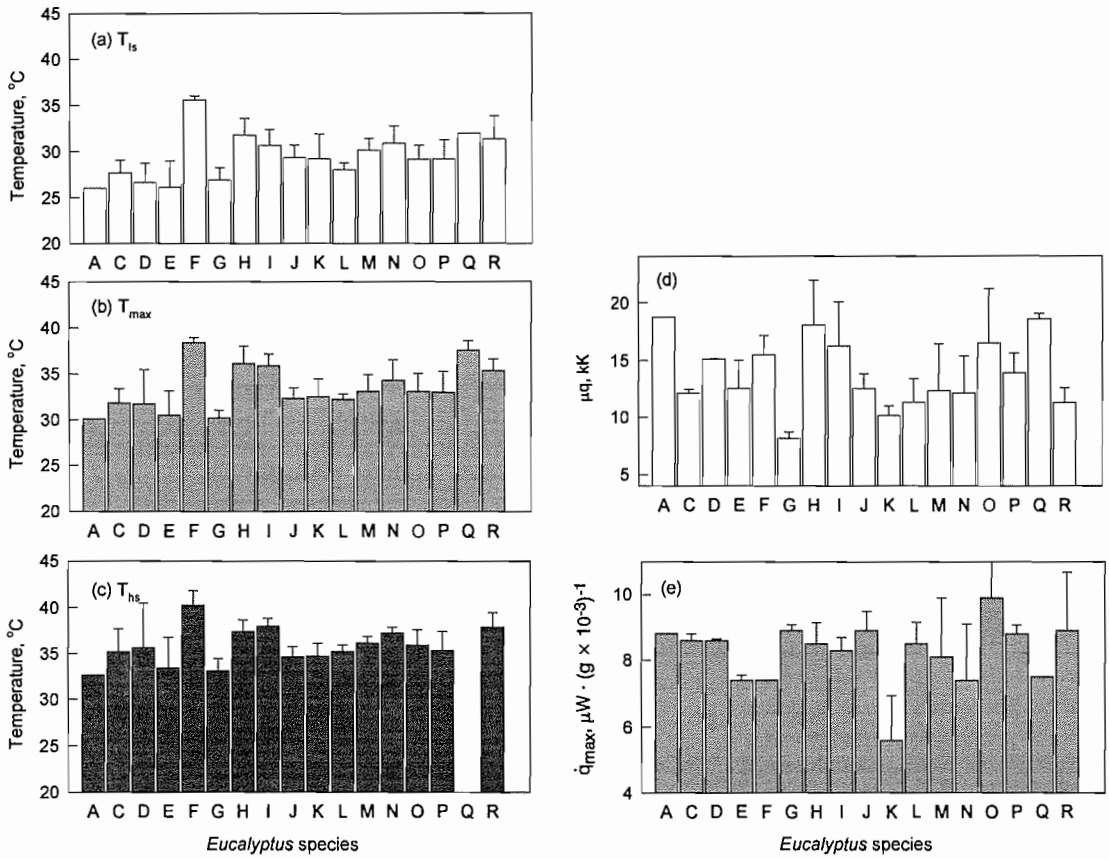

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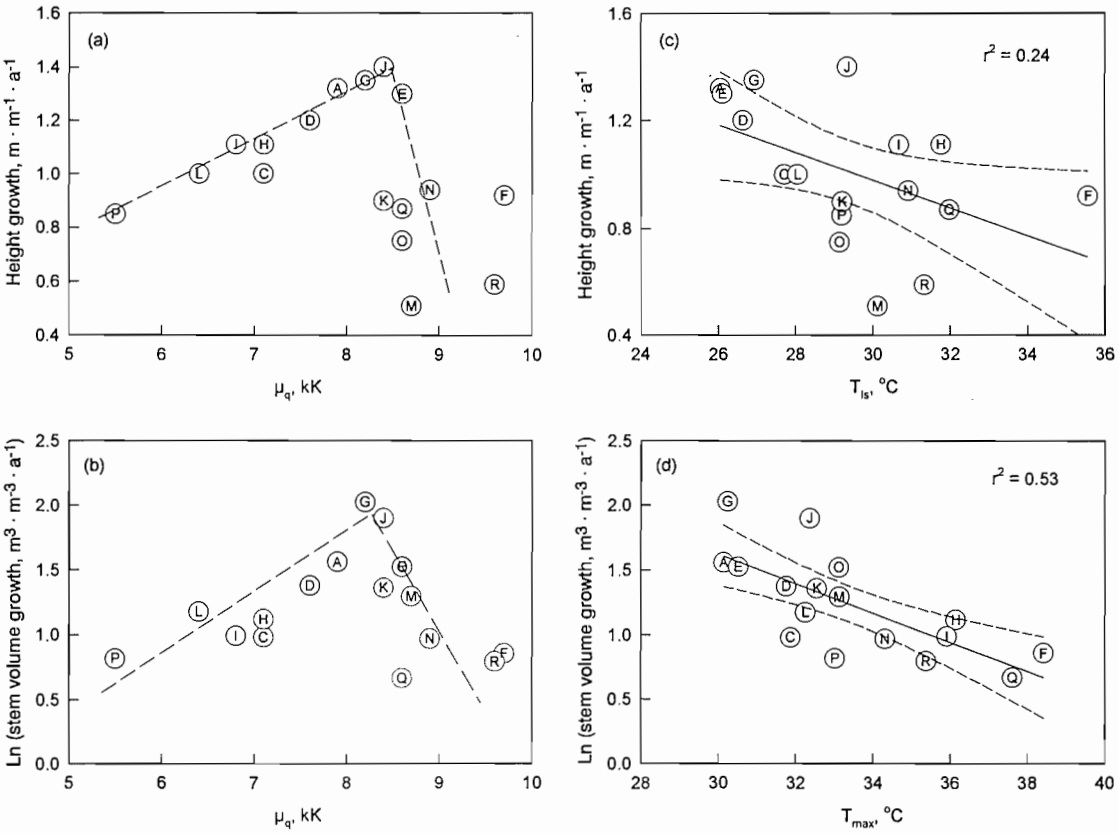
Fig. 4. (*a*) Relationship of the temperature coefficient of metabolism to height growth rates of 17 *Eucalyptus* species. (*b*) Relationship of the temperature coefficient of metabolism to stem volume index rates of 17 *Eucalyptus* species. (*c*) Relationship of T_{ls} to height growth rates of 17 *Eucalyptus* species. (*d*) Relationship of T_{max} to the stem volume index of 17 *Eucalyptus* species. The broken lines indicate 99% confidence intervals for regression lines. The letters indicate species as listed in Table 1.



temperatures. There is no apparent relationship between measured height growth of *Eucalyptus* at Corning and the maximum metabolic heat rate, $\dot{q}_{max}$. Therefore the maximum metabolic heat rate at high temperatures does not determine growth in the climate at Corning. No simple relationship between $\dot{q}_{max}$ and growth at Corning is expected because of the large diurnal and seasonal temperature changes at this location. If growth temperature and metabolic efficiency were constant, the tree with the highest $\dot{q}$ at that constant temperature would be expected to be the most rapidly growing.

