Effects of climate on growth traits of river red gum are determined by respiration parameters

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Abstract.   Temperature is the major uncontrollable climate variable in plantation forestry. Matching plants to climate is essential for optimizing growth. Matching is usually done with field trials because of the lack of a predictive relation between laboratory measurements of physiological responses and climatic factors affecting growth. This paper evaluates the potential of using respiration parameters for selection of appropriate drainage or seed sources within a drainage for superior growth in a particular climate. The growth traits measured are tree height, stem diameter and stem volume. The respiratory parameters measured are respiratory heat rate, rate of CO_2 production, and temperature dependence of respiratory heat rate. Five open-pollinated families from each of nine seed sources of river red gum (*Eucalyptus camaldulensis* Dehnh.) were studied following selection from a larger set of seed sources planted at three plantations in California. The three plantations differ in climate, particularly in extreme temperatures, diurnal temperature variability and total rainfall. Within each plantation, growth and respiration parameters show high genetic variation [overall coefficient of variation (CV) = 14–58%, family CV = 11–33%], with at least one of these traits showing significant ($P < 0.10$) difference due to drainage, or source within drainage, or families within source. The relationship of growth to respiration for each trait differs, depending on test plantation, origin drainage, source or family, suggesting a unique pattern for each trait. Correlation of drainage level averages between growth and respiration were strongly negative and significant ($P = 0.10$–0.01). Rankings for drainages between paired plantations were strong and significant ($P = 0.10$–0.05) only for respiration, but not for growth traits.

Keywords: climate, *Eucalyptus*, growth, metabolic rate, respiration efficiency.

Introduction

River red gum (*Eucalyptus camaldulensis* Dehnh.) is the most widely distributed of all eucalypts, covering most of the Australian continent (Pryor 1959*a*, *b*; Chippendale 1988). Because of its natural adaptation to both temperate and tropical climates with both winter and summer rains, it is also the most widely planted species in arid as well as semi-arid regions around the globe. Over 70 *Eucalyptus* species have been grown in California in the past 125 years since their introduction (Ledig 1983). Eucalypts are popular as windbreaks, roadside screens, and recently as sources of short-rotation fuel biomass and pulp for paper industries. Recognizing these uses, the University of California and the Institute of Forest Genetics initiated species trials throughout California (King and Krugman 1980). River red gum was one of the first species to be included in a detailed provenance test plantation established in 1976 at Concord, CA. In this test, the top performing provenances all came from the Murray and Darling River drainages and adjacent watersheds in Victoria, South Australia and New South Wales. This is a region of relatively low rainfall, cool maximum temperatures and a long season with frost (> 120 d) (Ledig 1983).

Although technologies for production and processing of eucalypt tree materials are well developed, the question of which trees to plant at any given plantation for maximal yield still poses difficult problems. This question applies to selection of species and to identification of seed sources and genotypes within a species (Zobel and Talbert 1984). Because trees require many seasons to mature, early selection of superior genotypes that match physiological characteristics to climate at a foreign growth site is essential for rapidly optimizing production. Presently, selection of exotic eucalypt trees for wood or fuel production at a foreign site is made largely on the basis of field trials, i.e. by growing a collection of seed sources at a site and selecting and breeding

the ones that perform best (Elridge *et al.* 1993). Note that knowledge gained at one site by these techniques is not transferable to a second site unless the two climates are similar (Booth and Pryor 1991). Because tree growth trials require many years of expense with little economic productivity, a laboratory method based on rapid determination of physiological parameters that are predictive of successful growth in a foreign climate would provide large savings for growers.

This study and others in our laboratories are addressing three questions. First, can seed sources or families within seed sources be selected for a foreign planting site on the basis of respiration parameters? Second, to what extent do eucalypts acclimate respiration to climate differences between the planting site and site of origin? Third, does this acclimation affect the relation between respiration and growth?

Rapid and accurate selection for fast growth in a foreign environment on the basis of metabolic measurements presumes knowledge of an accurate, quantitative relation between metabolic properties and growth rate and the effects of environment on that relationship. That respiratory and tree growth rates and growth temperature are related has previously been established (Larcher 1980; Levitt 1980; Criddle *et al.* 1991*a*, 1994, 1995, 1996, 1997; Anekonda *et al.* 1994*a*, *b*, 1996, 1999; Hansen *et al.* 1994, 1995; Jeffree and Jeffree 1994, 1996). However, what has not been well understood outside of our work is that direct calorimetric measurements of respiratory heat rates together with CO_2 or O_2 rate measurements are essential for quantifying the relation between respiration and growth rates. The rate of respiratory gas exchange is directly proportional to the energy produced by oxidation of substrate, and the respiratory heat rate is the rate of energy loss to the surroundings. The difference between these two is the rate of energy conservation by the plant, i.e. growth rate. Attempting to predict growth rate from gas exchange rate alone is thus like trying to balance a budget from information on income without knowledge of expenses. Such attempts (e.g. Wilson and Jones 1982) at best can only succeed under very narrow circumstances (e.g. Lambers 1985) and cannot provide general relationships valid across a wide range of environmental variables.

