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Contrasting adaptation of two *Eucalyptus* subgenera is related to differences in respiratory metabolism

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Summary

1. The largest eucalypt subgenus *Symphyomyrtus* survives and grows better in diverse native and exotic environments than the second largest subgenus *Monocalyptus*. Previously postulated reasons for this difference, including differential resistance to native insect pests and dependence on specific ectomycorrhizal symbiotic associations with soil fungi, do not fully explain the marked adaptive differentiation.

2. This work shows that differences between the subgenera in survival and growth performance are related to respiratory parameters. We propose that effects of climatic temperature on respiratory metabolism result in *Symphyomyrtus* being more successful than *Monocalyptus* in adapting to diverse environments. This suggests a new paradigm for adaptation and evolution of eucalypts.

Key-words: Calorimetry, canonical discrimination, energy-use efficiency, metabolic heat rate, specific growth rate, temperature coefficient

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Introduction

Species from the subgenus *Symphyomyrtus* commonly exhibit much higher growth potential and survival in both native and exotic sites than *Monocalyptus*. None of the morphological and physiological parameters previously measured, including water potential, photosynthesis properties and stomatal conductance, successfully account for growth and survival differences between the two subgenera on native sites (Noble 1989). Furthermore, none of the proposed ecological reasons offer satisfactory explanations for survival differences. Observed differences in growth dependence on nutrients, mycorrhizae and differences in germination rates, resprouting and growth period show that *Monocalyptus* species are more site specific than *Symphyomyrtus* (Noble 1989) but the fundamental causes for these differences remain unclear.

Outside their native Australian environments, nine of the 10 most successful *Eucalyptus* species are from the subgenus *Symphyomyrtus* (Elridge *et al.* 1993). The results of survival and growth tests at Concord, CA, are typical (King & Krugman 1980). Twelve years after planting species of both subgenera from overlapping native ranges, only one of 11 *Monocalyptus* species, but 14 out of 15 *Symphyomyrtus* species survived. Some species of *Monocalyptus* do perform well in exotic environments, but generally only in limited regions (Wilcox 1982; Elridge *et al.* 1993). For example, *Eucalyptus regnans* and *Eucalyptus fastigata* grow well in New Zealand, and *E. regnans* planted in south-eastern Australia and *Eucalyptus diversicolor* planted in south-western Australia often outgrow the local eucalypt species. Release from native insect pests or lack of appropriate ectomycorrhizal symbiotic association with specific soil fungi fail to satisfactorily account for many observations (Pryor 1959a,b; King & Krugman 1980; Noble 1989; Elridge *et al.* 1993). Because respiratory metabolism is directly related to plant growth and survival (McCree 1970; Thornley 1970; Amthor 1989; Hansen *et al.* 1994, 1995), we hypothesize that differences in respiratory metabolism may determine the subgeneric differences in growth and survival in different climates. Several species with overlapping native growth ranges from each of the two major eucalypt subgenera were studied to test this hypothesis.

The results show that differences in growth and survival of the two *Eucalyptus* subgenera in an exotic environment are associated with differences in respiratory metabolism, and further, that appropriate measurement and analysis of respiratory properties of *Eucalyptus* species allows their separation by species and more certainly by subgenera.

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Materials and methods

PLANT MATERIALS AND SITE PREPARATION

Plant material used in this study consisted of seed sources of nine *Symphyomyrtus* and six *Monocalyptus* species grown from individual seed collections obtained by the Simpson Tehama Fiber Farm, primarily from CSIRO Division of Forestry, Australian Tree Seed Center. Some additional collections were from other seed collectors in Australia and from the USDA *Eucalyptus* programme in Florida (Anekonda *et al.* 1996). These 15 species were planted in May 1992 at Corning, CA. The planting site was prepared by ripping to 1 m in August 1991, followed by disking in March 1992. The soil in the plantation is Corning–Newville gravelly loam (Soil Survey Tehama County, CA, May 1967) with north aspect and a 3% slope. Each species is represented by one to three seed sources. A seed source can be defined as a small number of trees in a small geographical area within the natural range of a species. Different seed sources often represent different habitats. Each seed source was grown in a 49-tree, square plot in each of two fields (replications). These two fields were different in site quality as shown by the growth and survival of trees at the end of third year, although they appeared similar at the time of planting. Trees were 3 months old at the time of planting and between-tree spacing within a plot was 3 m × 3 m. Seed sources were randomly assigned to the plots within the fields. This planting design allowed quantification of both the site-related differences and fundamental physiological differences between *Symphyomyrtus* and *Monocalyptus* species. Both fields were irrigated and fertilized uniformly throughout the growing season. Trees were also protected from insect and rodent pests with standard agricultural management practices.

