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Site-fitness and growth-rate selection of *Eucalyptus* for biomass production ☆

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Abstract

Calorespirometric investigation of the metabolism and temperature responses of tissues from *Eucalyptus* trees can be used to identify plants with superior growth characteristics. Measurements of the metabolic heat rate, rate of CO_2 evolution and O_2 uptake over a range of temperatures are analyzed with a mechanistic model of plant growth to allow early selection of superior trees. This analysis provides information about indexes of genetic characteristics to use in breeding programs and guidelines for matching trees to appropriate climatic conditions. These procedures can enhance the rate of production of biomass by shortening the time to harvest and can increase total economic returns.

Keywords: Biomass; Calorimetry; *Eucalyptus*; Metabolism; Model

1. Introduction

Application of calorespirometry to an understanding of the relation between plant respiration and growth rates has been reviewed by Hansen et al. [1] in this volume. The review outlines a wide range of applications of calorimetry to plant studies and discusses a growth model that can be used as a framework for

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interpretation of many plant respiration studies. This paper focuses on the practical application of calorespirometry methods and theory to studies of one group of trees, *Eucalyptus* species, which is being selected and intensively grown for biomass production. Practical questions arising during application of calorespirometry to improvement of biomass production rates are presented and answered to the extent currently possible. The results show that calorimetry can be an efficient tool for guiding programs aimed at producing trees with superior growth characteristics.

Our goal is the rapid production of high quality biomass. Applications of calorimetry for speeding or improving each of the following steps in the production process are illustrated.

1. Identification of suitable species and appropriate locations for obtaining seeds for an initial planting.
2. Optimizing nutrient and water inputs for growth and for economic production of biomass at the growth site.
3. Early selection of superior trees from initial plantings.
4. Matching *Eucalyptus* genotypes to the climate, and identification of cold- and heat-tolerant genotypes. This includes initial selection for growth at a proposed site and a further definition of which climates are best for growth of selected superior trees by means that do not require repetition of the entire planting program each time a new plantation site is developed.
5. Identifying multiple, readily measurable parameters defining growth rates to provide an improved rationale for breeding programs.
6. Identifying parameters to determine whether a genotype will produce more oxidized (better for paper) or more reduced (better for fuel) biomass product.
7. Identifying the optimum harvest age to maximize biomass yield.

Success in reaching each of these seven objectives is measured by effects on both short term and long term production rates. Traditional methods of tree selection, breeding, and production are slow, often requiring growers to plant trees that are less than optimal in growth performance in order to maintain a needed timber supply and to remain economically stable during tree improvement programs. Calorimetry will therefore have a maximum economic influence when used to guide selection of trees planted for early capital return along with a continuing program to optimize growth rates.

A broad distribution of tree sizes is found in even-aged stands of seedling populations of a single species. A portion of the growth rate heterogeneity is nutritionally related to microsite variability or physical factors, but a highly significant portion of variability is due to genetic differences. Use of selection techniques to increase the proportion of trees with better growth properties results in a large increase in overall biomass production. Consider for example Fig. 1, showing the distribution of stem volume index (SVI) of two-year-old seedlings from three different provenances of *Eucalyptus cypellocarpa* growing in a common garden at Corning, CA. Seedlings from the different provenances have different means and size distributions. The means vary from 2500 to 7000 cm^3. Thus, selecting seeds from the AU7 provenance for growth at Corning will produce a nearly three-fold increase in yield over growth of the AU6 provenance.

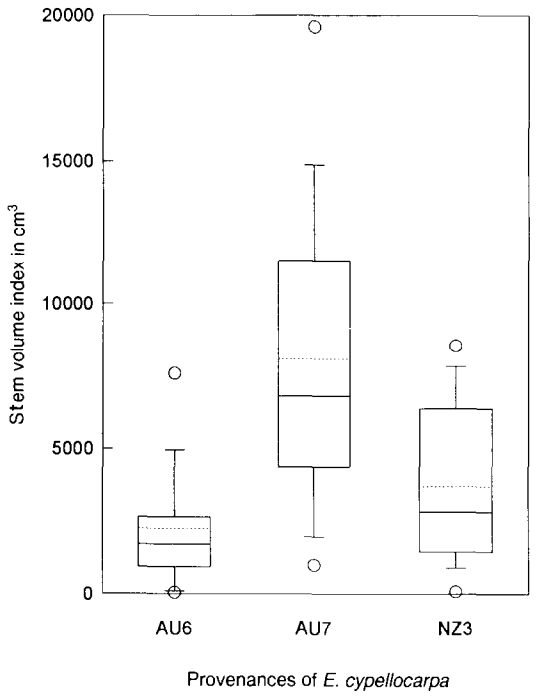

Fig. 1. Distribution of tree sizes in even-aged seedling populations from three provenances of *E. cypellocarpa* growing in Corning CA. The lines of the box plot mark the 10th, 25th, 50th, 75th and 90th percentile points of the data on stem volumes. The box encompasses the 25th through the 75th percentile. The 5th and 95th percentiles are shown as symbols below and above the 10% and 90% caps. The dotted lines are the volume means for the provenances.

