

# Ecology of Myrtaceae with special reference to the Sydney region

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## Abstract

*Myerscough, Peter J. (Institute of Wildlife Research, Macleay Building A12, University of Sydney, NSW 2006, Australia. Email: pmyerso@bio.usyd.edu.au) Ecology of Myrtaceae with special reference to the Sydney region. Cunninghamia 5(4): 787–807.* The well known differentiation of Australian members of Myrtaceae, with Myrtoideae in rainforest and Leptospermoideae in other types of vegetation, occurs in the Sydney region. The Sydney region is particularly rich in Leptospermoideae. They occur in almost all terrestrial habitats, ranging from fertile to infertile sites. The diversity of responses to fire, seed dormancy and dispersal, and breeding systems in the Leptospermoideae increases with decreasing fertility. It is thus appropriate that large areas of infertile habitat are conserved in the region, including the area of the Blue Mountains and surrounding plateaus, in which about 16% of the world's eucalypt taxa occur. The region's Myrtaceae support a wide range of invertebrates and vertebrates as well as fungi, including mycorrhizal fungi, and much of its vegetation is dominated by Myrtaceous plants, particularly eucalypts. This review examines patterns of distribution in the Myrtaceae across the Sydney region, particularly with respect to variation in fertility of habitats, examines processes underlying patterns of distribution, and suggests questions for research to increase understanding of these processes.

## Myrtaceae and Australian ecology

In Australia, members of the Myrtaceae, a family of woody plants, many of them large trees, including the tallest angiosperms in the world, are diverse, widespread and abundant, and are important components in many ecological patterns and processes in the continent. Indeed, it can be argued that a high proportion of plant biomass in Australia is Myrtaceous, that much of the gaseous exchange between plants and the atmosphere on the continent involves members of the Myrtaceae, and similarly much of the cycling of minerals between Australian biota and soils is through plants of the family, and that much of the plant material consumed in bushfires is of Myrtaceous plants.

In Australian vegetation, Specht (1981) noted the occurrence of genera of Myrtaceae in 11 of 13 major plant formations he recognised; only *Zygochloa* (cane grass) hummock grassland and chenopod low shrubland lacked them. Eucalypts are particularly widespread and often dominant in many types of Australian vegetation (Pryor & Johnson 1981, Wardell-Johnson et al. 1997).

Much of the high biological diversity of Australia relates directly or indirectly to the Myrtaceae. As Beadle (1981a) pointed out, the Myrtaceae contains the greatest number of species, but not genera, of any family of plants in Australia; nearly half of the world's approximately 3 000 species of Myrtaceous plants are Australian. A vast array of Australian invertebrates feed on them; for invertebrates on some eucalypts, see Majer et al. (1997); and, for a description of the range of insectivorous birds and bats preying on invertebrates in eucalypt forests and woodlands, see Woinarski et al. (1997). Several species of vertebrates feed on Myrtaceous plants, including the specialist folivore of eucalypts, the koala (see Landsberg & Cork 1997). Various species of insects, birds, possums and fruitbats take nectar and pollen from inflorescences which, in most members of the family, are showy and produce much pollen and nectar. Many of these animals are effective pollinators and often sustain significant levels of outbreeding in Myrtaceous plants; for a review of breeding systems in eucalypts, see House (1997).

Most Myrtaceae investigated to date have been found to be mycorrhizal, either ectomycorrhizal or with vesicular-arbuscular mycorrhizas, or with both (Stevens et al., in prep.), including *Osbornia octodonta* F. Muell., which Stevens et al. (in prep.) found had vesicular-arbuscular mycorrhizas, a new record of such mycorrhizas in a mangrove. Beside fungi that form mycorrhizas with members of the Myrtaceae, many fungi and bacteria act as pathogens on them, and several fungi, bacteria and invertebrates are involved in decomposition of litter and dead timber of Myrtaceous plants (e.g. May & Simpson 1997); these organisms in their turn serve as food for various species of ground-foraging birds, mammals and reptiles. Occasionally, some populations of eucalypts are episodically defoliated by activities of various organisms, as seen, for instance, in rural dieback (see Williams & Woinarski 1997). In addition to providing basic resources in food chains, Myrtaceous plants also afford shelter and breeding sites to many species of animals, for example, nesting hollows in old trees. In short, because of the high biomass of Myrtaceae in the Australian vegetation, the diversity of resources afforded to other organisms by Myrtaceous plants and their own high diversity, the family has a key role in supporting the high biological diversity of Australia.

The distribution of various taxa in Myrtaceae is far from random with respect to environmental variation, and shows distinctive patterns at all taxonomic levels in the family, as do distributions of various organisms associated with Myrtaceous plants. Much of the environmental variation critical in differentiating patterns of distribution of members of the Myrtaceae is apparently of some geological antiquity, has been a factor in the evolution of the high diversity of species in the family, and is evident in the contemporary distribution of members of the family in the Sydney region.