SAMPLE COLLECTION FOR CALORIMETRIC MEASUREMENTS OF RESPIRATORY METABOLISM

Among the available seed sources (one to three) for each species the best was selected based on its first-year height. In the selected source, the five tallest trees were chosen and labelled individually. Respiration measurements were made on only these five tallest trees based on first-year height of the best seed source from each species in field 1. Restricting sampling to the best trees in the best field reduced differential environmental influences on the sources and enhanced detection of inherent respiration differences among the species.

Actively growing, fresh shoot apices were collected near 07.00–10.00 h in the field and placed in small vials with cold, half-strength Hoagland's solution containing 1% sucrose. The vials were maintained at *c.* 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 of each tree. Samples were collected on five different dates between 2 June and 16 June 1993. A single sample was measured from each of five trees from the 15 species. In addition, respiration measurements were repeated twice at the end of the subsequent two growing seasons (August 1994 and June 1995) on a subset of eight of the 15 species. Sample collection order and the order of measurements of all samples and replicates were randomized.

CALORESPIROMETRIC METHODS AND DESCRIPTION OF RESPIRATION PARAMETERS

Calorespirometric measurements were made on *c.* 100 mg samples of meristematic and expanding foliage tissue excised with a razor blade and sealed in 1 cm^3 Hastelloy ampules of a heat-conduction, differential, scanning calorimeter (Hart Scientific Model 7707, Calorimetry Sciences Corp., Provo, UT, USA) operated in isothermal mode. Wound respiration is negligible in such tissues (Criddle, Breidenbauch *et al.* 1996). The respiration parameters measured or calculated were metabolic heat rate ($\dot{q}$, μW mg^{-1}), CO_2 production rate (R_{CO2}, pmol mg^{-1} s^{-1}), the amount of heat lost per mole of CO_2 formed ($\dot{q}/R_{CO_2}$), the temperature coefficient of metabolic heat rate (μ_q, kiloKelvin) and the calculated specific growth rate (R_{SG}, pmol C mg^{-1} s^{-1}) (Criddle, Breidenbach & Hansen 1991; Criddle, Fontana *et al.* 1991; Criddle *et al.* 1994; Hansen *et al.* 1994, 1995). R_{CO_2} and $\dot{q}$ were measured at 25 °C with an additional $\dot{q}$ value measured at 15 °C. The value of μ_q between 15 and 25 °C was calculated with the Arrhenius equation, i.e.

$$\dot{q} = A_q e^{-\mu_q/T},$$

where A_q is a constant and T the Kelvin temperature (Johnson, Eyring & Stover 1974; Criddle *et al.* 1994).

The μ_q-value was previously shown to be related to the climate of origin of woody perennials (Earnshaw 1981; Criddle *et al.* 1994). Plants from climates with a small range of daily and annual temperature fluctuations generally have high values for their rate of change in metabolic activity with temperature (i.e. higher μ_q). On the other hand, plants from climates where average temperatures are lower and temperature fluctuations greater, exhibit relatively small changes in metabolic rates with temperature (i.e. lower μ_q). Therefore, μ_q is a potential surrogate for predicting stability of plant performance across the common range of growth temperatures (usually between 10 and 30 °C).