Each of the provenances contains plants with widely diverse growth rates, showing the importance of careful screening of superior individuals within a prevenance in addition to screening for superior provenances. AU7 has the widest range of volume sizes as well as the largest mean volume. About 10% of the trees in AU7 have stem volume indices greater than 15 000 cm^3. Propagating only those trees that fall in the top 10% of AU7 would again increase yields by a factor of two.

The major conclusion from Fig. 1 is that growth of a mixed, unselected set of seedlings produces yields far lower than those yields obtainable from simple selection among the existing provenances and trees. Even with minimal selection for superior trees, major increases in biomass production rates are possible. Rapid and reliable early screening procedures similar to those described here are a requirement for realization of these increases.

2. Materials and methods

Field-grown plant tissues used in these studies were supplied by the Simpson Timber Co., Tehama Fiber Farm, Corning CA. Trees were planted in square plots

with a between-tree spacing of 3 m × 3 m. The trees were drip-irrigated at the rate of 0.8 m^3 ha^{-1} and fertilized at irrigation with nitrogen (as urea UN32) at a rate of 14.9 kg ha^{-1}. Trees were protected from insect and rodent pests using standard agricultural best management practices. Further details of planting site preparation and harvest techniques are described by Anekonda et al. [2]. Greenhouse plants were grown in 10 cm diameter, 200 ml pots in a peat/sand/perlite soil mix in a 50% shade house. Plants were irrigated with a 50% Hoagland nutrient solution.

Measurements of tree growth properties employed plant height and stem volume index determinations [3].

Tissue samples used in all studies were shoot apices, including terminal buds and subapical portions. Samples were generally collected near 7:00 am and placed in small vials with cold, half-strength Hoagland's solution containing 1% sucrose. The vials were maintained on ice during transport and stored at 5°C until measurement in the calorimeter.

Calorespirometric measurements were made using a Hart Scientific Model 7707 heat-conduction, differential scanning calorimeter. Most measurements were made in the isothermal mode [4–8]. Scanning procedures were used to examine the response of tissues to continuously changing temperatures [9,10].

3. Results and discussion

3.1. Selection of seed sources

The first step commonly followed in selecting seed for planting at a new site is identification of appropriate seed sources. Foresters have long attempted to identify and collect seed from trees within populations that exhibit good growth in their native location and have used these seeds in attempts to match seed-source-climate (or latitude and elevation) and planting-site-climate to enhance chances of getting favorable growth. However, making selections based on climatic factors is less effective than desired. Plants originating from within even a narrow geographical range may have a wide distribution of temperature responses. Accordingly, some are more suited to growth at a proposed planting site than others. One major difference may be in plant responses to high and low temperature extremes that can cause injury or stress that limits growth. High and low temperature tolerances are important determinants of where a plant can survive. Equally important, however, is the response of plants to changing temperature within the normal range of plant growth [11]. Matching the temperature coefficient (μ) of growth of a seed source to the optimum temperature coefficient for growth at a given planting site is critical for superior biomass production. Species differences among μ and T_{crit} values in *Eucalyptus* are directly correlated with growth rate differences among plants grown in common gardens [11,12].

Plants within any given *Eucalyptus* species exhibit a wide range of responses to temperature. Even plants within a narrow geographic area show a wide range of responses to changes in temperature. Identifying those plants with temperature

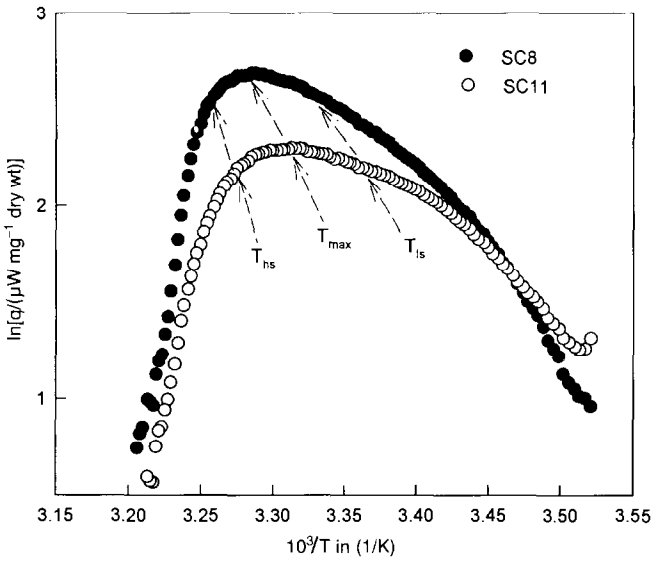

Fig. 2. Change in metabolic heat rate of meristematic tissue sections of *E. camaldulensis* clones SC8 and SC11 with increasing temperature. The data are plotted in Arrhenius form. Values of T_{ls}, T_{hs}, and T_{max} for each clone are indicated by arrows.