In contrast, Fig. 4*a* shows that height growth data for the 17 species is systematically related to μ_q measured over the range from 15 to 25°C. The lines drawn in this figure are visual best fits, meant only to display the general trends. Height growth is greatest for species with μ_q values near 8.4 kK. Growth rates are lower for species with either higher or lower values of μ_q. A similar conclusion is obtained when stem volume index is used as the measured growth parameter (Fig. 4*b*). Standard errors based on measurements of μ_q for different trees within each species range from 0.1 to 0.8 kK, with an average of 0.3 kK. Metabolic rates are exponentially related to μ_q so that small differences in μ_q can reflect very large changes in relative metabolic rates, and thus growth rates, of the species as growth temperature changes.

Values of T_{ls}, T_{max}, and T_{hs} also show a systematic relationship to growth of the species. Figures 4*c* and 4*d* show plots of T_{ls} and T_{max} against height and volume growth, respectively. T_{ls} and T_{max} have the lowest values in those species with highest growth rates. Table 2 shows that T_{max} varies across the species by more than 7°C, from 30 to above 37°C.

All of the plus trees show rapid growth rates at Corning, yet many do not have the values of μ_q, T_{ls}, T_{max}, and T_{hs} suggested from species analysis in Fig. 4 to be optimum for rapid growth. Temperature coefficients of the superior growing trees cluster around 6.5–8 kK, with an average value of 7.4 kK. T_{ls} has an average value of about 32°C. These data show that no single respiration parameter can be identified as a unique determinant of growth rates.