Specific growth rate (R_{SG}) was calculated from respiratory measurements with the equation derived in Hansen *et al.* (1994, 1995). This equation defines specific growth rate (R_{SG}) as the rate of incorporation of carbon into new growth per mass of tissue, as a function of the difference between the metabolic heat rate and CO_2 production rate.

$$R_{SG} = \{ -\dot{q} - R_{CO2}\,(1 - \gamma_p/4)\,\Delta H_{O2})\}/\Delta H_B,$$

where γ_p is the average oxidation state of photosynthate or substrate carbon, ΔH_{O2} is the enthalpy change for combustion of photosynthate per mole of oxygen (a constant equal to – 455 kJ mol^{-1}) and ΔH_B is the enthalpy change per mole of substrate carbon incorporated into biomass during biosynthesis as kJ mol^{-1} C. For these calculations, γ_p and ΔH_B were assumed constant and equal to – 1 and + 50 kJ mol^{-1}, respectively.

Energy-use efficiency is inversely proportional to the metabolic heat energy lost per mole of CO_2 respired during dark respiration (i.e. $\dot{q}/R_{CO2}$). If the energy lost is large, the plant is inefficient in conserving energy for use in biomass formation and tree growth rate is thus limited (Hansen *et al.* 1995).

GROWTH MEASUREMENTS

Field data were collected on percentage survival, tree height in cm and stem diameter at half-height in mm on all seed sources of each species at the end of the third growing season during January 1995. Stem volume index in mm^3 was estimated by equating volume to height × $(diameter)^2$.

ANALYSES

Analysis of variance was carried out on survival and volume traits of 3 year-old trees and on respiratory parameters of 1 year-old trees for which respiration data on all 15 species were available. Variance components associated with replications, subgenera, species within subgenera, and seed source within species or error were estimated for the measured volume and survival traits using the VARCOMP procedure for unbalanced nested classification (SAS 1992). Replication component of variance was not estimable for respiration measurements because these measurements were made only on trees from the best replication. Canonical discriminant analysis was performed on respiration measurements of the species. If distinct subgeneric differences exist in respiration, then canonical discriminant analysis of multiple respiration parameters should accurately assign each species to either the *Monocalyptus* or *Symphyomyrtus* subgenus (Manly 1986; SAS 1992).

Results

Trees of all species in field 1 survived better than those in field 2, indicating large site-specific differences. *Symphyomyrtus* species generally had a larger stem volume and survival rate than did *Monocalyptus* species in both fields (Table 1). These results support previous observations that *Monocalyptus* is more sensitive to site conditions than *Symphyomyrtus* (King & Krugman 1980; Noble 1989; Elridge *et al.* 1993). The stem volume index for each species studied is plotted against percentage survival in Fig. 1. Data for *Symphyomyrtus* and *Monocalyptus* species are clearly separated in this plot as shown by the dashed lines. Rapidly growing sources are expected to have high survival but no simple relation exists between volume and survival. Even those *Symphyomyrtus* species with low growth rates have higher percentage survival than the *Monocalyptus* with similar growth rates. The differences between subgenera are magnified under the poorer conditions in field 2. These results clearly demonstrate differences in the inherent nature of survival and growth characteristics of the subgenera.

All the measured respiration parameters showed systematic differences between *Symphyomyrtus* and *Monocalyptus* (Fig. 2a–e), particularly during the first year of growth. The specific respiration rate (both $\dot{q}$ and R_{CO2}), temperature coefficient (μ_q) of metabolic heat rate, efficiency as indicated by $\dot{q}/R_{CO2}$ and calculated growth rate (R_{SG}) were significantly higher for *Symphyomyrtus*. Note that the metabolic rates, $\dot{q}/R_{CO2}$ and R_{SG} all vary with temperature. The values in Fig. 2 are an illustration of differences in respiratory parameters among species at 25 °C rather than an indication of efficiency and growth rates in the variable temperature environment at Corning. Although geographic distribution of both *Symphyomyrtus* and *Monocalyptus* species included in this study generally overlap in their native range (Chippendale 1988), systematic temperature-coefficient differences were found between species of the two subgenera. Substrate carbon conversion efficiency (i.e. the frac-

Table 1. Mean plot survival and mean tree volume with standard errors of means for two eucalypt subgenera planted in two fields