This paper provides further evidence that tree respiration properties are related to rates of biomass accumulation as a function of climate, and thus calorespirometric methods can provide a means to rapidly match exotic tree seedlings to planting sites for biomass production. Respiration rate (metabolic heat rate and CO_2 rate), temperature dependence of respiration rate, and growth performance data for nine seed sources of river red gum planted at three California plantations with different climates are reported in this study. There are basically two approaches to determine the ability of trees to acclimate their metabolism to a change in climate. One approach searches for correlation between metabolic properties of trees in their native environment and climate

gradients across a cline. This approach assumes that native plants have evolved to an optimum match with their environment. However, it is survival, not growth, that is optimized, and plantation forestry seeks to optimize growth. Another approach is to search for metabolic characteristics that make a genotype adaptable to exotic environments by studying plants growing in foreign environments. Two main objectives of this study were:

(i) to assess the extent of genetic variation in respiration and growth traits at different growth sites; and

(ii) to determine the influence of origin factors on the relationship between these traits.

Materials and methods

River red gum (*Eucalyptus camaldulensis* Dehnh.*)* seeds from three river drainages and a valley in northwestern Victoria, Australia were obtained by the Institute of Forest Genetics at Placerville, CA for establishing three plantations at Anderson, Arvin and Concord, CA. Climate data for the three planting sites are presented in Table 1. Drainages, seed sources, and families for the subset of trees used for this study are presented in Table 2. The plantation sites were prepared by removing pre-existing stumps and ripping the land 1 m deep in June 1987. The land was drip irrigated prior to planting. Seedlings were raised in containers from seed sown in October 1986. Tree seedlings were planted 7–12 August 1987 in 10 cm soil-augured holes and were drip irrigated at 2–3 L week^{-1} during the first two seasons after planting. Competing vegetation was hand-released around each plant in January 1988, controlled by applying herbicide (Roundup, Monsanto) around each plant in March 1988, by mowing between rows in March 1988 and again by applying herbicides (Roundup and Princep, Monsanto) in January 1989.

Seedlings were planted in eight completely randomized blocks with 21 seed source plots in each block. Each source plot contained 24 trees, with two trees representing each of 12 families in a source. Each plantation site thus has 4032 trees (8 blocks × 21 sources per block × 12 families per source × 2 trees per family = 4032 trees). Of the 12 families, three top-ranked and two bottom-ranked families from each source were selected based on their 5½-year average volume at all three plantations.

Growth data

Tree height and stem diameter at breast height were measured on 5½-year-old trees during January–February 1993. Stem volume index (volume) was estimated using the equation: volume = (diameter at breast height)^2 × tree height.

Samples for calorespirometric measurements

This study used nine of the total 21 seed sources, including four sources from Wimmera drainage, two from Yarriambiack drainage, one from Lowan Valley and two from Avon drainage (Table 2). These nine sources represent an even north–south sampling of seed sources across their native Australian range. The origin of each seed source is given in column 3 of Table 2. In each seed source, the 12 families were ranked by 5½-year average stem volume and the three largest (top-ranked) and two smallest (bottom-ranked) were selected for this study. Each selected family was given a two-letter code (see column 4 of Table 2). The last column gives the average of stem volumes for top- and bottom-ranked families at each plantation.

Three to five trees were chosen randomly from each family for respiratory measurements. Therefore, at each plantation, 135–180 trees were sampled (9 sources × 5 families per source × 3–4 trees per family = 135–180 trees). Sample collection was designed for maximum effi-

Table 1. Climatological data (1992–1994) for three provenance test plantations

Only the active growth periods during April through September of 1992–1994 were considered for compilation of values for DHIGH, DLOW, HLDIF, STDHI, STDLO, and STDIF. SD, standard deviation

