

Respiration rates predict differences in growth of coast redwood

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ABSTRACT

The relation between growth rate traits (height, basal diameter, stem volume and branch diameter) and two measures of respiration rate [metabolic heat rate (q) and CO_2 production rate (R_{CO_2})] and their ratio (q/R_{CO_2}) was examined on a collection of 192 different genotypes of coast redwoods [*Sequoia sempervirens* (D.Don) Endl.]. Branch diameter was not correlated with any of the respiratory measures, but the other three growth traits gave highly significant ($P<0.001$) correlations with positive slopes. Combining the four growth traits and the three respiratory variables (q , R_{CO_2} and q/R_{CO_2}) to give two canonical variates, one representing growth and one representing respiration, gives an even stronger linear correlation ($r=0.85$). These data suggest that simultaneous assay of multiple respiratory measures on juvenile trees can be used to predict their longer-term growth rates.

Key-words: calorimetry; coast redwood; respiration; *Sequoia sempervirens*.

INTRODUCTION

Although photosynthesis is responsible for carbon fixation, respiration is necessary for processing photosynthate into structural biomass. Many investigations have demonstrated strong correlations between respiration rates and growth rates (e.g. Wilson & Jones 1982; Geider & Osborne 1989; Hansen *et al.* 1989, 1992; Anekonda *et al.* 1990, 1993; Poorter, Remkes & Lamberts 1990; Thornley & Johnson 1990). However, as Amthor (1989) has stated, ‘the precise nature of the relationship between growth and respiration . . . is unknown’. This is evident since both positive and negative growth-respiration correlations have been found. The use of diverse plant sources, growth conditions and methods for measurement, as well as the lack of a general quantitative theory capable of describing the diverse relations experimentally found between

growth and respiration rates have made it difficult to interpret and generalize results.

The three most direct measures of plant respiration rates are CO_2 production rate, O_2 use rate, and metabolic heat rate i.e. the rate at which heat is produced by respiration (Criddle *et al.* 1991a). Ratios of the various measures of respiration rate such as heat/ CO_2 or heat/ O_2 can be particularly informative about individual differences in the growth energetics of plants because they are related to growth efficiencies of metabolism (Yamaguchi 1978; Criddle, Breidenbach & Hansen 1991b; Hansen *et al.* 1993) and oxidation states of substrates and products. Thus, simultaneous measurement of multiple measures of respiration rate can lead to a better understanding of the relationship of respiration to growth traits.

The objective of this study is to investigate the relationships between a set of commonly used growth traits and a set of multiple respiration measurements in coast redwood trees. The long-term goal of this work is to develop rapid, early means for selection of trees for increased productivity.

MATERIALS AND METHODS

Experimental design and sample collection

The overall study included 192 clones (genotypes) sampled systematically from the entire native range of coast redwood in California and Oregon, USA (Professor John Kuser, personal communication). A replication of an international range-wide provenance test including these 192 clones was planted in December 1988 at Russell Reservation of the University of California. The Reservation is situated at the narrow eastern end of Briones valley near Lafayette, California. Field design at the Russell test consists of three independently randomized replications that are interlocked, with plot members arranged non-contiguously within each block (Libby & Cockerham 1980). Spacing between any two adjacent trees is 3 m. The trees were drip irrigated

weekly during the dry season for the first 2 years. Weeds were controlled by cultivation for the first 2 and by mowing in the subsequent 2 years. A detailed account of the Russell plantation establishment is presented elsewhere (Anekonda 1992).

Measurements focused primarily on 30 clones chosen from the 192 clones on the basis of preliminary measurements on all clones. These 30 are a combination of two subsets of trees. The first subset includes 16 clones purposely picked from different parts of the native range to provide the broadest characterization of redwoods (Anekonda, Criddle & Libby 1990). The second subset of 14 clones was selected from a preliminary study to include individuals exhibiting the extremes of combined growth and respiratory variables (Anekonda 1992; Anekonda *et al.* 1993). This subset includes four groups of trees: (1) tall trees with high metabolic heat rates; (2) tall trees with low metabolic heat rates; (3) short trees with high metabolic heat rates; and (4) short trees with low metabolic heat rates.