The assumption that origin data are successful predictors of appropriate planting sites is tested with the data of Fig. 5. The growth rates in Corning of trees from the 15 species with available geographical origin information for the selected provenance are presented as a function of

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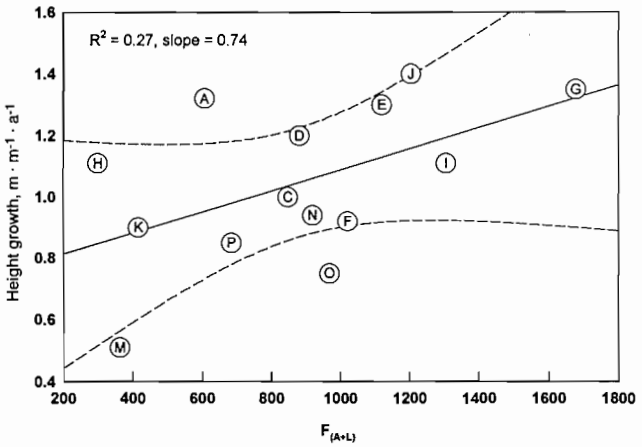
Fig. 5. Relationship of height growth to a function of altitude and latitude of species origin, (F_{A+L}) = (85 m) (L − 35°C) + (A − 200 m). The letters indicate species as listed in Table 1. The broken lines indicate 99% confidence intervals for regression lines.



latitude and altitude (F_{A+L}) of seed origin. Longitude is not considered here because latitude and longitude are largely covariant for our samples.

Figure 5 shows a weak correlation between latitude and altitude of species origin and height growth at Corning. For these species, as seed source latitude and altitude increase, i.e., as origin climates become generally cooler, growth rate at Corning increases. A similar relationship is observed when growth is measured as stem volume growth. Each of the respiration parameters summarized in Tables 2 and 3 was examined to determine whether any could account for this growth–origin relation. Regression analyses investigating relations among all measured respiration parameters and seed origin parameters for the 17 species (Table 4) showed that regression of μ_q (i.e., the temperature coefficient of metabolic heat rate) on latitude yielded a significant linear fit. A small (11%) but significant ($p < 0.001$) portion of the variation in μ_q with species is attributable to differences in latitude. This analysis indicates that species from lower latitudes and altitudes, i.e., plants from generally warmer climates have higher values of μ_q (see also similar conclusions from previous examination of other species, Criddle et al. 1994). Using additional terms (quadratic and cross-product) in the regression equation indicates additional complex dependence of respiration parameters on origin (lower portion of Table 4). Stem volume growth at Corning and temperature at maximum metabolic heat rate still showed no apparent relationship with origin, but other respiratory parameters showed significant but weak ($0.01 < p < 0.0001$) degrees of complex relationships with the origin factors. Thus, climate as represented by origin factors does show significant, but complex, relationships with respiratory parameters. We conclude that species native to different climates have unique combinations of respiration parameters.

Canonical correlation analysis was used to investigate whether combinations of individual effects among respiration and species origin factors define growth rates at Corning without assuming any growth model. Respiration measurements were made on two different trees of four different species, in replicate, for each provenance of eight different respiration parameters and three origin factors. Canonical correlation analysis of the combined respiratory and origin factors is summarized in Table 5. Altitude, with a coefficient of 1.15, was the strongest contributor to the origin variables in this study. The sign of the coefficient for longitude is negative; as expected, since the longitude of our samples generally decreases as latitude increases across the sample collection area. R_{CO_2} at 15°C has the largest coefficient (6.23) among the respiration variables. The value of μ_{CO_2} is the second largest (3.31) term. Coefficients of $\dot{q}$, R_{CO_2} at both 15 and 25°C, $\dot{q}/R_{CO_2}$ at 25°C, and μ_{CO_2} are all positive. $\dot{q}_{15}$, $\dot{q}/R_{CO_2}$at 15°C, and μ_q all have significant negative coefficients.

Figure 6 plots the averages and standard deviations for the first pair of canonical variables, respiration and origin, for each of the eight provenances from the four species. The values yield a linear relationship between the origin and respiration parameters. This plot shows that respiratory parameters of trees grown in a common garden at Corning vary in a systematic fashion with geographic origin and climate.