Climatological data (CODE)	Red Bluff (Anderson)	Tejon (Arvin)	Concord
Av. daily high temp. (DHIGH) (°C)	30.7	31.8	27.9
Av. daily low temp. (DLOW) (°C)	14.3	13.6	13.1
Av. difference in daily high-low temp. (HLDIF) (°C)	16.4	18.2	14.8
SD in daily high temps (STDHI) (°C)	6.4	5.4	4.7
SD in daily low temps (STDLO) (°C)	4.1	5.4	2.3
SD in daily high–low temp. difference (STDIF) (°C)	4.1	3.1	3.8
Av. number of daily lows per year below 0°C (BEL0)	22.0	41.3	5.3
Av. number of daily highs per year above 37°C (ABO37)	27.7	23.7	3.7
Av. rain fall per year (RAIN) (cm)	66.9	31.2	46.2

ciency. Beginning at one end of the plantation, available trees were sampled until the prescribed number from each family was achieved. All the samples were collected and measured from April 17–June 7, 1994 (6½-year age). Seasonal variation was minimized by taking only fresh and actively growing meristems. Sampling times were 16–19 May and 6–7 June (Anderson), 6–12 May (Arvin), and 17–18 April and 1–6 June (Concord).

Trees were up to 15 m tall. Shoot apices and subapical portions with fresh leaves were collected from the highest secondary branches that could be reached (up to 10–12 m) and placed in small vials with cold, half-strength Hoagland's solution containing 1% sucrose. The vials were placed on ice during transport and stored in an aerated refrigerator at 5°C during the period of calorespirometric measurements. Respiratory rates of the samples declined during the first 0.5 h and then remained constant for 3–4 d. Metabolic rates on about half the samples from Arvin were measured near the plantation site, while the remaining half were measured at UC Davis. All samples from Anderson and Concord were measured at UC Davis.

Calorespirometric measurements

Measurements of metabolic heat rate (q)* and CO_2 production rate (R_{CO2}) were made using a Hart Scientific Model 7707, heat-conduction, differential, scanning calorimeter operated in the isothermal mode (Criddle *et al.* 1991*b*; Criddle and Hansen 1999). Metabolic heat rate, q or dQ/dt, is the time derivative of heat production due to plant metabolic activity in the dark. R_{CO2}, is dn_{CO_2}/dt, the time derivative of CO_2 production in the dark. Sections approximately 1 cm long, including the apical meristem with subtending developing stem and leaves, were placed in the 1-cm^3 calorimeter ampules along with a 50-µL vial. q was measured with the vial empty. Then, 40 µL of 0.4 M NaOH was added to the vial and the CO_2 rate measured as an increase in total heat rate that is proportional to R_{CO_2} (Criddle *et al.* 1991*b*; Criddle and Hansen 1999). q and R_{CO_2} were measured at 25°C on all samples. Measurements of q were made at 15°C on one half of the samples chosen randomly. The Arrhenius temperature coefficient of metabolic heat rate (μ_q) in kK and the ratio of heat rate to CO_2 rate (q/R_{CO_2}) in kJ mol^{-1} were derived from the original variables (Criddle *et al.* 1994; Hansen *et al.* 1994).

Statistical analyses

Differences in growth and respiration traits between top- and bottom-ranked families (objective 1) were tested for each plantation using Cochran's approximate '*t*'-statistic for unequal variances (TTEST pro-

cedure, SAS Institute Inc., 1992). In addition, plantation averages were plotted to visualize the differences in respiration and growth between the ranks.

Top-ranked families were deemed commercially more important than the bottom-ranked families, thus analyses of variance were performed on each respiration and growth trait in both of these sets of families for comparison in each plantation. Variance components for each respiration and growth trait were associated with differences due to drainages, sources within drainage or sources (drainage), families within source or families (source), and trees within family or error by use of the VARCOMP procedure for unbalanced nested classification (SAS Institute Inc., 1992). Note that the differences between three river drainages and the valley are combined under the variance-due-to-drainages component. River drainages occupy much broader environments than individual seed source populations or families within populations. Thus, the influence of origin factors on these three levels of variance components (drainage, seed source, family) must be different. The GLM procedure of the SAS statistical software was employed to test the significance of these components.

The influence of origin factors on the relationship between growth and respiration traits (objective 2) was examined using phenotypic correlations at three levels (drainage mean, seed source mean, family mean) in each plantation again using trees only from the top-ranked families. In this same set of trees, rank changes between plantations for drainages, sources and families in respiration and growth traits were also examined.

