

### Contrasts between *Eucalyptus* subgenera

Anekonda *et al.* (1999) interpreted the results of their study of growth and respiration by shoot apices from nine *Symphyomyrtus* and six *Monocalyptus* species, as 'a new paradigm for adaptation and evolution of eucalypts'. Far from a new paradigm, this paper contains errors of fact and a liberal view of what might constitute a fair contrast – as found in many previous publications in which these subgenera have been 'contrasted'.

First, while there are ≈600 species of *Eucalyptus* (>440 *Symphyomyrtus*, >140 *Monocalyptus*), plus a further 110 or so species of the closely related genus *Corymbia*, most published contrasts, like that presented by Anekonda *et al.*, have been based on a handful of species of any one subgenus. Similarly, these studies have seldom, if ever, been based on truly representative species, and instead focus either on sympatric species or on those species chosen for 'field trials' where the basis for choice is either not stated or has been biased by previous, equally unfair, contrasts. The most common contrasts have been based on growth and nutrition (see review by Noble 1989, and especially Florence 1964, 1981). For example, Anekonda *et al.* have iterated others in suggesting symphyomyrts have a 'much higher growth potential and survival ... than monocalypts', when no such general distinction has been satisfactorily proven. On the other hand, a comprehensive contrast of the subgenera (Judd *et al.* 1996) included 110 species and more than 500 references from around the world. There we noted that 'both *Monocalyptus* and *Symphyomyrtus* cover the range of growth, productivity and biomass accumulation from low ... to high ...'. Despite iteration, assertions that growth and survival of symphyomyrts are better than those of monocalypts, and that symphyomyrts have greater nutrient requirements and prefer more fertile soils, have a poor basis (e.g. Judd *et al.* 1996).

Secondly, the authors argue that '*E. regnans* planted in south-eastern Australia and *Eucalyptus diversicolor* planted in south-western Australia often outgrow the local eucalypt species'. Unfortunately, *E. regnans* is the 'local' species for large areas of south-east Australia (including Tasmania) and the same is true for *E. diversicolor* in south-west Australia. Worse, rates of growth of 'exotic' eucalypts (for example *E. globulus* – a symphyomyrt) are sometimes better than those of either plantations or natural forests of *E. regnans* in south-east Australia or *E. diversicolor* in south-west Australia (e.g. Grierson & Adams 1999). Even here, though, the contrast is still spurious. As is all too commonly the case, comparing attributes of a 'species' that has been highly modified by selective breeding

(in this case *E. globulus*) with those of the natural population is hardly a fair test. Similarly, the (mainly) arboreta-based comparisons of species in either region are few in number and seldom on either prime *E. regnans* or *E. diversicolor* sites.

Anekonda *et al.* used seed from a mixture of sources ('... primarily from CSIRO ...', 'from ... other seed collectors ...', '... including seed from the USDA *Eucalyptus* programme in Florida ...'), but could not definitively identify their sources or the parentage of the seed. Unless we know the lineage of the seed, and the degree of human-assisted selective breeding, it is difficult to assess the value of their contrast between monocalypts and symphyomyrts.

While Anekonda *et al.* have produced some interesting data, their 'paradigm' remains as weak a hypothesis as the many others generated about subgeneric variation in the eucalypts, at least until tested 'on a level playing field'.

### References

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### Response to M. Adams

We thank Dr Adams (Adams 2000, this issue) for identifying an unintentional error in our published paper (page 675, column 2, lines 7–10, Anekonda *et al.* 1999), '... and *Eucalyptus regnans* planted in

south-eastern Australia and *E. diversicolor* planted in south-western Australia often outgrow the local eucalypt species'. The correct statement is '... and *Eucalyptus regnans* planted in south-western Australia and *E. diversicolor* planted in south-eastern Australia often outgrow the local eucalypt species'. Prior to receiving Dr Adams's letter, we had recognized this error, informed the editor of *Functional Ecology*, and an Erratum was published in issue 14:4 of the Journal (page 400).