properties matched to optimum responses for trees at a proposed planting site is important for selection of trees to be used as seedling sources. Trees with optimum temperature response are more likely to produce seedlings with equally well-matched temperature responses than are trees from the population as a whole. Thus, an early identification of which trees are to be used for seed collection, based on temperature responses, can significantly increase the proportion of seedlings well suited to growth at a selected climate. Foresters have traditionally had no rapid, quantitative means of judging tree and seedling responses to temperature. Calorimetric measurement of meristem respiration rates as a function of temperature now allows quantification of these responses and provides a means for identifying source trees that may produce seedlings well-suited to a new growth environment.

Fig. 2 employs an Arrhenius-type plot to demonstrate responses of metabolic heat rate of two *Eucalyptus camaldulensis* clones to temperature changes over the range of normal growth and at high temperatures where the plant is stressed. Each genotype has a distinct pattern of temperature response in such studies. Several growth–temperature-related parameters are defined in this figure. The most apparent is the high temperature beyond which metabolic rate rapidly declines (referred to as the high shoulder temperature, T_{hs}) in the plot. This is a measure of the high temperature limit to survival. More important to biomass production rates, however, are T_{max} and T_{ls}. Thus, T_{ls} is an indication of the temperature at which the plant begins to be stressed by high temperature and metabolic rate (growth) slows.

The slope of the near-linear portion of the curve in the range 15°C up to T_{ls} indicates the rate at which metabolic activity changes with temperature, i.e. the temperature coefficient of metabolism μ, in a common temperature range for growth. Growth rate at a specific location depends critically on a match between the value of μ and the growth climate [11,13]. A significant proportion of trees with SVI values in the lower portion of Fig. 1 are slow growing because their values of μ and T_{crit} (where T_{crit} is used to refer to T_{max}, T_{ls}, or T_{hs} depending on which is limiting for a given genotype) are not matched to the growth climate.

In Fig. 2, the broken arrows connect values of T_{max}, T_{ls}, and T_{hs} for the two clones of *E. camaldulensis* SC8 and SC11. The values of these temperatures differ significantly for these two clones. SC8 metabolic rate continues to increase with temperature well beyond stress temperatures for SC11. In addition, the slopes of the plots between about $1000/T = 3.43$ and T_{ls} differ considerably, indicating different values of μ. SC8 has a much larger temperature dependence than SC11 in this range.

Simple scanning calorimetric measurements [9] made on tissues from trees that are considered as potential sources for seeds can identify sources with T_{crit} and μ values matched to the requirements for growth at a planting site. This selection will improve the probability that seedlings from these trees will also be matched to conditions at the growth site and thus enhance the number of seedlings with high rates of growth. Thus, prior to selection based on growth trials at a selected site, calorimetry may be used as a first guide for collection of seed from sources and can give enhanced initial production rates at a new plantation. Breeding programs guided by calorimetry can be applied to further improve planting stocks.

3.2. *Optimizing nutrient and water supply*

Maximizing the economic yields of biomass requires intensive agricultural practices. Water and fertilizer requirements for optimum growth depend upon the crop variety, the climate and the soil. Requirements must be established at each site individually. Economic considerations require that neither too little nor too much water and nitrogen be applied. However, it has been difficult to define optimum conditions for cultivation of long rotation crops such as *Eucalyptus*. The effects of added nutrients are not linear and cannot be defined by changing one factor at a time. The most informative and efficient approach is to employ multifactorial design methods [14]. Growth at Corning CA for clone 4016 of *E. camaldulensis* as a function of water and urea (as nitrogen source) was investigated to illustrate the usefulness of these methods. Fig. 3A shows a contour plot of 6-month growth of 4016 trees as a function of water and urea. The contours show that with ample urea present, the benefits from increasing water maximize at about 0.9 m^3 ha^{-1}. At this level of water, increasing urea above about 20 kg ha^{-1} results in little increased growth. Yield can be estimated at any urea and water combination in this plot, allowing comparisons of the costs of increasing either water or urea with the yield benefits from higher nutrient levels.