		Field 1		Field 2		Field difference (%)*	
Subgenera	*n*	Survival (%)	Volume (cm^3)	Survival (%)	Volume (cm^3)	Survival (%)	Volume (cm^3)
Symphyomyrtus	835	93·3 ± 1·4	4778 ± 225	81·3 ± 2·5	928 ±85	12·9	80·6
Monocalyptus	375	86·2 ± 2·3	1656 ± 160	52·0 ± 4·5	115 ± 50	39·7	93·1
†Subgeneric difference (%)		7·6	65·3	36·0	87·6		

*100 × (Field 1 – Field 2)/Field 1. †100 × (*Symphyomyrtus – Monocalyptus*)/*Symphyomyrtus*.

tion of photosynthate carbon incorporated into structural biomass) as indicated by a lower heat loss per mole of CO_2 formed (i.e. lower $\dot{q}/R_{CO2}$) was greater for *Symphyomyrtus* than for *Monocalyptus*. Specific growth rates calculated from the measured respiratory parameters yielded much larger values for *Symphyomyrtus* over all 3 years of tests, with predicted differences of the same relative magnitude as the measured volume differences for the entire population of plants studied (Table 1).

Analysis of variance of survival, growth volume and respiration for plants from the two subgenera are summarized in Table 2. Variance in survival was predominantly owing to subgeneric difference (55%); species differences within subgenera had no effect on survival. Variance in volume was also mainly the result of subgeneric difference (17%), however, the species-within-subgenera component was 10% of the total variance. Variance in respiration measurements owing to subgeneric difference (23–49%) was two to three times greater than the variance owing to species within subgenera (8–22%). The consistently higher subgeneric variance component in survival, volume and in all measured respiration traits strongly indicates a relationship among early respiratory metabolic activity, later growth rates, and survival.The first two canonical discriminant functions (or canonical variables) describing relations among respiration parameters, their coefficients and eigenvalues are given in Table 3. The eigenvalue for CAN1 is by far the largest and is highly significant ($P < 0{\cdot}0001$) accounting for 82% of the total variation among all the respiration parameters. Therefore, fundamental differences in survival and stem volume between the two subgenera are primarily associated with differences in respiratory metabolism accounted for by CAN1. Table 4 gives the quantitative relations between the measured and canonical variables. Figure 3 shows CAN1 plotted *vs* CAN2. All species in the right half of the figure belong to *Symphyomyrtus* and all those in the left except *E. cypellocarpa* (C) are *Monocalyptus* species. Canonical analysis thus demonstrates fundamental differences in respiration parameters of the species in the two subgenera. There is also some separation of species within the subgenera.