Field data collection on growth characteristics

Field data were collected at the end of the second (1990) and the third (1991) growing seasons after planting. The growth traits and measures of respiration included in this study are listed in Table 1.

Tissue-sample collection and calorespirometric experiments

Calorespirometric experiments were conducted during

June and July 1991. Metabolic heat rates and CO₂ production rates were measured on the two tallest trees (ramets) of each clone in the 16-clone subset and for all the selected (mostly single) ramets in the 14-clone subset. On average, 3·3 tissue samples were measured from each of one or two ramets per clone. Shoot apices were collected from the two most recent secondary branches of the two topmost primary branches. These samples were collected near 0800 h and immediately placed in small vials with cold, half-strength Hoagland's solution containing 10 kg m⁻³ sucrose. The vials were placed on ice and transported to UC Davis for calorespirometric measurements. The transport time was about 1 h. Respiration rates decreased slightly during the first 30 min after collection. The rates then remained nearly constant for the subsequent 12–24 h at 5 °C. Fresh samples were collected for each day of experiment.

Calorespiration measurements were made using a Hart Scientific model 7707, heat-conduction, differential, scanning calorimeter in the isothermal mode (Criddle *et al.* 1988). An approximately 1-cm-long section, including the apical meristem with subtending developing stem and needles, was placed in a 1-cm³ calorimeter ampule along with a 50-mm³ vial. Metabolic heat rates were measured with 40 mm³ of H₂O in the vial. Then the H₂O was removed and replaced with 40 mm³ of 400 mol m⁻³ NaOH in the same vial. CO₂ produced by the respiring tissues was absorbed by the NaOH to produce Na₂CO₃ and liberate additional heat at a rate proportional to the CO₂ production rate. All respiration measurements were made at 26 °C. For further details of the methods refer to Criddle *et al.* (1991a,b).

Code	Specific growth-rate traits	Mean ($\times 10^{-2}$)	SD ($\times 10^{-2}$)
Height	Main-stem height (m m ⁻¹ year ⁻¹)	0·36	0·17
Basal diameter ¹	Main-stem basal diameter (m m ⁻¹ year ⁻¹)	4·70	2·10
Branch diameter ²	Branch diameter (m m ⁻¹ year ⁻¹)	3·40	4·70
Stem volume ³	Stem volume index (m ³ m ⁻³ year ⁻¹)	2·05	1·00

Code	Respiration measurements	Mean	SD
q	Metabolic heat rate, mWatt g ⁻¹ , dw	12·16	4·59
R _{CO₂}	CO ₂ rate, nmol g ⁻¹ s ⁻¹ , dry wt	27·78	8·33
q/R _{CO₂}	Heat rate/CO ₂ rate, kJoule mol ⁻¹	460·23	84·00

Table 1. Description of specific growth-rate traits and respiration measurements for 30 selected clones

¹ Main-stem basal diameter was measured 5 cm above the ground.

² The branch located closest to the end of the first-year height was selected based on the observable growth pause on the main stem. This was done to avoid bias in picking the measured branch and to maintain a consistency of the trait measured at a specific position related to developmental stage of the tree. The selected branch diameter was measured 5 cm away from the main stem.

³ Stem volume index = [(Main-stem quarter height diameter/10)² × (Height)].