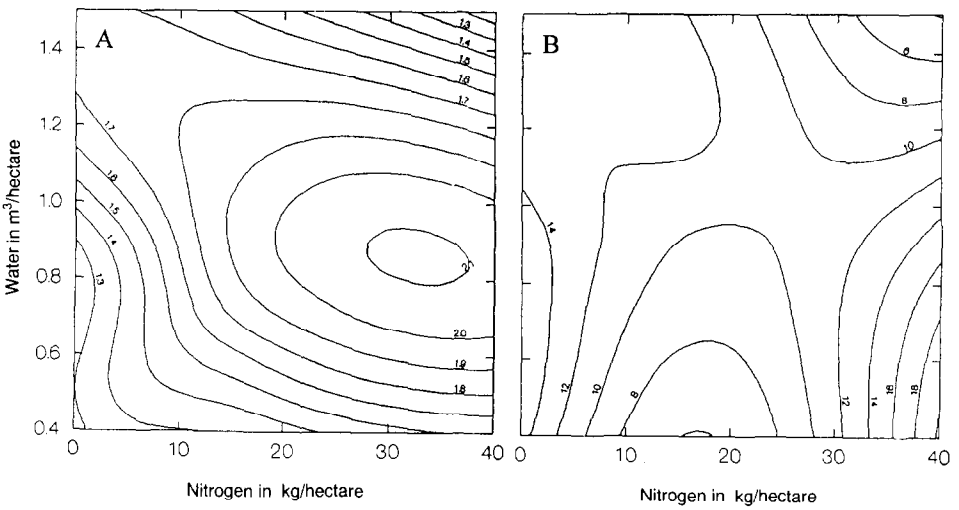

Fig. 3. Contour plots showing growth rate of clone 4016 of *E. camaldulensis* as a function of added water and nitrogen (3A) and specific metabolic heat rate as a function of water and nitrogen (3B). Values on the contours of 3A are growth rate in m^3. Values on the contours of 3B represent metabolic heat rate in μW per mg dry wt. tissue.

Fig. 3A is based on measured growth as a function of urea and water application levels. Accurate growth rate measurements are only possible when trees are small and increases in biomass can readily be determined. Fig. 3B shows a contour plot of isothermal (at 25°C) metabolic heat rates of meristem tissue sections from the same trees as a function of urea and water. When properly interpreted, metabolic rate can be used as a surrogate for growth that leads to conclusions about optimum nutrient levels similar to those based on growth and provides additional information about stress and energy-use efficiency.

Limiting nitrogen causes stress to plants, slowing growth, reducing metabolic efficiency and generally causing increased specific heat rates q. Ample nutrients also lead to increased q, due to more rapid metabolism, but with a parallel increase in efficiency and growth. Measuring both q and R_{CO_2} allows determination of when increased q corresponds to an increase or decrease in growth rate. Fig. 3B shows the net result of these effects. Water in the range 0.9 m^3 ha^{-1} with nitrogen above about 25 kg ha^{-1} where both water and nitrogen are ample to support rapid growth, produce a broad saddle in the contour plot of heat rates. Thus, it appears possible to measure metabolic rates of actively growing tree tissues at a given age with trees supplied both different water and nitrogen levels to determine optimum water and nitrogen application rates. Testing for optimum conditions by simultaneously measuring metabolic heat rate and CO_2 rate does not necessitate long term trials with a dedicated planting of trees. Varying the application rates of nitrogen and water is relatively easy, so that, with calorimetric analyses as a guide, optimization of nutrient levels can be rapidly performed.

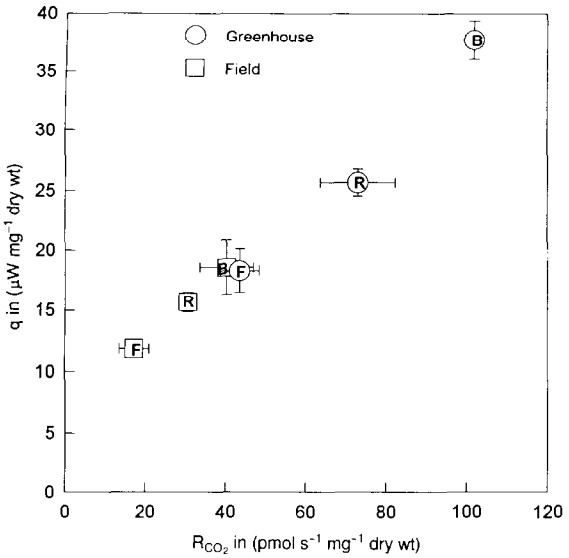

Fig. 4. Relation between respiratory parameters of field-grown vs. greenhouse-grown *Eucalptus* species. The linear relation shows that values of q/R_{CO_2}, the strongest single respiratory parameter for predicting *Eucalyptus* growth rate potential, are the same for greenhouse- and field-grown trees. Constant values of q/R_{CO_2} for *E. fastigata* (F), *E. camaldulensis* (B), and *E. viminalis* (R) grown in greenhouse and field show that this parameter does not change with age through the growth period examined.