Table 5. Canonical correlation analysis of four selected *Eucalyptus* species.

(A) Provenance geographic origin information

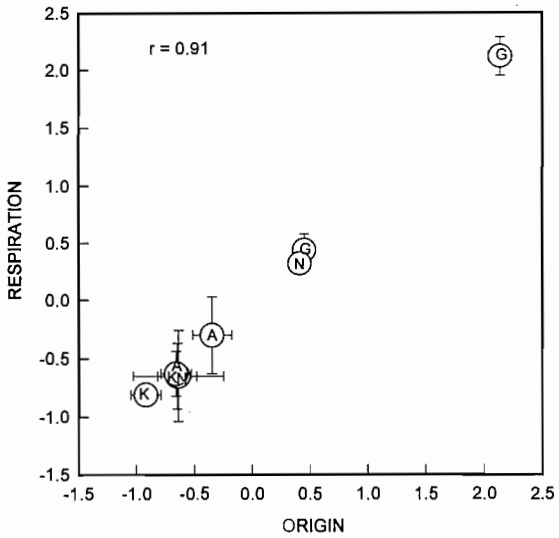
Species	Provenance	Alt. (m)	Lat. (°S)	Long. (°E)
E. brookerana	1	440	42.3	147.9
E. brookerana	2	500	38.6	143.8
E. fraxinoides	1	1750	36.5	149.4
E. fraxinoides	2	1100	36.5	149.3
E. obliqua	1	1000	29.0	152.1
E. obliqua	2	370	37.9	145.9
E. regnans	1	450	42.4	147.9
E. regnans	2	900	37.6	145.5

(B) Coefficients for the first pair of canonical variates for respiration and origin parameters.

Respiration[a]		Origin	
Parameter	Coefficient	Parameter	Coefficient
$\dot{q}$ at 15°C	−0.29	Latitude	0.18
$\dot{q}$ at 25°C	0.72	Longitude	−0.19
R_{CO_2} at 15°C	6.23	Altitude	1.15
R_{CO_2} at 25°C	2.19		
$\dot{q}/R_{CO_2}$ at 15°C	−0.35		
$\dot{q}/R_{CO_2}$ at 25°C	3.14		
μ_q	−1.96		
μ_{CO_2}	3.31		

[a]Respiration values used for calculation of values in this table are given in Table 2. μ_{CO_2} was measured in kK.

Fig. 6. The canonical correlation between the first pair of canonical variates representing origin factors and respiration properties of two provenances of each of four *Eucalyptus* species; A, *E. brookerana*; G, *E. fraxinoides*; K, *E. obliqua*; and N, *E. rubida*. The letters indicate species as listed in Table 1.



Discussion

In establishing production sites, a common assumption is made that geographic origin factors (longitude, latitude, and altitude) for *Eucalyptus* species and other trees are useful predictors of planting locations where good growth rates may be expected (Eldridge et al. 1993). Longitude, latitude, and altitude act as surrogates for climate with this assumption. Our results thus far confirm the strong relations between growth and origin temperature that form the basis for this assumption, but the relation of growth rate to μ_q suggest that temperature fluctuations may be an important part of climate not necessarily reflected by origin parameters.

The most readily apparent overview of differences in temperature responses among species and among individual plants within a species is shown with the scanning experiments (Fig. 2). Each thermogram for the different *Eucalyptus* species and plus trees describes the short-term responses of respiration rate to temperature, over much of the temperature range commonly encountered during rapid growth. The curves in Fig. 2 suggest that *E. rubida* and *E. nitens* may continue rapid growth at temperatures well above those that cause stress in species such as *E. delegatensis*. The thermograms differ both in metabolic responses at high temperatures and in the temperature coefficient of metabolism at lower temperatures. Both these differences can be important determinants of growth rate differences in a given climate.

Consider first the consequences of differences in metabolic responses at high temperatures. Metabolic rates and hence growth rates of *Eucalyptus* will not continue to increase with temperature beyond some stress limit (Fig. 2). At T_{ls} the metabolic rate first begins to deviate downward from a linear extrapolation of the Arrhenius plot at lower temperature. At this temperature, the rate of metabolism no longer increases as rapidly as expected from chemical kinetics, but slows as a result of limitations within the plant. A tree that does not undergo this rate limitation until higher temperatures might, if other factors are equal, have a growth rate advantage at high temperatures.