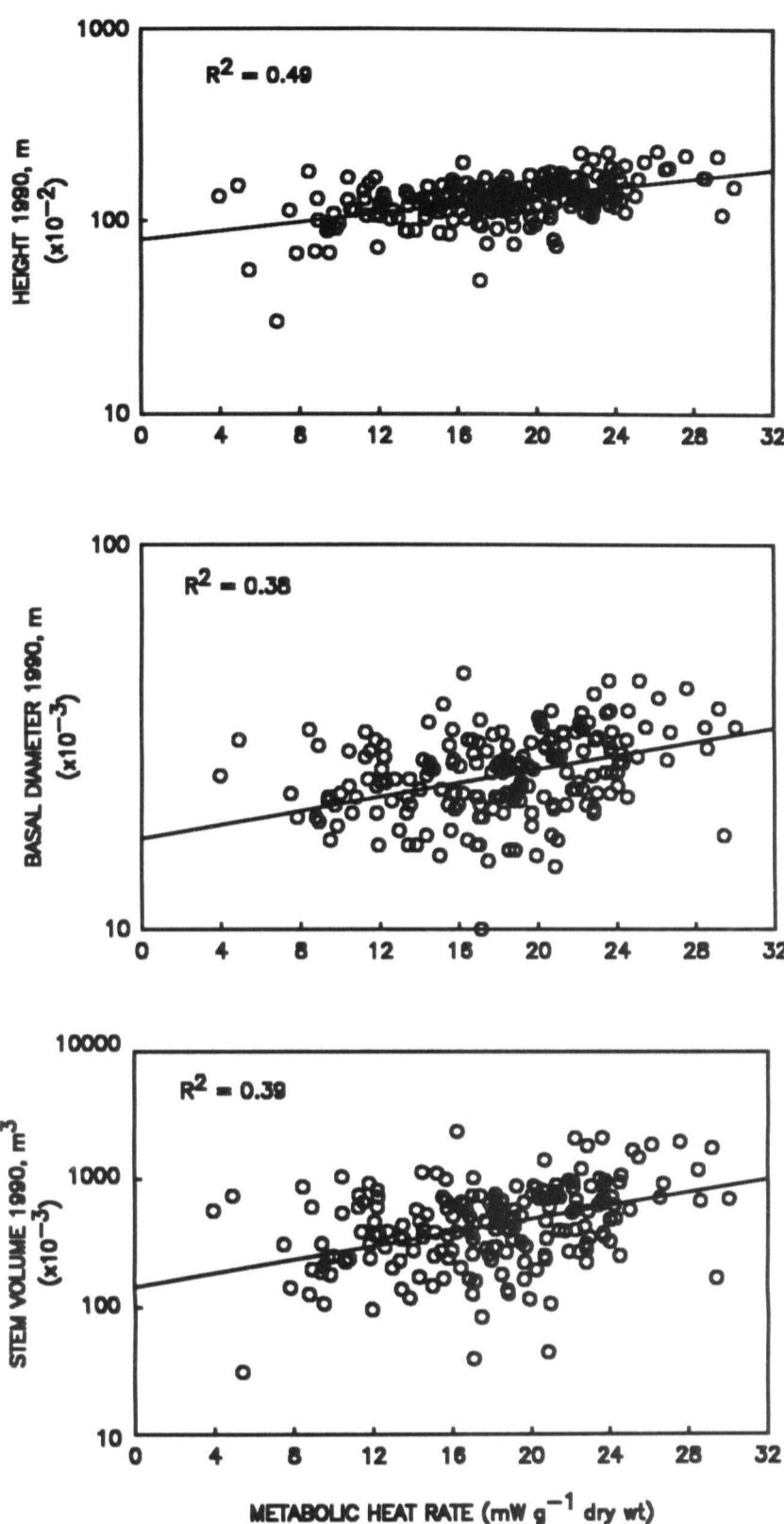


Figure 1. Three growth traits (on log scale) plotted against metabolic heat rates for 192 clones of coast redwood.