Results

Plantation averages for growth and respiration traits differ between top and bottom ranked families

Figure 1 shows height, diameter, and stem volume, respectively, for top- and bottom-ranked families averaged over all trees in nine seed sources and plotted for each of the three plantations. Average growth was best at Anderson and worst at Concord for both top- and bottom-ranked families. The difference in size between top and bottom families is significant ($P < 0.05$) in all growth traits at all three plantations, but the difference is smaller at Concord than at the other two sites, apparently because top families grow slower at Concord.

*Abbreviations used: CV, coefficient of variation; q, metabolic heat rate; R_{CO_2}, CO_2 production rate; μ_q, Arrhenius temperature coefficient of metabolic heat rate.

Table 2.   Selected geographic seed sources, top and bottom-ranked families and family averages for stem volume from three plantations at Anderson (And), Arvin (Arv) and Concord (Con), CA, USA

Lowan is a valley, the rest are river drainages. Seed sources are given in ascending order from southern- to northern-most regions in Australia. Latitude, longitude, and elevation of seed sources are given in the third column. For seed source 1 at Anderson, the average volume of the 3 top-ranked families (BF, BI, BD) is 3.42 m^3 and of the 2 bottom-ranked families (BC, BM) is 2.2 m^3. Similarly, 3.53 and 1.82 at Arvin and 2.06 and 1.50 at Concord are the volume averages for top- and bottom-ranked families in source 1, respectively. These two values are paired for comparison purposes, hence three pairs of comparisons are possible for each source, totaling 27 such comparisons for all sources at all plantations

River damage or valley	Seed source	Seed source origin variables			Families selected in each seed source (largest or top-ranked and smallest or bottom-ranked) and family codes	Average volume (m^3) for 3 largest and 2 smallest families at each plantation		
		Latitude (° S)	Longitude (° E)	Elevation (m)		And	Arv	Con
Wimmera	1	37°13′	143°16′	325	3 largest: BF, BI, BD	3.42	3.53	2.06
					2 smallest: BC, BM	2.20	1.82	1.50
	3	36°35′	142°00′	100	3 largest: CA, CC, CD	2.66	1.97	1.46
					2 smallest: CK, CG	1.47	2.40	1.02
	6	35°49′	141°56′	75	3 largest: DM, DL, DN	2.91	3.33	2.63
					2 smallest: DR, DO	2.68	3.67	2.08
	12	35°24′	141°53′	45	3 largest: GQ, GP, GO	2.83	2.58	1.68
					2 smallest: GM, GI	1.75	2.20	1.64
Yarriambiack	13	36°20′	142°24′	110	3 largest: GS, HC, GY	3.07	2.95	2.86
					2 smallest: GU, GT	2.69	1.54	2.01
	15	35°44′	142°23′	75	3 largest: IA, HU, HS	3.45	3.33	2.35
					2 smallest: HV, IC	2.74	1.42	2.02
Lowan Valley	17	36°50′	141°50′	135	3 largest: IQ, IS, JB	3.59	2.85	2.11
					2 smallest: IU, IT	1.57	0.72	1.71
Avon	19	36°52′	143°11′	280	3 largest: JU, JS, JY	2.74	3.46	2.11
					2 smallest: JP, JX	2.65	1.58	0.84
	21	36°17′	142°58′	100	3 largest: KO, KT, KU	3.86	2.11	1.77
					2 smallest: KS, KN	2.17	2.01	1.80

Figure 2 shows average values for respiration parameters of top- and bottom-ranked families plotted for each plantation site. As in Fig. 1, each point is the average value for trees in nine seed sources. Average values of q and R_{CO_2} are higher for bottom-ranked than for top-ranked families at all three plantations, and the differences were significant ($P < 0.10$) at Arvin and Concord, but not at Anderson. Thus, the smaller trees have higher respiration rates measured at 25°C either as q or as R_{CO_2}. Respiration rates at 25°C increase from Anderson to Arvin to Concord. Values of q/R_{CO_2} at 25°C are significantly ($P < 0.10$) larger for bottom-ranked families at Anderson and Concord, indicating lower energy use efficiency, but bottom- and top-ranked families have equal q/R_{CO_2} values at Arvin. The temperature dependence (μ_q) of respiration from 15–25°C is also larger for smaller families.

Genetic variation in growth and respiration among the top-ranked families

Trees from the top-ranked families grown in three plantations differed markedly in both growth and respiration traits, with a CV 19–58% and 14–48%, respectively, for these traits (Table 3). In addition, family ranges and family CVs were also large in growth and respiration traits, suggesting that substantial genetic variation is present in these traits within families.