3.3. *Early selection of superior trees*

Because both absolute and relative growth rates of trees change from juvenile to mature growth, it has not been possible in the past to predict satisfactorily the long term growth of individual trees from early growth rate measurements. To be successful in this goal, characteristics related to growth but either independent of maturation state or changing predictably with growth rate must be defined. Calorespirometric measurements show respiratory metabolism changes with age, but *Eucalyptus* maintain the same relative respiratory values during maturation. Fig. 4 presents data on plants of three species grown in a greenhouse plotted against data for the same species growing in the field. Note that the absolute values are different for greenhouse vs. field-grown trees, but that a proportionality is maintained. Thus, it appears possible that (with development of a sufficient database covering the early stages of growth) measurements of q, R_{CO_2}, R_{O_2} and the temperature dependence of these parameters, all as a function of age, can be used for predictions of growth.

3.4. *Matching* Eucalyptus *genotype to climate*

Environmental temperature is one of the key determinants of relative growth rates of eucalypts. A tree will not produce biomass as rapidly as it is genetically capable unless the temperature response of a tree is matched to the local climate.

Trees identified as superior growers at one site may perform poorly at a site with a slightly different climate. Therefore, in addition to the importance of temperature responses in selection of trees as seed sources, as discussed above, it is also important to identify trees most suited to the local climate. The two key metabolic parameters for such selections are the critical high temperature where activity increase with temperature deviates from Arrhenius predictions (T_{ls}), and the temperature dependence of metabolism μ. T_{ls} is a measure of ability to grow near the climatic extreme high temperature. The temperature dependence of metabolism is an indicator of growth performance across the temperature range normally encountered by the trees during growth. Trees adapted to growth in a warm climate have high μ values. Trees from high latitudes and high elevations have lower μ values. Relative growth rates of plants with different μ values will change with the growth temperature.

Each *Eucalyptus* genotype has genetically determined values of μ and T_{crit}. The values of these two parameters may change as a plant adapts to a specific climate, but the range of values accessible to a genotype by adaptation is limited. If a plant cannot achieve optimal μ and T_{crit} values for a given climate, it will not grow well at that site.

The responses of two different clones of *Eucalyptus* to changes in growth temperature are illustrated in the curves inset at the top of Fig. 5. Growth rates, measured in controlled environment chambers at 15, 20, and 30°C, for clones of 4016, which grows well at high temperatures, and GD11, which grows well only at lower temperatures, are shown for comparison. Growth, measured as biomass weight increase over a fixed time interval, is plotted against growth temperature. In addition, the metabolic response of tissues from each clone grown at each temperature to changes in temperature were examined to define the short-term temperature responses of the two *Eucalyptus* clones adapted to growth at three different temperatures. The value of μ for each genotype at each growth temperature is equal to the slope of the line given in the inset Arrhenius plots. Note that for both genotypes, μ is higher at 20°C than at 15 or 30°C. GD11 grows very poorly at 30°C and the measured temperature dependence of tissues grown at this temperature is also low. These response patterns are typical of the changes seen when large numbers of trees are examined.

When values of μ and T_{crit} for 17 different species of *Eucalyptus* trees are plotted against average growth rates of seedlings of each of these species in a common garden, the growth rates of the species are systematically related to μ and T_{crit}, as shown in the lower pair of inset graphs in Fig. 5. Species with too small μ values do not grow well in the climate at Corning CA. Increased growth rates are observed for species with higher values of μ, up to an optimum value. When values of μ are too high, growth is again reduced. The relation between growth and T_{crit} appears to be approximately the reciprocal of that shown in the μ vs. growth plot.

The central part of Fig. 5 is a schematic diagram of an Arrhenius-type plot deduced from the effect of growth temperature on μ. A single clone grown at different temperatures (temperature increases from lines 1 to 7) adapts to the change in growth temperature by changing μ according to the slopes of these lines.