RESULTS

Figure 1 shows the simple linear regressions between three of the growth traits and metabolic heat rates for all 192 clones. The slopes of all three plots are positive ($P < 0.0001$), showing that metabolic heat rate is positively correlated with tree height, basal diameter and stem volume. The second subset of 14 clones, of the 30 selected for intensive studies, were chosen on the basis of the data in Fig. 1. A summary of the respiration and growth measurements, with their symbols, units, mean values and standard deviations for the 30 clones are listed in Table 1. The three respiration variables and the four specific growth-rate measures are plotted in Figs 2 and 3, respectively.

Correlation analyses

Pearson correlation coefficients (SAS 1989) among the three respiration variables, among the four specific growth-rate traits and between the variables of the two sets are given in Table 2. Positive and highly significant ($P < 0.001$) intra-set correlations occur among growth traits, except for branch diameter. Strong ($P \leq 0.01$) correlations also occur among the three measured respiration traits. All growth traits except branch diameter are strongly ($P < 0.01$) and positively correlated with q , R_{CO_2} and q/R_{CO_2} .

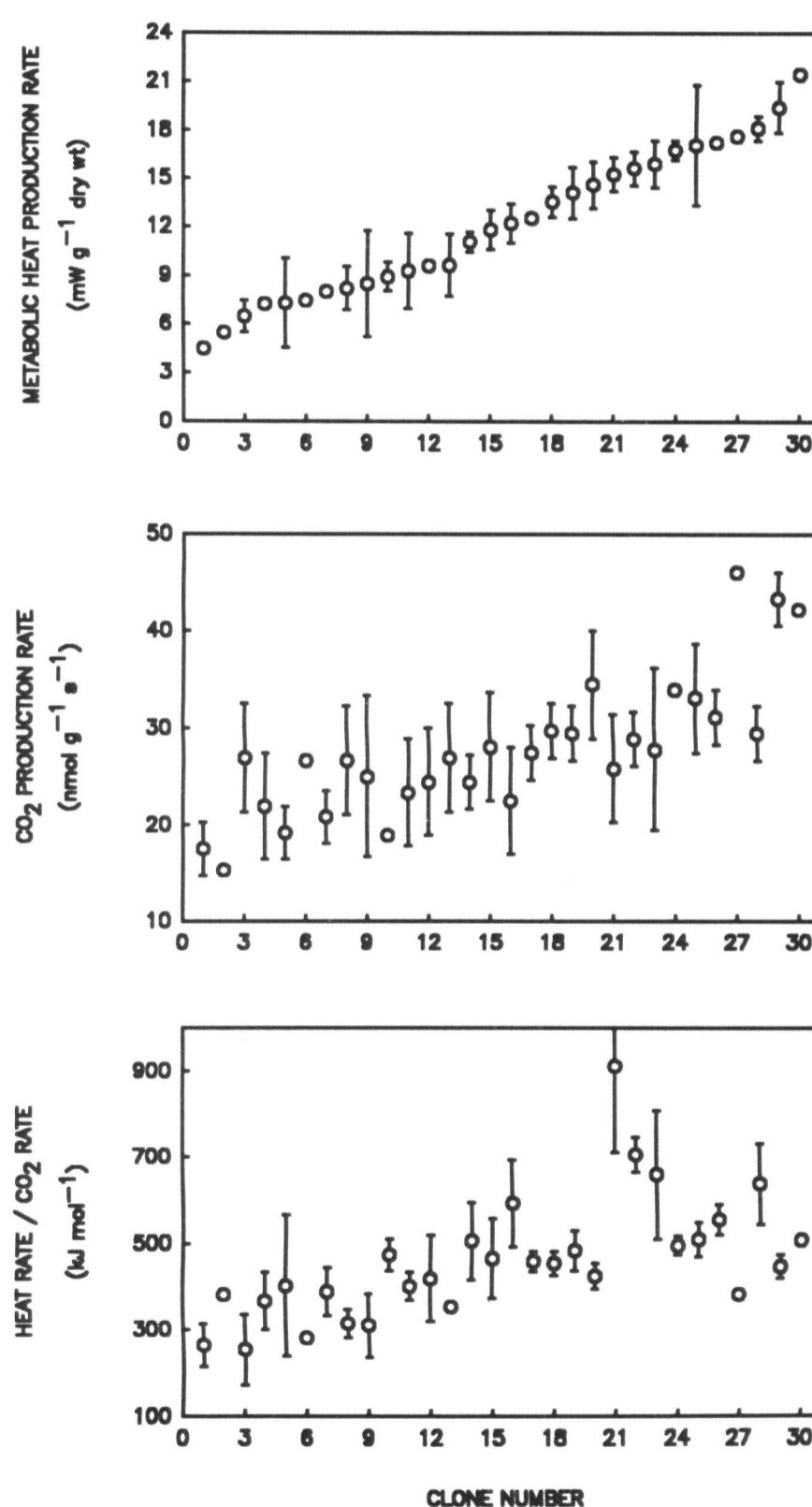


Figure 2. Two respiration measures and their ratio plotted against clone number assigned by increasing order of metabolic heat rate. The vertical coordinate is the mean of the values measured for a clone and the error bar shows the SEM based on between two and six measurements made on samples collected from one or two ramets a clone. Samples from two different ramets were usually collected on different days. Where no error bar is shown, the standard error is within the size of the symbol.