Across all plantations in all traits, 70–93% of the total variance was due to differences in trees within families (Table 3). The remaining 7–30% variance was due to differences in drainages, sources within drainages, and families within source. The latter three components differed among plantations, among individual traits, and between growth and respiration traits. Variance components for only μ_q values for drainages were positive at all plantations, and these values differed significantly ($P < 0.05$) at Anderson and Arvin.

Relationships between growth and respiration traits

All significant ($P < 0.10$) drainage and source mean correlations between growth and respiration traits were strongly negative (mean $r = -0.88$; range = -0.77 to -0.99) (Table 4). On the contrary, all but one of the significant family mean correlations between growth and respiration were positive. The discrepancy of the relationship at different levels appears to be due to differences between local climates within sources relative to broader climatic conditions that influence variation at the drainage level.

Ranking drainages, sources and families for growth and respiration traits

For the same growth or respiration trait, estimated drainage mean, source mean, and family mean correlations between paired plantations are presented in Table 5. Correlations between Anderson and Arvin were poor for all growth traits, strongly negative and significant for q at all three levels, and positive for q/R_{CO_2} at the drainage level. Between Anderson and Concord, correlations were again poor and inconsistent for all growth traits, strongly positive and significant

($P < 0.10$) for R_{CO_2} and μ_q at the drainage level. However, between Arvin and Concord all growth traits showed significant ($P < 0.10$) and moderately positive correlations at source and family levels, while correlations for all respiration traits were low. In general, relative rankings for drainages can be predicted more reliably using respiration than growth traits.

Discussion

Top- and bottom-ranked families represent two extreme ends of the normal curve for growth traits. Therefore, the families analysed in this study can be visualized as two extreme groups of genotypes in each drainage or seed source population. When these two groups of genotypes are compared, the relationship between respiration rates at 25°C and growth is largely negative. In general, bottom-ranked, poor growing families had higher q, R_{CO_2}, μ_q, and q/R_{CO_2} values than the top-ranked, superior families (Fig. 2). These results strongly suggest that a rapid calorimetric-based analysis of unknown families to identify plants with low respiration rate, small temperature dependence and high efficiency (low q/R_{CO_2}) can select river red gum families producing higher yields at these growth sites. Previous studies have demonstrated that the temperature coefficient of q accounts for the effects of fluctuations in daily temperatures on growth of wide variety of species (Criddle *et al.* 1994). Temperature coefficients of plants growing in harsher climates, where wide temperature fluctuations exist, are generally lower than trees from milder climates. At the Arvin site, plantation average in μ_q for top-ranked families is lower than at the Concord site (Fig. 2). In addition, μ_q values for bottom-ranked families are higher than those for the top-ranked families. Therefore, bottom-ranked families may have difficulty growing in the widely fluctuating temperatures at Arvin and Anderson. Also, the growth differences between top- and bottom-ranked families at Concord are small. Although the growth at Concord is uniformly lower than at the other two sites, the smaller range of temperatures allows narrowly adapted families to grow nearly as fast as the top families; the family level difference in both growth and respiration traits is significant ($P < 0.10$) only at this site (Table 3).

Genetic variation among top-ranked families is high both in growth and respiration traits, and this variation is partitioned primarily among trees within families (average over all traits across all traits = 84%) and the remaining three components accounted for only 16% of the total variation (Table 3). Differences among drainages were detected only by respiration traits, sources within drainage differences were shown by both growth and respiration traits, while family differences were shown predominantly by growth traits, suggesting a strong influence of plantation sites on the origin factors. Seed sources at Arvin differed significantly ($P = 0.05$–0.01) for all growth traits, indicating that environment at the Arvin site may have provided the best
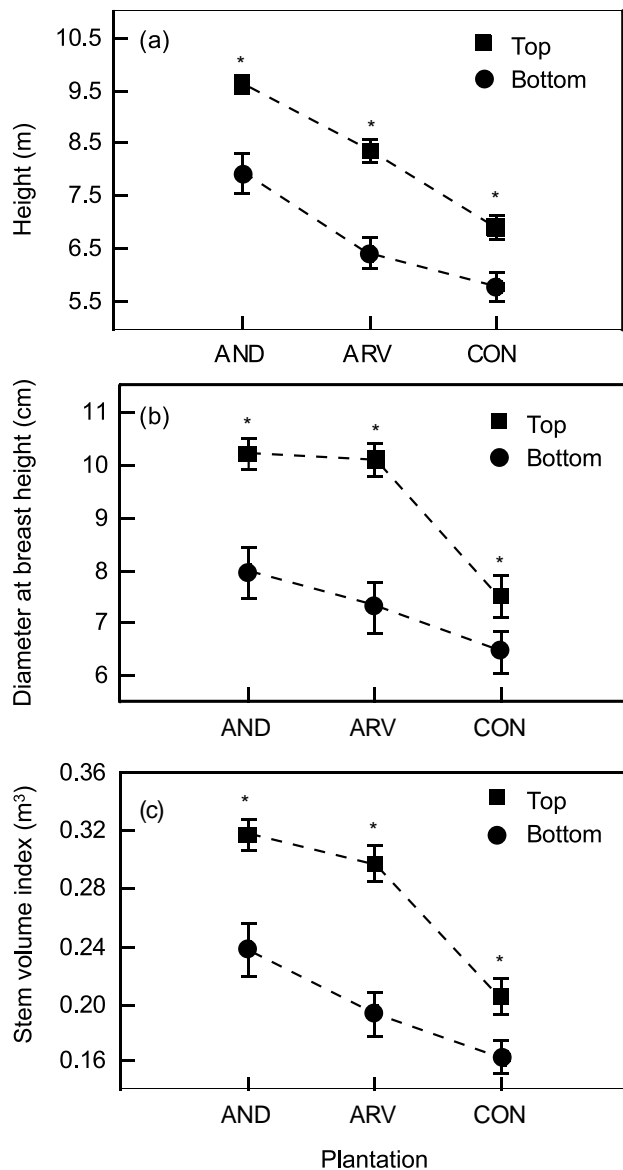