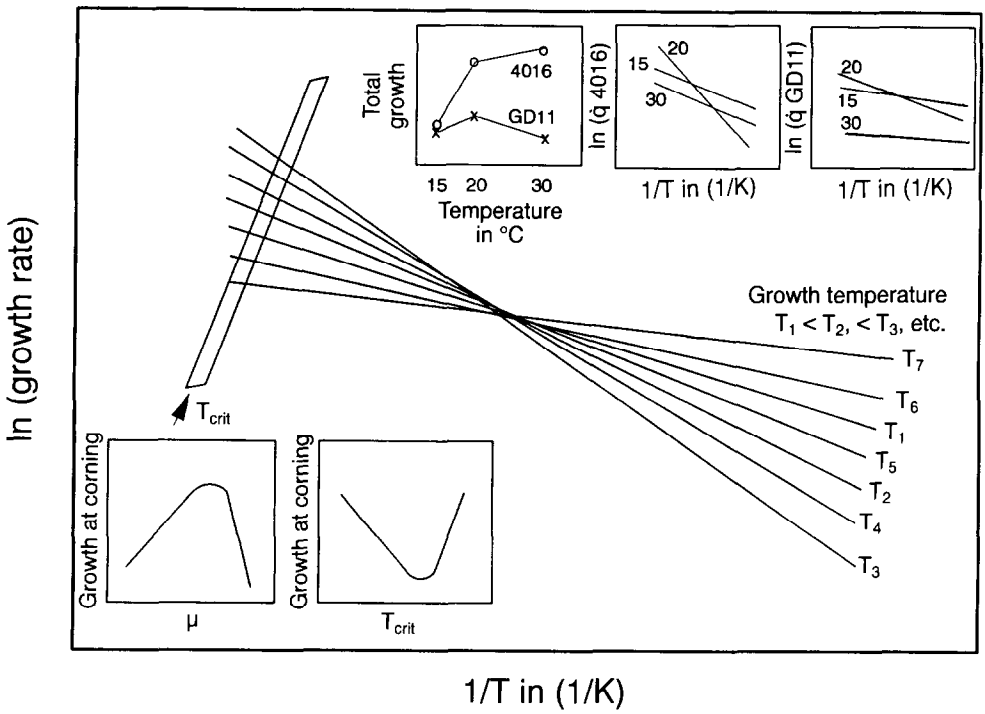

Fig. 5. Growth rate and related temperature coefficient trait dependences on temperature. In the upper inset, growth rate vs. temperature data are shown for ramets of two *Eucalyptus* species (*C. camaldulensis*, 4016 and *E. gundal*, GD11). Growth rates change differently with temperature. Also, the changes in respiratory rates with rapid change in temperature are shown for plants grown at each temperature. The lower inset shows how growth rate for 17 *Eucalyptus* species at Corning CA is correlated with μ and T_{crit} values for those species. The central portion of the figure combines these results into a model showing how changes in growth temperature of a single genotype alter μ and T_{crit} and therefore growth, in a given climate.

Each line indicates how the value of μ, established by growth at a fixed temperature, determines the growth vs. temperature response when temperature is rapidly changed. As found for clones 4016 and GD11, μ is shown to increase and then decrease as growth temperature is increased from T1 to T7. Growth rates increase and then decrease with μ as shown in the lower inset figure. T_{crit} values are given by the intersection points of the lines with a line approximately perpendicular to the log growth vs. reciprocal temperature curves. Growth decreases then increases with T_{crit} as shown in the lower inset.

Because of the presence of an isokinetic point (Fig. 5), the relative specific growth rates of plants adapted to a given growth temperature change with short term changes in temperature. Note that the order of growth at low temperatures is reversed from the order at temperatures above the intersection point. Genotypically defined plant response to temperature thus involves a complex adaptation of plant metabolism to the long term running average temperature and a response to

short term, daily fluctuations in temperature. Successful prediction is possible only over a limited range of temperature for each plant. This range varies among plants, both within and among species. Therefore, μ values within a species vary with origin climate, and there is a systematic increase in μ for plants from successively warmer climates. Selection of plants with the ability to adapt μ and T_{crit} to the range of temperatures commonly encountered at a growth site is therefore a very important factor in choosing trees for rapid growth at that site. The information produced by plots such as those in Fig. 5 can be used to guide selection of plants for growth at locations other than the test site. For example, trees with values of μ slightly lower than optimum at a given growth site are the best candidates for optimum growth at a site with a somewhat cooler climate.

Selection of cold-tolerant eucalypts is important for growth in many areas such as northern California and the southeastern United States. This selection is difficult because the extent of cold damage is a strong function of the degree of cold hardening, which in turn depends upon temperatures in the time period preceding a damaging freeze. Calorimetry can be used to identify freeze-tolerant plants in two ways. An indirect method is by measurement of μ. We have demonstrated that μ values for plants adapted to high latitude, high elevation locations are relatively low [11]. Thus, μ values determined for a collection of plants by isothermal measurements at several temperatures can often be used to predict which plants are likely to be the most cold tolerant. The second method involves measurement of metabolic heat rates as a function of time and temperature of exposures to cold [15,16]. This second procedure has to date only been used to characterize *Eucalyptus* responses to onset of winter hardening. Considerably more information is needed before the method can be used to quantify cold tolerances.