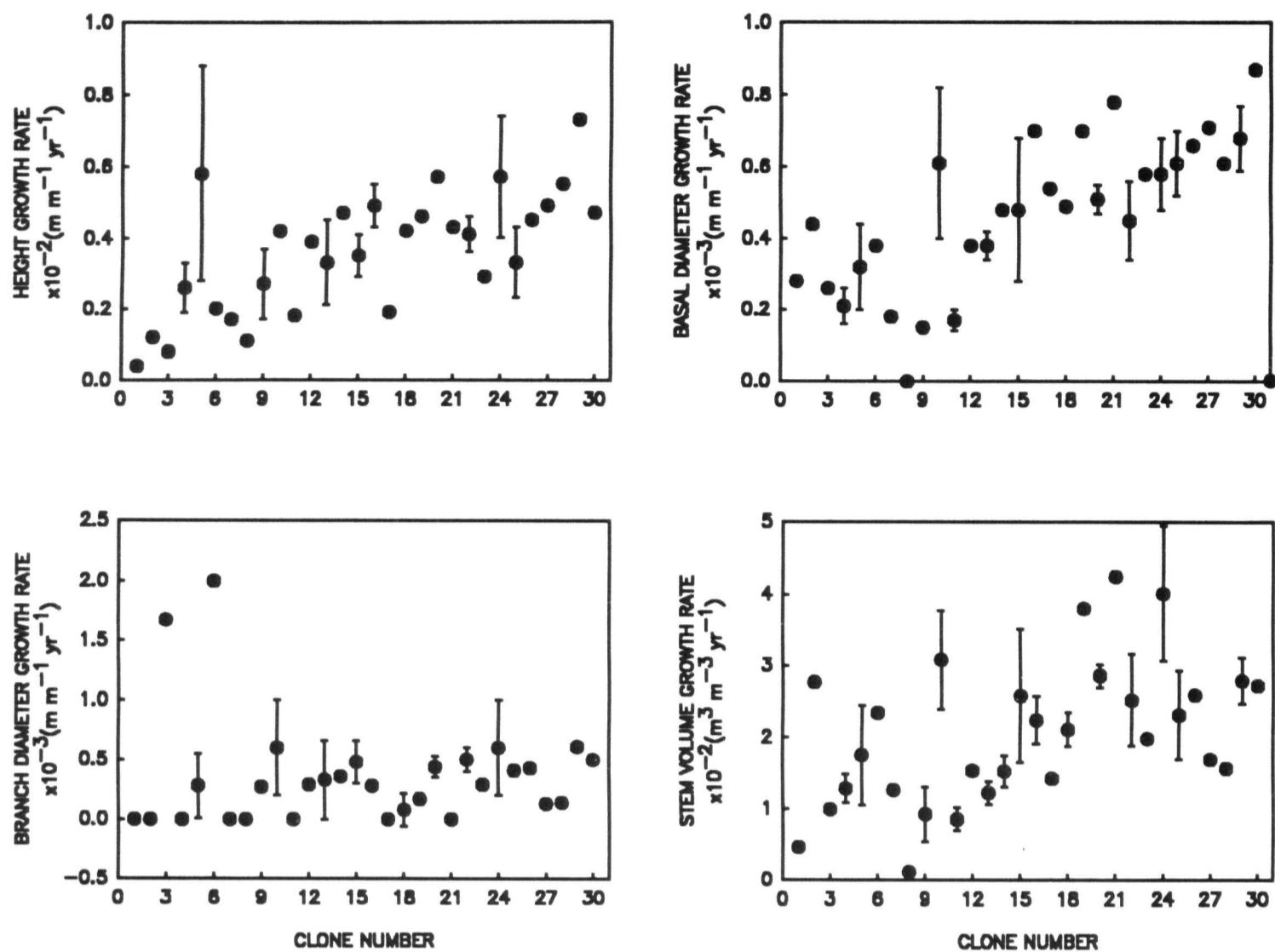


Figure 3. Four specific growth traits of coast redwood plotted against clone number assigned by increasing order of metabolic heat rate. The vertical coordinate is the mean of the values measured for a clone and the error bar shows the SEM based on measurements made on two ramets of a clone. Where no error bar is shown, the standard error is either within the size of the symbol or no standard error because a single ramet was sampled for that clone.

	Height	Basal diameter	Branch diameter
<i>Among growth traits</i>			
Basal diameter	0.57***		
Branch diameter	0.15	0.14	
Stem volume	0.65***	0.76***	0.13
q	R _{CO₂}		
<i>Among respiration measures</i>			
R _{CO₂}	0.70***		
q/R _{CO₂}	0.40***	-0.29**	
	Height	Basal diameter	Branch diameter
			Stem volume
<i>Between growth and respiration variables</i>			
q	0.64***	0.63***	0.13
R _{CO₂}	0.37***	0.35***	0.13
q/R _{CO₂}	0.33***	0.35***	0.01

Table 2. Pearson correlation coefficients among and between the original variables given in Table 1

* 0.05 ≥ P > 0.01.

** 0.01 ≥ P > 0.001.

*** P ≤ 0.001.

For each variable, the number of observations is n = 92.