Fig. 1. Average growth traits for top- and bottom-ranked families of river red gum plotted *vs* planting sites in California. Error bars are standard error of means. * above the symbol indicates a significant difference ($P < 0.05$) between the means of top- and bottom-ranked families at a given plantation.

Fig. 2. Average respiration parameters at 25°C for top- and bottom-ranked families of river red gum plotted *vs* planting sites in California. Error bars are standard error of means. * above the symbol indicates a significant difference ($P < 0.05$) between the means of top and bottom-ranked families at a given plantation.
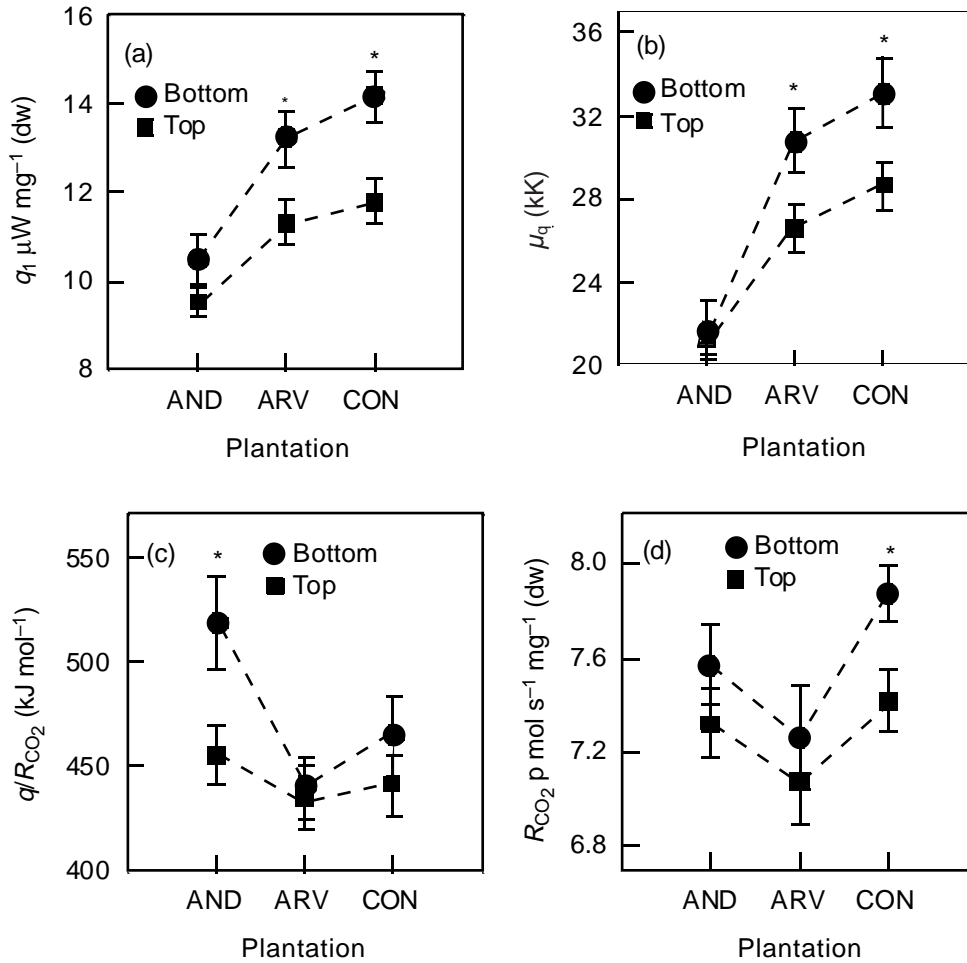
opportunity to express genetic differences among the seed sources (Table 3). Also, the maximum difference (26.6%) for μ_q was expressed among drainages at the Arvin site.