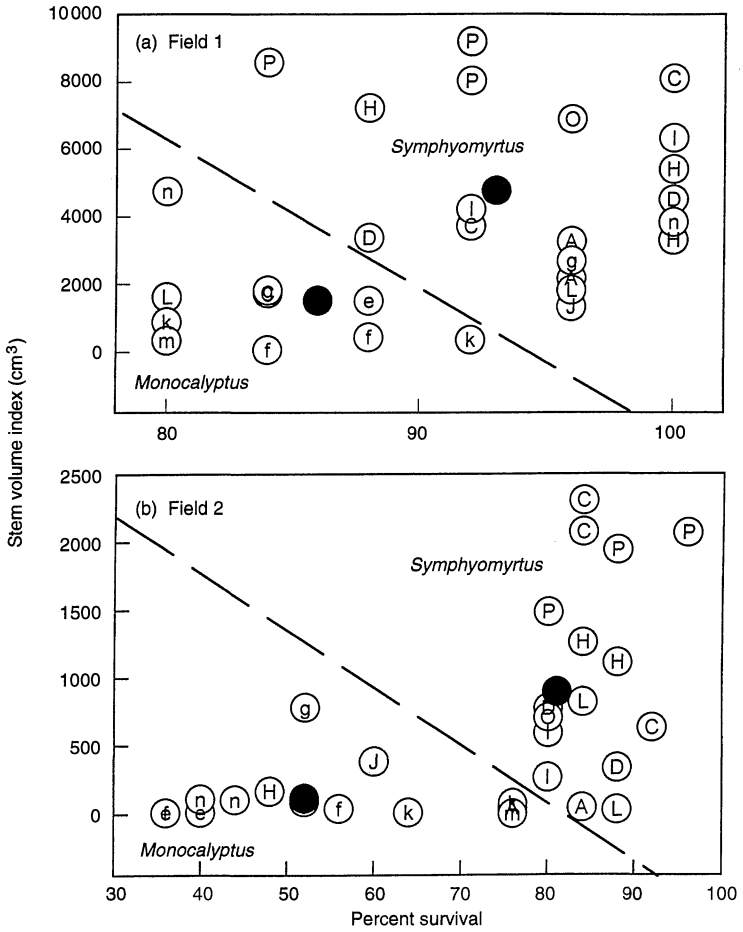

Fig. 1. Stem volume index plotted against percentage survival of *Eucalyptus* species in two fields: A, *E. brookerana*; C, *E. cypellocarpa*; D, *E. dalrympleana*; e, *E. delegatensis*; f, *E. fastigata*; g, *E. fraxinoides*; H, *E. maidenii*; I, *E. glaucescens*; J, *E. nitens*; k, *E. obliqua*; L, *E. ovata*; m, *E. radiata*; *n*, *E. regnans*; O, *E. rubida*; P, *E. smithii*. *Symphyomyrtus* species are represented by upper case letters and *Monocalyptus* species by lower case letters. Multiple symbols represent different seed sources (populations) of the same species. The dashed line separates the subgenera. Solid circles are average values for the subgenera.

Discussion

This study shows that selective forces giving rise to eucalyptus subgenera and species have operated on respiratory metabolism. Figure 3 establishes that a unique combination of respiratory parameters exists for each of the *Eucalyptus* species and that the combinations of respiratory patterns characteristic of *Symphyomyrtus* differ from those of *Monocalyptus*. Because respiratory properties are major determinants of plant growth rates and responses to environment, a tight link exists between respiration properties and adaptation to a given environment (Anekonda, Criddle & Libby 1994; Anekonda, Criddle, Libby, Breidenbach & Hansen 1994, Criddle *et al.* 1994, 1995; Anekonda *et al.* 1996; Criddle, Anekonda *et al.* 1996; Criddle, Smith & Hansen 1997).

The most likely selective environmental force causing respiratory metabolic adaptation is climate and the most likely climatic factor is temperature (Levitt 1980; Berry & Raison 1981; Davidson & Reid 1985; Sakai & Larcher 1987; Booth & Pryor 1991; Criddle *et al.* 1994, 1995; Jeffree & Jeffree 1994, 1996; Criddle, Anekonda *et al.* 1996). Plant distributions are closely linked to seasonal temperature, and metabolic responses are closely linked to diurnal and seasonal temperature changes (Criddle *et al.* 1994; Anekonda *et al.* 1996). Respiration parameters measured over a range of temperatures successfully predict the growth temperature ranges of plants as diverse as tomato and cabbage (Criddle, Smith & Hansen 1997).

Adaptation to broad temperature ranges offers survival advantages to a species because growth and