Table 3. Canonical correlations and eigenvalues of paired canonical variates

Paired canonical variates ¹	Canonical correlations ± SEM	Squared canonical correlation	Eigenvalues	Cumulative	F-Stat	Pr>F
v ₁ , u ₁	0.85 ± 0.05	0.72	2.56	0.85	4.41	0.0001
v ₂ , u ₂	0.54 ± 0.13	0.29	0.42	0.99	1.66	0.1500
v ₃ , u ₃	0.17 ± 0.18	0.03	0.03	1.00	0.37	0.7000

¹ v₁ = a*(Height) + b*(Basal diameter) + c*(Branch diameter) + d*(Stem volume) (see Table 1).

u₁ = x*(Metabolic heat rate) + y*(CO₂ rate) + z*(Heat rate/CO₂ rate).

Where a, b, c, d, x, y and z are coefficients chosen to maximize the correlation between v₁ and u₁.

The multivariate relations between the four specific growth-rate traits and three measures of respiration were determined by canonical correlation analysis. Two canonical variates, v_x and u_x, were constructed. One canonical variate, v_x, is a linear combination of the four specific growth-rate traits. The other, u_x, is a linear combination of the three respiration traits. The first pair of canonical variates (v₁, u₁) was chosen to maximize the correlation between them. Succeeding pairs of canonical variates were uncorrelated with any of the preceding pairs (Gittins 1985; Manly 1986; SAS 1989).