The decline in heat rates above T_{max} and T_{hs} is evidence of a decreased rate or alteration of metabolic reactions. Changes in metabolic activity near T_{hs} and above appear to be irreversible in our studies with detached tissues. Activity loss of this type has generally been attributed to structural changes within a cell (Johnson et al. 1974; Levitt 1980; Berry and Raison 1981; Steponkus 1981; Lambers 1985). Currently it is not possible to identify T_{ls}, T_{max}, or T_{hs} with the growth-limiting high temperature, since all change in parallel. Events at each temperature possibly play a role.

Plants grown at Corning spend most of the time at temperatures below T_{ls}, but much summer growth occurs during periods of higher temperatures. Since average growth rates of species at Corning increase and then decrease with an increase in T_{ls} and T_{max} (Fig. 4), some high-temperature response appears to critically affect growth.

Next, consider the effects of differences in μ_q on relative growth rates. At the lower temperatures, metabolic rate increases with temperature approximately as expected from chemical reaction rate theory (Fig. 2). Any two plants with differing values of temperature coefficients in this range will have continuously changing differences in their relative rates of metabolism. Plants with higher μ_q will increase metabolic rates and growth rates faster with increases in temperature than plants with lower μ_q. The plants may switch orders of metabolic rates (and growth rates) on either side of the crossover temperature showing an interaction with temperature change (also see Criddle et al. 1994). In the constantly changing temperatures during field growth, the average kinetic temperature can determine which of these plants grows fastest. The crossover in relative respiration rates with temperature appears to be common among other species such as maize, lettuce, poplar, in addition to *Eucalyptus* (Criddle et al. 1994).

Values for μ_q and T_{ls} for the plus trees do not show the simple relations with growth rates noted for the species. The scatter in these data demonstrate that an assumption of constant substrate carbon conversion efficiency for all plants is not valid for this group of plus trees. μ_q, T_{ls}, and possibly T_{max} values still play a central role in relating growth rates to climate, but it is the combined contributions of all respiratory factors and their interaction with the environmental that defines growth rate. This conclusion is verified in a related study (Criddle et al. 1996), where three *Eucalyptus* clones with different μ_q values were grown in controlled environment conditions to measure the precise relations among their metabolic rates, biomass production rates, and temperature.

Though all of the respiratory parameters contribute to the temperature–activity relationships evident in Fig. 2, only μ_q gave a significant first-order correlation with origin (Table 4). Earlier studies (Criddle et al. 1994; Hansen et al. 1995) showed that μ_q plays a strong role in determination of the fitness of a plant for a particular climate. Plants with origins from warmer climates (lower latitudes and lower altitudes)

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have relatively high values of μ_q. Plants from high latitudes and altitudes have low values of μ_q. Therefore, values of μ_q may indicate the ability of a plant to survive and grow well in a given environment. As a consequence, some correlation between μ_q and *Eucalyptus* growth in the Corning climate was expected. Still, the nature of this relation was not simply predictable.

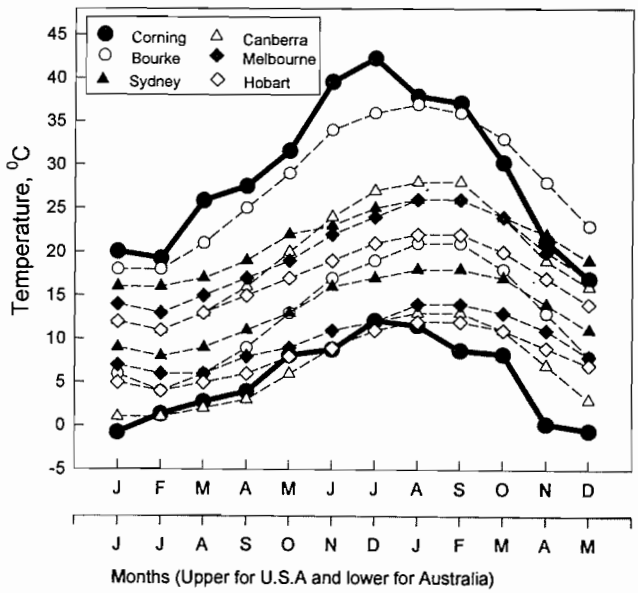
The 17 *Eucalyptus* species are separated into two classes, with major differences in growth for plants with μ_q less than or greater than 8.4 kK (Fig. 4). The class with μ_q less than 8.4 has higher growth rates with higher μ_q. In this same region, the lower the value of T_{ls}, and T_{max}, the better the growth. In the second class, species with μ_q greater than 8.4 have lower growth rates as μ_q gets larger. In a different growth climate, the distribution of *Eucalyptus* species between these classes is expected to change. The order of growth rates of the species would also change. The best growing plants would be those with μ_q and T_{ls} values matched to the new climate. For colder climates, the optimum μ_q value will be below 8.4 kK and optimum T_{ls} may be higher (Fig. 4).