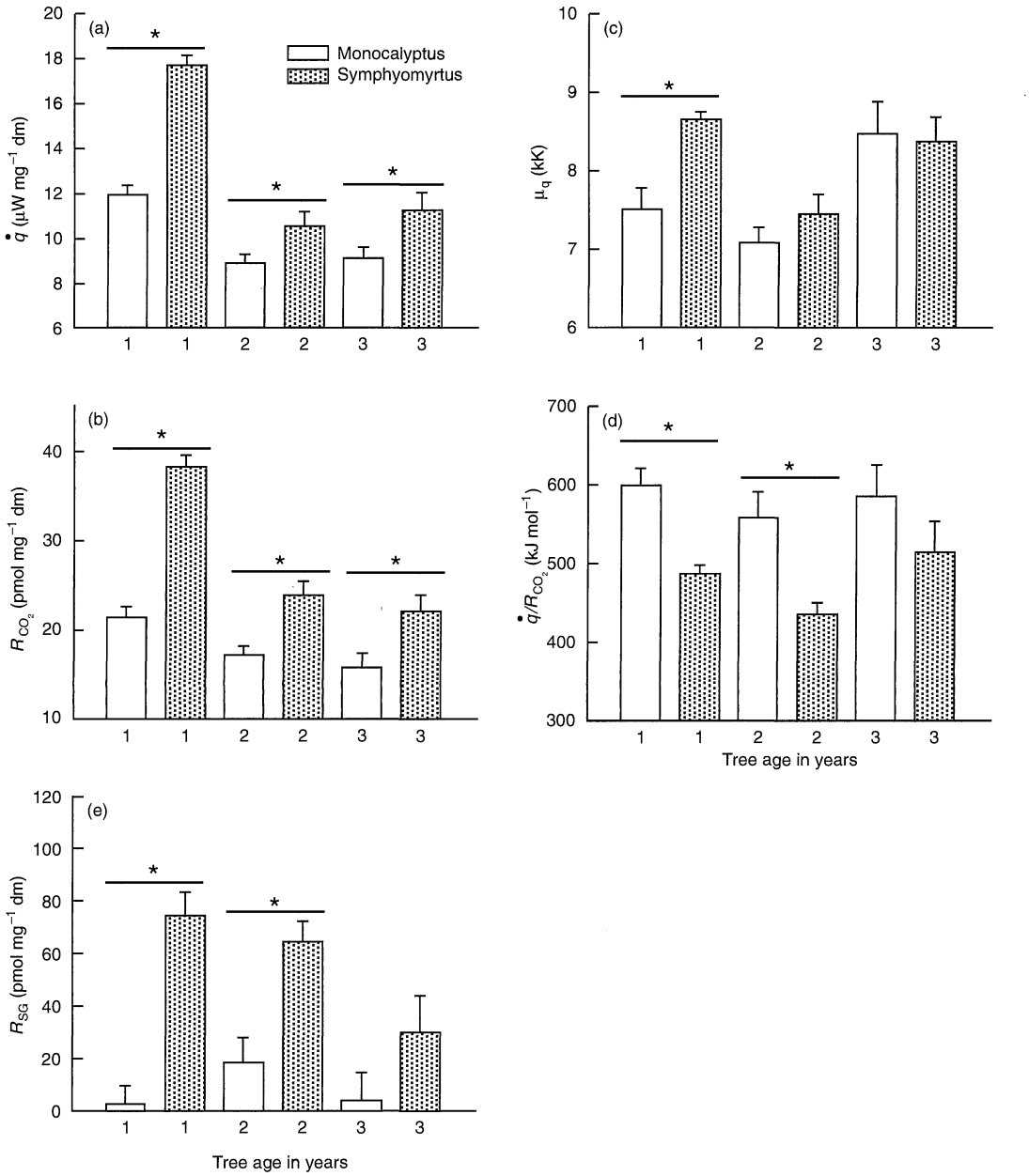

Fig. 2. Mean estimated respiration parameters for *Symphyomyrtus* and *Monocalyptus* subgenera plotted against tree age since planting: (a) metabolic heat rates ($\dot{q}$); (b) CO_2 production rates (R_{CO2}); (c) temperature coefficient of metabolic heat rate (μ_q); (d) the ratio of metabolic heat rate to CO_2 production rate ($\dot{q}/R_{CO2}$); (e) predicted specific growth rate (R_{SG}). An asterisk above the horizontal line indicates a significant ($P \leq 0{\cdot}05$) difference between the two subgenera within a same-age comparison. dm, dry mass.