Variation in u₁ (Table 3) accounted for 72% of the variation in v₁. The eigenvalues from the multivariate analysis are coefficients describing the contribution of each parameter to the total effect. The higher the value, the greater the contribution of that parameter. The first eigenvalue (2.56) accounted for 85% of the patterned variation and was highly significant ($P < 0.0001$). The two other paired canonical variates were not statistically significant, accounted for only 15% of the remaining variation, and therefore, were disregarded.

The first canonical variate, v₁, of specific growth-rate traits was highly correlated with specific basal diameter growth rate ($r = 0.94$), specific height growth rate ($r = 0.81$) and specific stem volume growth rate ($r = 0.69$) (Table 4). The first canonical variate, u₁, of respiration measurements was also highly correlated with q, R_{CO₂} and q/R_{CO₂} ($r = 0.67$ to 0.97). Redundancy analyses provided the fraction of variance of growth traits explained by the canonical correlation of the respiration measurements, and vice versa (Table 4).

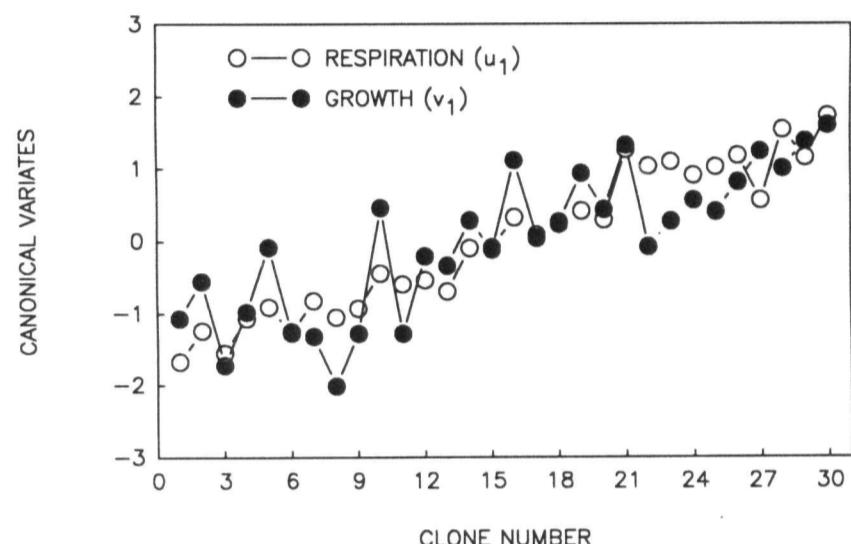


Figure 4. Canonical variates plotted against clone number, assigned by increasing order of metabolic heat rate.

Forty-two per cent of the variance in standardized specific growth traits is explained by u₁ and 57% of the variance in standardized respiration measurements is explained by v₁. The relationship between u₁ and v₁, based on redundancy, was considerably weaker than the relationship based on squared canonical correlation. Redundancy analysis is more conservative than canonical correlation analysis.

Values of v₁ and u₁ are plotted against the ordered clone numbers in Fig. 4 and values of v₁ are plotted against values of u₁ in Fig. 5, showing covariance of v₁ and u₁ (Figs 4 & 5), and the relationship of both to

Correlation of v ₁ with growth traits	r	Correlation of u ₁ with respiration variables	r
Height	0.81	q	0.97
Basal diameter	0.94	R _{CO₂}	0.67
Branch diameter	-0.16	q/R _{CO₂}	0.78
Stem volume	0.69		
<i>Redundancy</i>			
Growth traits by respiration measurements			0.42
Respiration measurements by growth traits			0.57

Table 4. First pair of canonical variates (v₁, u₁) and their correlations with specific growth traits and respiration measurements