We agree completely with Dr Adams comments that conclusions about the differences in growth and survival of the two *Eucalyptus* subgenera, *Symphomyrtus* and *Monocalyptus*, in exotic sites, are based only on numerous observations, but have not been proven definitively. The first sentence in our introduction was not intended as a universal description of responses of all species in each subgenus. Our use of the terms, growth potential and survival, refer to the subgenera as a whole, and to the number of successful plantings at different sites. This does not mean that individual *Monocalyptus* species cannot successfully grow at certain exotic sites around the world, just that *Symphomyrtus* can grow at more, and more varied, sites.

We take exception to several other points in the letter. The paper by Anekonda *et al.* (1999) was not just one more report of attempts to correlate the success of *Symphomyrtus* and *Monocalyptus* in exotic locations with geographical, soil nutrient, symbiosis, etc., differences. Using species that were all growing at a common location, we measured responses of energy metabolism to changing reaction conditions. We observed differences among species and a statistically significant distinction between energy-use efficiency responses to changing environmental conditions for the two subgenera. The metabolic studies show that *Monocalyptus* species in general have evolved as temperature specialists and *Symphomyrtus* species as generalists.

Plants adapt to environmental conditions with contrasting strategies linked to their metabolic energy-use efficiency in changing environments. Metabolic rate studies show that *Symphomyrtus* have adapted a generalist strategy that emphasizes survival across a broad range of changing environmental conditions. However, adaptation to widely changing environmental conditions comes at the cost of less efficient use of energy (a result dictated by the second law of thermodynamics), and thus a reduced ability to compete for growth resources. The *Monocalyptus* species studied have metabolism adapted to a second strategy, i.e. they are specialists adapted to a narrower range of environmental conditions. This strategy allows better competitiveness in a given environment, but at the risk of being unable to tolerate extraordinary fluctuations in environmental conditions. Such plants may be widely distributed, but are successful only in narrow, well-defined conditions. Transfer of *Monocalyptus* species

to exotic sites has a low probability of success in finding an appropriate match to required conditions, but would be expected to grow with high efficiency when the correct site is located.

Both growth rationales offer successful paths for adaptation to climatic conditions. Because plants at all locations must achieve a compromise between growth and survival potential, it is not uncommon to have islands of specialists surrounded by generalists with much broader temperature range.

Adams contends that sympatric (overlapping) species and 'field tests' do not provide an accurate test for identifying differences between symphyomyrtes and monocalypts. This is true for traditional correlation studies. However, in our analysis these conditions are an advantage because overlapping species experience similar climatic conditions, yet our measurements allowed differentiation of the subgenera based on patterns of species responses to environmental conditions. The currently observed differences in metabolic energy-use requirements of overlapping species can be attributed directly to adaptation of different survival rationales or to species' response to the historic climate change.

Contrary to Adams's assertion, we did not attempt to show that symphyomyrtes have greater nutrient requirements and prefer more fertile soil than monocalypts. We only quoted literature sources on this point. However, our study did show that survival and volume differences between symphyomyrtes and monocalypts are much higher in the poor field (36% for survival; 87.6% for volume) than the better field (7.6% for survival; 65.3% for volume) (Anekonda *et al.* 1999).

Finally, Adams criticized our selection of seed sources for this study. Despite our using seed from a variety of sources where rapid growth in the local climate was the major objective, all seed came from wild seed collection, and we have excellent records on origin (latitude, longitude, elevation, and provenance location in Australia) of all the seed sources used in this study. This information was published in another article (Anekonda *et al.* 1996). Adams's concern that we are making inappropriate comparisons using selected populations may stem from the fact that the original seed collection by the Simpson Timber Company included somewhat genetically selected sources from *E. camaldulensis*, *E. tereticornis*, and *E. viminalis*. However, we did not include any of these species in our current study. Some selection does occur whenever seed is gathered in Australia for planting at locations such as California or Florida with a goal of rapid biomass production. We note, however, that even though our samples may contain a mix of unselected trees and selected trees that might represent species and subgenera extremes, this strengthens rather than weakens our conclusions. This shows that eucalypts, from whatever their history of collection and selection, whether from overlapping

or distinct native ranges, all fall into recognizable patterns of energy metabolism that are characteristic of their subgenus.

### References

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