### **Patterns of ecological distribution in the Myrtaceae**

Variation of climate and soils provides a framework against which the most obvious features of ecological distribution in the Myrtaceae can be viewed. On the old land surface of Australia, differentiation into habitats of low and somewhat higher soil fertility is of long standing, probably existing back in the mid-Cretaceous (Johnson & Briggs 1981). Beadle (1981a) suggested that new genera evolved in low-fertility habitats possibly in early Tertiary times with several of these genera being endemic

to Australia. In the Myrtaceae, genera of the subfamily Leptospermoidae, such as *Eucalyptus*, *Melaleuca*, *Baeckea*, *Calytrix*, are dry-fruited and, as Johnson and Briggs (1981) pointed out, largely occur outside rainforest, whilst the fleshy-fruited genera of the subfamily Myrtoideae, such as *Acmena* and *Syzygium*, are largely confined to rainforest on more fertile soils in wetter parts of the continent. In rainforest, vascular plants are usually relatively soft-leaved, whilst under similar climates plants on infertile soils are normally sclerophyllous, their hard leaves having much lignin and thick cuticles at maturity (Beadle 1954, 1962). Beadle also showed that the soils on which rainforest occurred generally had higher levels of phosphate than those on which sclerophyllous vegetation occurred, and that leaves of rainforest plants had higher amounts of phosphorus per unit dry weight than sclerophyllous plants. Furthermore, Beadle (1966) postulated that, through the Tertiary, levels of soil phosphorus directed evolutionary change in development of plants with xeromorphic features on soils of low fertility.

Through the Tertiary, the climate of Australia became more arid, changing from one in the late Eocene, approximately 40 million years ago, that supported forest across the whole continent to one in which forest is confined to its wetter regions, south-western Western Australia, the eastern and south-eastern coastal regions and Tasmania (Martin, 1998). Rainforest does not now occur in south-western Western Australia, probably due to lack of suitably fertile soils (Beadle, 1981b), and, as aridity increased, the xeromorphic flora that had evolved on soils of low fertility under moist climatic conditions was split between south-western Western Australia and eastern Australia with few taxa of this flora persisting in central Australia. As Beadle (1981b) recognised, in this flora there are several genera in the sub-family Leptospermoidae, as defined by Johnson & Briggs (1981), that occur only in south-western Western Australia, and some genera, *Babingtonia* (*Baeckea* in Beadle 1981b), *Callistemon*, *Calytrix*, *Darwinia*, *Kunzea*, *Leptospermum*, *Melaleuca*, *Micromyrtus* and *Thryptomene*, that occur in both south-western Western Australia and eastern New South Wales (see Table 4.7, p. 98 of Beadle, 1981b).

Pryor & Johnson (1981) see Australia as the centre for origin of the eucalypts and, indeed, for the Leptospermoideae as a whole, and note that eucalypts have been successful since the mid Tertiary. By the mid Miocene, about 15 million years ago, rainforest was in decline on the western slopes of the Great Dividing Range in south-eastern Australia, but charcoal and Myrtaceous pollen were more plentiful than in earlier deposits, suggesting that rainforest was being replaced by eucalypt vegetation (Martin 1987, 1998). Present-day Australian vegetation is dominated by *Acacia* and *Eucalyptus* sens. lat. Many eucalypts share with several phyllodinous acacias a nearly vertical stance for their flattened photosynthetic surfaces in their mature leaf canopies, particularly eucalypts with concolorous leaves (King 1997). Increasing aridity can be postulated as having been the dominant agent in selection of this attribute. In periods of drought when stomata are closed and insolation is high, temperatures of tissues will rise much more in a horizontal leaf than in a leaf whose flattened surfaces are held vertically. There are two reasons for this: firstly, a vertically held leaf will absorb less radiation, and, secondly, a leaf whose flattened surfaces are held vertically is more streamlined to convective movement of air across its surfaces and thus will lose sensible heat more efficiently to the air than a horizontal leaf. This would suggest that changing leaf stance is more easily accomplished in evolution under increasing aridity than is increasing the tolerance of tissues to heat stress.

Thus, in Australia, the differentiation of the Myrtoideae largely into well-watered fertile habitats and of the Leptospermoideae into well-watered less fertile ones appears to be ancient. Less ancient is the increased aridity of the continent superimposed on it, eliminating rainforest from central and western parts, separating xeromorphic flora of better watered parts into a south-western and an eastern segment and allowing some members of the Leptospermoideae, particularly *Eucalyptus* sens. lat., and to a lesser extent *Melaleuca*, rapid evolution and expansion into new habitats. The outcrossing nature of their breeding systems and the enormous production of seeds by most eucalypts (up to 150 million Jacobs (1955) estimated to be produced by an individual of *Eucalyptus camaldulensis* during its lifetime) may have been important factors in this rapid evolution.

Eucalypt woodland is widespread in sub-humid and semi-arid regions of Australia. Eucalypt forest occurs in the south-western tip of the continent and down its eastern and south-eastern coasts and in Tasmania. The major centres of diversity of the Myrtaceae remain in the moist climatic zones of the continent in its south-western tip, where the diversity now resides solely in the Leptospermoideae, and in its eastern regions, where, due to existence of both fertile and infertile soils, both the Myrtoideae and the Leptospermoideae continue to occur, still largely differentiated in their occurrence with the diversity of Myrtoideae increasing with soil fertility and that of Leptospermoideae conversely increasing with decreasing soil fertility. The Sydney region well illustrates this ancient continuing differentiation of habitat between members of the two sub-families, and rather less well illustrates differentiation between forest and woodland associated with variation in rainfall, though even this pattern is present.