These findings suggest that it is possible to use rapidly measured respiratory values of μ_q and T_{ls} to identify trees from a population that are suitably matched for optimum growth in the current growth site or are suited for growth at other sites with defined climates. However, a greater understanding of the relation between climate, T_{ls} and μ_q is required to make specific predictions of growth at a given location without first acquiring a database on growth and respiration at that site. The major problem lies with our understanding of factors related to T_{ls}. The observation that species with relatively low values of T_{ls} grow most rapidly at the Corning plantation is unexpected because of the frequent exposures of trees to high summer temperatures at this site. Optimal growth with low T_{ls} appears contrary to intuitive conclusions that temperature stress at high temperatures could play an important role in limiting total growth. Our results indicate, however, that μ_q and some interplay between μ_q, T_{ls}, and the climate at the growth site may be major growth rate determinants for these species at this site.

If common latitude and altitude between origin and planting sites were the primary determinant of which species would have the fastest growth rate at a given site, maximum growth would be expected for those species with $F_{(A+L)}$ near 625, the value for Corning (Fig. 5). But growth rates of the species at Corning continue to increase up to $F_{(A+L)}$ values at least as high as 1800. Thus, the best growing species at Corning have geographical origins at much higher latitudes and altitudes than the Corning site. Species from locations in Australia with lower average temperatures than those at Corning are most suited for rapid growth at Corning. Average temperature, while sufficient to correlate growth at different sites is clearly not sufficient for direct comparison. Seasonal temperature fluctuations must also be considered.

Figure 7 is a plot of mean monthly high and low temperatures for Corning and for Australian cities near the seed collection sites. The months are offset by six months to account for differences in hemispheric growth seasons. Temperature fluctuations are much larger at Corning than

Fig. 7. Seasonal temperature fluctuations at Corning, Calif. and at five locations in Australia. Average monthly high and low temperature values are shown for Corning, Bourke, Sydney, Canberra, Melbourne, and Hobart.



at any of the Australian seed collection sites. The range of diurnal and seasonal fluctuations is apparently a factor in determining plant growth rates. Plants with a temperature dependence of metabolism, μ_q, matched to the range of temperature fluctuations at a given climate grow better than those that are not matched. Note that a regression analysis identified μ_q to be inversely related to latitudes of seed source origin (Table 3).

While Fig. 5 Shows species growth at Corning is correlated with latitude and altitude of origin, there is considerable scatter in this plot. Canonical analysis of combined respiratory variables and origin factors for four eucalypt species shows a precise relation between respiration properties of individual trees and their origins when variables are weighted correctly (Fig. 6). In spite of a complex relationship between individual respiration and growth parameters, multiple measures of respiration considered together can provide an accurate relationship with the origin factors.

Since combined measures of respiration parameters are related to both tree growth rates and origin factors, measurements of respiration parameters can provide an understanding of the relation between origin and growth parameters and in turn the process of adaptation of species to the environment. Several important conclusions are apparent from these correlations among temperature responses of growth, temperature dependencies of metabolic parameters, and the absolute values of metabolic rate and efficiency. The combined data from Figs. 2, 3, and 4 suggest that definition of which species will grow most rapidly at Corning is strongly dependent on understanding the differences in the metabolic activity responses of each species to temperature change. Temperature fluctuations and the amount of time of growth at each temperature must be considered in matching species to growth sites. These

observations make it possible to understand why latitude and altitude of origin are useful, but not sufficient, parameters for identifying which Australian species will grow well at Corning. Growth over a season is determined by the response of the tree metabolic rates to temperature integrated over time.

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