The relationship between growth and respiration varies from plantation to plantation and among variance components of the seed origin (drainages, sources, and families) (Table 4). Distinct drainage and sources within drainage differences were observed when grown at Anderson, Concord or Arvin (Table 5). Respiration parameters appear to undergo only limited acclimation to sites. Acclimation may be due to the differing temperature variation patterns at the sites or to additional factors such as soil and water differences, although this investigation did not collect any information on soil characteristics. The trees studied are obviously limited in their ability to acclimate to changed growth conditions because the best performing drainages at one site were in some cases the poorer performers at another site. Mismatch between Anderson and Arvin and between Arvin and Concord, and a better match between Anderson and Concord

are better shown by rankings for drainages in respiration traits than in growth traits (Table 5).

All seed sources of this study originated from regions with relatively low rainfall, cool maximum temperatures, and more than 120 d with frost in the growing season. Although none of the three study sites fully match native climate, average number of daily lows below 0°C per year, an indicator of frost events, was much higher at Arvin (41) than at the remaining two sites (28 at Anderson and 5 at Concord) (Table 1). Thus, Arvin appears to match the native climate somewhat better than other two plantations. However, the Anderson site has the most fertile soil and receives the highest average rainfall per year (669 mm). Although trees grew taller at Anderson, plantation average for diameter is similar between Anderson and Arvin (see data for top-ranked families in Fig. 1). Rankings for drainages based on q ($r = -0.95$; $P < 0.05$) and q/R_{CO_2} ($r = 0.91$; $P < 0.05$) are significantly high between these plantations (Table 5). Arvin is the southernmost site of the three in California, has a warmer

and longer growth season than Anderson, and ambient temperatures are warm enough that growth may be possible throughout the year. Although December is the coldest month at all sites, the mean daily high at Arvin in December is 22°C, which may still be warm enough for growth. The temperature seems to have an overriding positive effect on

growth at Arvin. This study by itself may not be sufficient to develop a solid strategy to match respiration parameters to current growth environments, however, respiration parameters can be used to aid identification of superior drainages, or seed sources for establishment of a foreign plantation. Measurement of respiration parameters at more

Table 3. Estimated overall and family means, ranges, coefficients of variation (CV) and variance components for growth and respiration traits of river red gum in three California plantations (Anderson, Arvin, and Concord)

Significant level ($P < 0.10 = +$; $P < 0.05 = *$; $P < 0.01 = **$) for F-statistic of each variance component was tested using the SAS GLM procedure

Plantation/traits	Mean	Overall Range	CV	Family Range	CV	Variance components (%) Drainages	Sources (Drainage)	Families (Source)	Error
Anderson:									
Height	9.63	1.1–13	19	5.13–11.4	13	0.5	0.0	23**	76.5
Diameter	10.2	0.27–1.93	28	0.063–0.137	16	0.0	9.4+	0.0	90.6
Volume	0.320	0.056–0.657	33	0.159–0.462	20	0.0	7.1+	5.3	87.6
q	9.54	2.20–19.6	36	5.90–13.2	21	18.3**	0.0	0.0	81.7
R_{CO_2}	21.3	4.10–48.8	36	13.5–30.9	20	8.6+	0.2	0.0	91.2
q/R_{CO_2}	456	139–977	31	324–645	18	0.0	8.7+	0.0	91.3
μ_q	7.32	5.14–10.2	14	6.07–9.92	11	12.7*	0.0	0.0	87.3
Arvin:									
Height	8.34	4.00–13.4	24	6.27–10.6	15	0.0	15.0*	0.0	85.0
Diameter	10.1	0.44–1.64	27	0.069–0.126	18	0.0	26.3**	3.4	70.3
Volume	0.299	0.088–0.600	36	0.183–0.413	24	0.0	23.3**	0.0	76.7
q	11.31	2.10–24.5	40	5.50–16.4	25	0.0	8.1+	0.0	91.9
R_{CO_2}	26.6	1.80–51.2	37	17.3–42.0	19	4.1	6.2+	0.0	89.7
q/R_{CO_2}	435	156–829	31	276–596	21	5.4	0.0	11.0	83.7
μ_q	7.08	3.32–8.38	17	4.78–8.20	13	26.6*	0.0	0.0	73.4
Concord:									
Height	6.92	1.70–11.7	33	1.70–9.90	20	4.1	0.6	11.7+	83.6
Diameter	7.50	0.40–1.56	45	0.036–0.123	25	3.3	0.0	8.7	88.0
Volume	0.207	0.005–0.524	58	0.070–0.387	33	3.9	0.0	11.1+	85.0
q	11.8	1.70–29.0	42	4.20–19.3	24	6.3	4.5	0.0	89.2
R_{CO_2}	28.61	1.80–70.5	46	4.10–41.0	23	0.2	7.1+	0.0	92.7
q/R_{CO_2}	441	97–890	33	177–814	21	0.0	0.0	18.9*	81.1
μ_q	7.42	1.70–9.62	17	4.54–8.32	14	7.7	19.6*	0.0	72.6