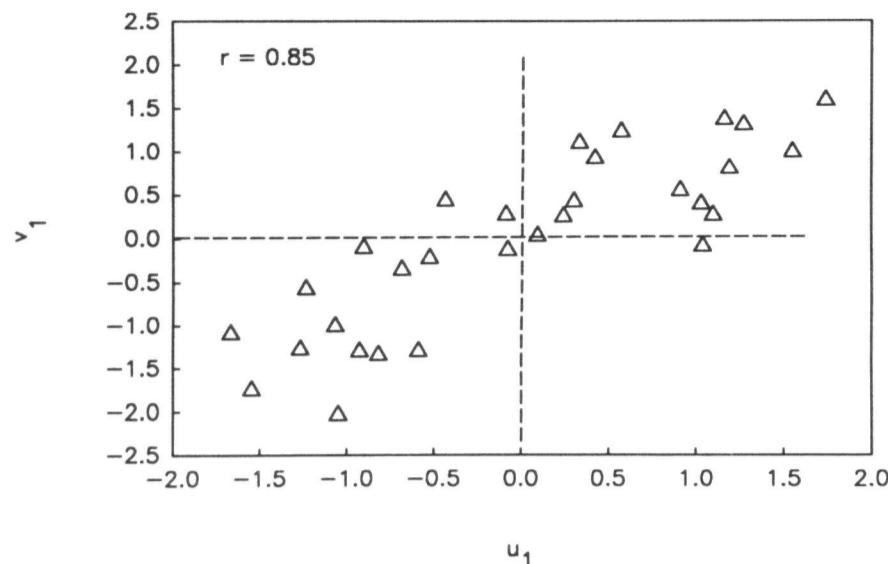


Figure 5. A canonical variate (v_1) of growth traits plotted against a canonical variate (u_1) of respiration measurements.

metabolic heat rate (Fig. 4). The points in Fig. 5 fall close to the diagonal from lower left to upper right, demonstrating a strong, unbiased correlation.

DISCUSSION

This study estimated the strength of the relationship between four specific growth-rate and three respiration rate traits in coast redwoods. Except for branch diameter growth, all other growth rate traits measured were strongly correlated with metabolic heat rate, CO_2 production rate and the heat to CO_2 ratio (cf. Fig. 1 and the combined results of Figs 2 & 3). Therefore, respiration rate can likely be used to guide early selection for tree growth rate. Furthermore, a combination of q , R_{CO_2} and their ratio (i.e. values of u_1) provide better correlation with specific growth-rate traits than any single measure of respiration (i.e. Fig. 5 with $r=0.85$).

The apparent redundancy of using two parameters and their ratio is justified because q and R_{CO_2} reflect metabolic rates, whereas the ratio is related to efficiency of energy metabolism. Assuming the same oxidation state of the substrate carbon (i.e. photosynthate), a plant producing large amounts of heat per mole of CO_2 produced is less efficient at retaining energy for production of biomass than one with lower heat loss per CO_2 . Thus, the ratio q/R_{CO_2} shows that the rapidly growing plants in this study may be less efficient than slower growing ones (Table 2).

Because the trees used in this study are growing in a common garden, and temporal and spatial effects have been largely accounted for (Anekonda *et al.* 1993), differences in growth and respiration traits must be mostly genetic in origin.

This study shows that simultaneous measurements of multiple respiratory parameters can be combined for use in prediction of growth rates of individual redwood trees. Figure 4 establishes that respiration rates are highly correlation with current growth rates of redwoods. The fastest and the slowest growing among

the 30 clones are easily distinguished by the respiratory variable u_1 . Moreover, growth performance, as predicted by respiratory measures, appears to remain in the same relative order over the life-span of one sample population of redwood trees (Hansen *et al.* 1992). Thus, short-term respiratory measurements made on juvenile trees (2–3 years old) might be useful in prediction of the potential growth performance of individual genotypes. This ability to relate respiratory parameters to plant growth rate may allow early genetic selection for improved biomass production. Short-term methods of selection can provide substantial time savings in tree selection programmes and accelerate improvements in production.

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