Table 2. Estimated variance components owing to subgenera, species within subgenera and seed sources within species or error for survival, volume and respiration traits

	Percentage of toal variance†						
			Respiration				
Components of variance‡	Survival	Volume	$\dot{q}$	R_{CO2}	$\dot{q}/R_{CO2}$	μ_q	R_{SG}
Subgenera	55**	17**	45**	49**	29**	23**	31**
Species within subgenera	< 0	10**	22**	19**	8*	14**	11**
Error	25	55	33	31	63	63	59

†Variance component owing to replication difference in survival and volume is 20 and 18%, respectively. ‡Significance levels for *F*-statistics: *0·05 > *P* > 0·01; **$P < 0{\cdot}01$.

survival can persist through a wide range of changing conditions. Broadly adapted plants can survive well in many locations outside their native range. However, there are energy costs associated with the production of plants physiologically and morphologically able to survive over a broad range of temperatures. To the extent of these costs, energy available for growth, reproduction and competition for resources is reduced. In contrast, growth of plants adapted to a narrow range of conditions has lower energy costs and, therefore, a competitive advantage for growth within the appropriate narrow range. However, narrow adaptation is accomplished at the risk of incurring greatly reduced metabolic efficiency and major damage or death if temperatures outside the narrow adaptive range occur. Although structural changes may be associated with plant responses to a temperature change, a change in the structure need not be the ultimate cause of the response or the damage eventually observed as a consequence of the temperature change. Cells are compartmentalized and concentration gradients of ions and molecules exist across the membranes of compartments. These gradients, both of concentration and of electrical potential, are the immediate energy source used to drive biosynthesis in the cell. Biosynthesis creates not just new molecules from substrate but also new structures. Thus, energy gradients cannot exist without structure and structure cannot exist without energy gradients. At any temperature where respiration is either too slow or too inefficient to provide energy at a rate sufficient to maintain the energy gradients in at least a steady state, the gradients will diminish until the structure can no longer be maintained and the system will then begin to lose structures within the cell. If the process continues too long, the cell will be unable to repair itself and death ensues. Narrowly adapted plants thus fail to grow or grow poorly at most sites outside their native range. Exotic growth sites must be closely matched to the narrow native growth conditions to ensure growth.

The two temperature adaptation rationales (broad and narrow) have major effects on ability to successfully move plants from their native site to an exotic location. Broadly adapted plants may be successfully planted in a wide range of exotic sites. Narrowly adapted plants are difficult to move successfully. Our studies indicate that *Symphyomyrtus* species have lower metabolic efficiencies over a broad temperature range and are thus capable of survival at many exotic sites. *Monocalyptus* are adapted to rapid growth and competition in a narrow temperature range and may grow very well at a few sites carefully matched to their native sites but are unlikely to survive at most locations.

The species growth studies at Corning allowed a good test of *Symphyomyrtus* and *Monocalyptus* adaptation to temperature patterns. The trees were all well watered and fertilized so that the major uncontrolled variable affecting growth was temperature. Diurnal temperature variation at Corning is generally greater than at the growth sites of the test species in Australia

Table 3. First two †canonical discriminant functions (CAN1 and CAN2) generated from the analysis of respiration parameters

	CAN1	CAN2
Adjusted canonical correlation ± SE	0·85 ± 0·02	0·37 ± 0·07
Eigenvalue	3·1 ****	0·3 **
Proportion (%)	82	9

†Each canonical variable (CANx) is a linear combination of the measured respiration variables such that CANx = $a_1 \times \dot{q} + a_2 \times R_{CO2} + a_3 \times \dot{q}/R_{CO2} + a_4 \times \mu_q$, where a_1, ... a_4 are canonical coefficients of CANx. Each succeeding canonical variable measures patterning not accounted for by its preceding canonical variable(s). In order to avoid redundancy in the canonical coefficients, R_{SG} is not included in CANx. $^{**}P \leq 0{\cdot}01$; $^{****}P \leq 0{\cdot}0001$.