Table 4. Estimated drainage mean ($n = 4$), source mean ($n = 9$), and family mean ($n = 27$) correlations between growth and respiration traits in top-ranked families at Anderson, Arvin, and Concord plantations

Correlations were significant at 0.10 (+), 0.05 (*), and 0.01 (**) level

Trait	Origin	Anderson Height	Diameter	Volume	Arvin Height	Diameter	Volume	Concord Height	Diameter	Volume
q	Drainage	−0.96*	0.09	−0.40	−0.60	−0.99**	−0.93*	0.51	0.41	0.50
	Source	−0.61+	0.18	−0.02	0.06	−0.15	−0.07	0.11	0.05	0.09
	Family	−0.18	0.19	0.09	0.16	0.03	0.06	0.28	0.16	0.21
R_{CO_2}	Drainage	−0.97*	0.09	−0.38	−0.83*	−0.37	−0.54	0.04	−0.08	0.20
	Source	−0.77*	0.002	−0.19	0.08	0.10	0.10	−0.08	−0.04	−0.03
	Family	−0.37+	−0.08	−0.17	0.22	0.14	0.17	0.14	0.16	0.17
q/R_{CO2}	Drainage	−0.54	−0.44	−0.69	0.16	0.19	−0.29	−0.41	−0.44	−0.37
	Source	0.26	0.29	0.28	−0.08	−0.16	−0.12	0.26	−0.00	0.13
	Family	0.32+	0.42*	0.41*	0.05	0.01	0.01	0.32+	0.22	0.25
μ_q	Drainage	−0.95*	−0.15	−0.60	−0.11	−0.36	−0.29	−0.01	−0.06	0.02
	Source	−0.35	0.24	0.07	0.15	−0.04	0.04	0.30	0.27	0.34
	Family	0.03	0.24	0.18	0.04	0.01	0.02	0.58**	0.42*	0.50**

Table 5. Estimated drainage mean ($n = 4$), source mean ($n = 9$), and family mean ($n = 27$) correlations between plantations for the same growth or respiration trait in top-ranked families

Correlations were significant at 0.10 (+), 0.05 (*), and 0.01 (**) level

Trait	Origin	Correlations between paired-plantations		
		Anderson & Arvin	Anderson & Concord	Arvin & Concord
Height	Drainage	−0.24	0.29	0.51
	Source	−0.23	0.14	0.60+
	Family	−0.09	−0.33+	0.56**
Diameter	Drainage	0.41	−0.34	−0.20
	Source	0.14	−0.02	0.48+
	Family	−0.02	−0.20	0.32+
Volume	Drainage	0.06	−0.19	0.06
	Source	0.05	−0.01	0.54+
	Family	−0.07	−0.26	0.43*
q	Drainage	−0.95*	0.69	−0.46
	Source	−0.69*	0.36	−0.11
	Family	−0.50**	0.09	0.18
R_{CO_2}	Drainage	0.27	0.80+	−0.07
	Source	0.17	0.44	−0.06
	Family	0.02	0.17	−0.13
q/R_{CO_2}	Drainage	0.91*	0.43	0.27
	Source	0.16	−0.12	0.21
	Family	−0.02	−0.16	0.10
μ_q	Drainage	−0.04	0.81+	0.30
	Source	0.14	0.25	0.33
	Family	−0.04	0.13	0.30+

temperatures for seedlings grown at each site will be required to allow identification of genotypes best matched to the planting site.

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