3.5. *Identifying multiple, readily measurable parameters related to growth rate*

Parameters so far identified as useful for prediction of *Eucalyptus* growth rates at a particular site are listed in Table 1. Measurements of these parameters do not yield enough information to solve completely the growth rate equation of Hansen et al. [17] for R_{SG} values. Values of ΔH_B, the enthalpy of biosynthesis per mole of carbon, and of γ_p and γ_B, the chemical oxidation states of carbon in photosynthate and plant biomass, are needed for a complete solution. However, in many conditions, these parameters can be estimated if a sufficient database of information is obtained for the species under study. This appears possible with *Eucalyptus* trees and thus allows relative specific growth rate predictions from measured values of the parameters listed in Table 1. A fast growing *Eucalyptus* tree commonly has a relatively high value of q (metabolizes rapidly), a low value of q/R_{CO_2} (metabolizes efficiently and/or with optimal metabolic pathways), values of μ matched to the growth climate, and a value of T_{crit} also matched to the growth climate. The relative importance of each of these variables differs from species to species. For example, in eucalypts, q/R_{CO_2} values are the strongest determinants in differentiating species; q is of greater importance as a variable to sort differences in redwoods [18].

Table 1
Parameters measured for predictions of tree growth rate

Always measured

1. q, the metabolic heat rate per mg tissue (μW (mg dry wt)$^{-1}$)
2. CO_2 rate, measured as an increase in q due to carbonate formation in the presence of an NaOH trap (mmol (mg dry wt)$^{-1}$)
3. The temperature coefficients of metabolic heat rate (μ_q) and R_{CO_2} (μ_{CO_2}) (kK)
4. q as a continuous function of temperature by scanning measurements to determine critical temperatures where metabolism is impaired.

Less commonly measured but important to measure for a subset of the samples measured

5. O_2 consumption rate (measured as a pressure change in a sealed vessel with an NaOH trap for CO_2)

Calculated parameters

6. R_{SG}, the specific growth rate
7. ε, the substrate carbon conversion efficiency

Other parameters of the growth model [17]

8. ΔH_B, the enthalpy change per mole of carbon incorporated into biomass
9. γ_P, the chemical oxidation state of photosynthate used for biomass synthesis
10. γ_B, the average chemical oxidation state of plant biomass

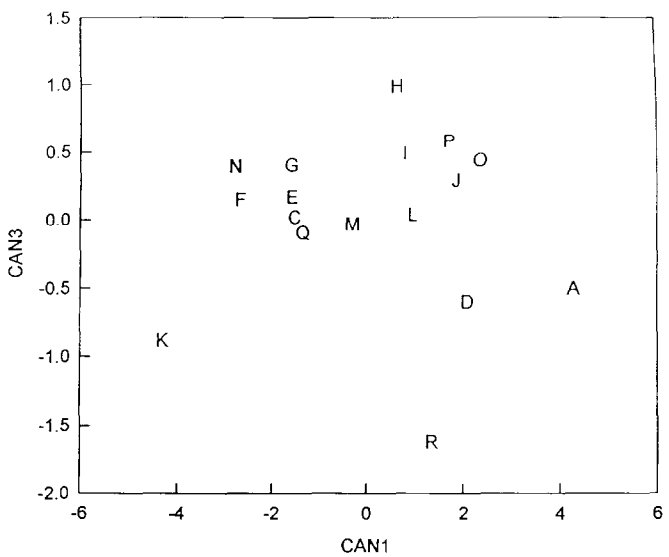

Fig. 6. Canonical discriminant analysis separating *Eucalyptus* species into distinct categories based on respiration parameters. Each letter represents coordinates for a different *Eucalyptus* species. Identities of these species are tabled in Anekonda et al. [2].

Evidence that these measurements can in many cases be sufficient to distinguish growth and respiration properties among a wide range of *Eucalyptus* species can be seen in Fig. 6. Canonical discriminant analysis using the measured respiratory properties q, R_{CO_2}, q/R_{CO_2}, and μ, and the calculated properties R_{SG}, (specific growth rate) and ε (carbon use efficiency) for 17 *Eucalyptus* species shows distinct

separation of species. CAN1 includes mostly q, μ and a positive dependence on R_{SG}, while CAN3 contains q/R_{CO_2}, and ε and a negative dependence on R_{SG}. A similar analysis comparing respiratory properties of individual trees also produces a separation within a species that identifies trees with the best combination of metabolic parameters for optimum growth at a given location. Plots of this type indicate that values of respiratory parameters are genetically stable, distinct characteristics. Each of the species has a characteristic distribution of growth rates and range of temperatures in which it can grow. These are successfully predicted by the respiratory parameters of Table 1. The morphological differences used by plant taxonomists in classifying *Eucalyptus* thus carry over into distinct metabolic differences. It is therefore possible to use respiration parameters to distinguish among *Eucalyptus* species. Identification of eucalypt species by morphological differences is difficult in many instances and could be aided by calorimetry.