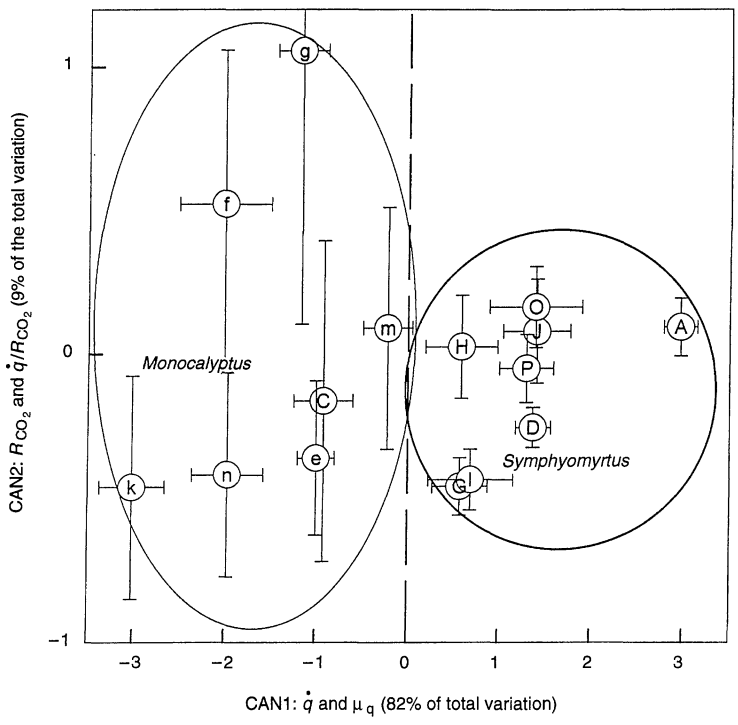

Fig. 3. Mean estimated first and second canonical variables, CAN1 and CAN2, for species respiration traits. Error bars are the standard errors of the means of CAN1 and CAN2. Because CAN3 and subsequent functions were not statistically significant and together added < 10% of the total patterning, they are not discussed further. For species names, refer to Fig. 1. The dashed vertical line emphasizes the separation of subgenera on the basis of the respiratory traits.

Table 4. Pattern of variation explained by the first two canonical discriminant functions of Table 3

Respiration variables*	Standardized canonical coefficients for CAN1	CAN2
$\dot{q}$	1·2	−1·4
R_{CO2}	0·4	2·0
$\dot{q}/R_{CO2}$	−0·2	1·6
μ_q	0·7	0·4

*These variables are presented in Fig. 2.

(Anekonda *et al.* 1996). The trees therefore experience temperatures outside their normal range for much of the growth season at Corning. Clearly, the more broadly adapted *Symphyomyrtus* species are better able to tolerate this range. The narrowly adapted *Monocalyptus* spend considerable time at temperatures outside the normal limits where ATP metabolism is well controlled.

Assuming our conclusions based on 15 species can be generalized, further molecular and respiratory physiology studies should provide an understanding of the evolutionary significance of respiratory adaptation in plants. For now, we speculate that metabolic adaptation has allowed progenitor eucalypt species to minimize competition by occupying unique habitats and niches. We further propose that differing solutions to the problem of metabolic adaptation to a given niche has produced differing patterns of respiratory properties that allow plants to occupy a common environment. Populations within a niche could include, for example, geographically overlapping *Symphyomyrtus* species, adapted to a broad range of environmental conditions including those of the niche, and *Monocalyptus* species, adapted to the specific set of conditions peculiar to the niche. Differences in respiration parameters between the subgenera seem to have been developed as two solutions to dealing with patterns of prehistoric temperature change. It is not uncommon that species with current overlapping geographical distributions may have differing responses to environmental factors (Jeffree & Jeffree 1996).

The multiple pathways of adaptation of metabolic responses for survival in changing environments that led to *Monocalyptus* being narrowly adapted and site specific while *Symphyomyrtus* from the same geographic range are more broadly adapted, could also easily lead to differential effects on a range of important, metabolically dependent functional properties of plants, including reproductive properties. Thus, metabolic differences among geographically overlapping plants with different adaptation strategies could readily restrict ability to cross. We propose, therefore, that metabolic differences could produce a 'metabolic isolation' that ultimately results in reproductive isolation and thereby contributes to evolutionary divergence in a manner similar to sympatric speciation.

Understanding how plants match their respiratory metabolism to climate should contribute to improvement of the match between plant growth and growth climate and therefore help guide ecological management and agricultural production.

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