3.6. Quality of wood

The model of Hansen et al. [17] predicts that plant growth rate is dependent on the oxidation states of photosynthate γ_P and biomass γ_B (or ΔH_B). In addition, γ_B is an important indicator of wood quality. Trees that are largely cellulose have a relatively high oxidation state of biomass product and small ΔH_B. Also, they have potentially higher values of substrate carbon use efficiency, because less sugar must be combusted to CO_2 to provide the energy necessary for production of cellulose biomass than for high-lignin biomass. Trees that are high in lignin and resins have a lower γ_P and hence a larger ΔH_B. We are not yet capable of defining ΔH_B directly from calorespirometry; however it is possible to estimate relative values of ΔH_B from a sufficiently large database of respiratory data on plants of the same species. Measurements of γ_B are possible by several techniques. γ_B can be calculated from elemental analysis for C, H, O and N, by scanning calorimetric analysis of oxidative reactions near 250°C for cellulose and hemicellulose, and near 450°C for lignin [19].

3.7. Harvest age

Determination of tree age for harvest and replanting cycles to produce maximal economic biomass yields is an important factor in tree cultivation, yet defining the optimum age has largely relied on long term growth observations. Calorespirometric measurements can simplify and accelerate identification of appropriate times for early selection. Variation in overall carbon use efficiency (ε) with maturation of eucalypts suggests that harvest at about 6–8 years is optimum for economic production. Fig. 7 shows that growth per year maximizes at about age three for *E. camaldulensis*. The drop-off at older ages is accompanied by a decrese in efficiency. Metabolic heat rates follow the same curve as growth rate and q/R_{CO_2} the inverse, and both can thus be used as indicators of growth.

Calorespirometric measurements can be made on a population of existing trees with different growth ages in a matter of a few days. Thus, measurements on trees growing at a given site, or measurements over the first few years of growth on trees

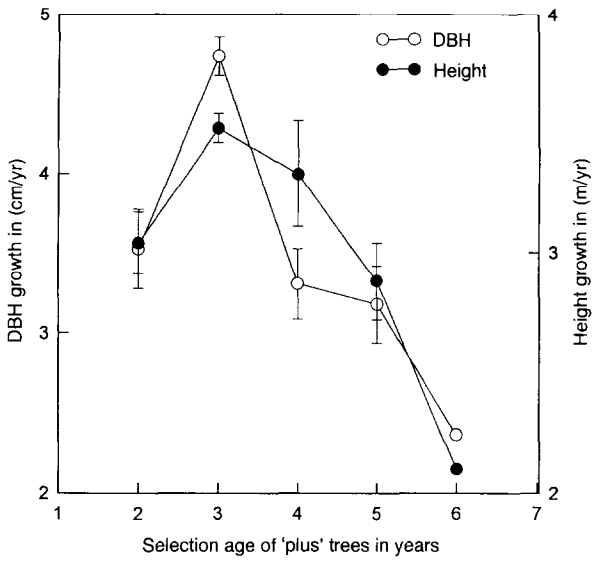

Fig. 7. Dependence of growth rate on age of selected, rapidly growing "plus trees" of *E. camaldulensis*. DBH is diameter at breast height.

newly planted at a site, can accurately guide decisions on cycling times. In addition, the age of clones or cuttings is defined by the age of their parent trees. Thus, clonal propagation of older trees yields plantlets with growth characteristics corresponding to the age of the parent. Two consequences of this are: cuttings from older trees may be past optimum when harvested at the end of a normal 8-year cycle, and early identification of superior trees for clonal propagation will enhance clonal performance.

4. Conclusions

Calorimetry can accelerate the rate of selection of superior trees within available populations for immediate yield increases, guide breeding programs for further enhancement of yields, determine harvest times, identify appropriate seed sources, match trees to a suitable climate and define the maturation state of clones. Eventually, calorimetrically identified respiration traits can be linked to quantitative biomass traits by using tools such as RAPD/RFLP analyses. Manipulation of such traits to genetically engineer suitable respirogenetic trees will further increase the rate of biomass production.

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