### **Ecological distribution of Myrtaceae in the Sydney region**

In the Sydney region, major patterns of variation in vegetation have been described in relation to variation in climate and other features of landscape by Pidgeon (1937, 1941), Burrough et al. (1977) and Benson and Howell (1990). Much of the region's vegetation is dominated by eucalypts. Beside variation of vegetation in relation to rock type, soils and landform, Pidgeon (1941) explored variation in distribution of eucalypt species with respect to variation in temperatures with increasing altitude from the coast into the Blue Mountains and with variation in rainfall from areas of higher rainfall on the coastal plateaus and in the mountains to areas within the rain shadow of the basin that forms the Cumberland Plain. Variation of eucalypt vegetation with variation in rainfall is apparent on Wianamatta shales. Soils on these shales support the Blue Gum High Forest of Benson & Howell (1990, 1994) in areas of high rainfall on Sydney's north shore, with *Eucalyptus saligna* and *Eucalyptus pilularis* giving an open-forest canopy up to 40 m. In areas of low rainfall on the Cumberland Plain, they support Benson's (1992) Grey Box Woodland, with *Eucalyptus moluccana* and *Eucalyptus tereticornis* on flat to gently undulating country, or, on more hilly country, Grey Box-Ironbark Woodland, with *Eucalyptus crebra* also forming the tree canopy with the other two species. Though climatic variation obviously influences distribution of vegetation and species of Myrtaceae across the region, the most striking aspects of variation in their distribution are in relation to soil fertility in which rock type has a commanding influence.

As already indicated, the major and apparently long-standing differentiation of habitats between members of the Leptospermoideae and members of the Myrtoideae is along gradients of soil fertility. In the Myrtoideae, only about seven species occur in the Sydney region, of which *Acmena smithii* is perhaps the most prominent member in the region's vegetation. *Acmena smithii* is an important component of rainforest both in coastal areas, on fertile soils on Permian rocks in the Illawarra and shales and sandstones of the Narrabeen series, as in Royal National Park (Beadle 1954) or in the Gosford to Lake Macquarie area (Benson 1986), and in the Blue Mountains on fertile soils again on Permian rock, as in closed-forest of the 'Escarpment Complex' of Keith & Benson (1988), and on basalt, as in rainforest on Mount Wilson (Brough et al. 1924), the 'Montane Rainforest' of Keith & Benson (1988). It also occurs in small pockets of rainforest in deep gullies incised into Hawkesbury and Narrabeen sandstones in the Colo Gorge and Wheeny Creek area, the 'Gully Rainforest' of Ryan et al. (1996). As with many rainforest trees, the leaves of *Acmena smithii* have a predominantly horizontal stance, and, unlike that of most eucalypts, its canopy usually casts deep shade. Its fleshy one-seeded fruit are eaten by various species of birds (see Floyd 1989) and are thus probably dispersed by them, as claimed by Beardsell et al. (1993b). Its fruit are also eaten by flying foxes (Eby 1995) and by brushtail possums (T.D. Auld personal observation). The seed is relatively heavy, mean seed weight of 0.13 g (Ashton & Frankenberg 1976), and the seedling is very shade-tolerant (Ashton & Frankenberg 1976). All other species of the Myrtoideae in the Sydney region are less common but are all trees, probably with similar reproductive traits, confined to rainforest except *Austromyrtus tenuifolia*, a shrub which generally occurs in riparian scrub on sandstone.

By contrast, the Leptospermoideae are very diverse and widespread in the Sydney region. Eucalypt species tend to form the overstorey in all native vegetation in the region ranging from the most fertile soils, when these are not exclusively occupied by rainforest, to all but the most infertile or periodically waterlogged soils. Eucalypts, a term used in this paper to cover all species of *Angophora* and *Corymbia* as well as of *Eucalyptus*, range from species such as *Eucalyptus saligna* that inhabits fertile soils to *Eucalyptus haemastoma*, *Corymbia eximia* and *Angophora hispida* that inhabit shallow infertile soils on sandstone. Within *Angophora*, the species cover a wide range of fertility, with *Angophora subvelutina* on fertile soils to *Angophora hispida* on infertile soils. In the Sydney region, species of *Corymbia* are largely restricted to infertile soils, though *Corymbia maculata* inhabits more fertile sites than do *Corymbia gummifera* and *Corymbia eximia*. Within *Eucalyptus*, species of the subgenus *Symphyomyrtus* are more numerous on fertile than infertile soils, though they are not entirely absent on the latter, while species of *Monocalyptus* occur equally on fertile and infertile soils. *Monocalyptus* includes the scribbly gums, a group of species that are entirely confined to infertile soils.

No other group in the Leptospermoideae covers as wide a range of soil fertility as do the eucalypts. Some non-eucalypts do occur on reasonably fertile soils. *Syncarpia glomulifera* tends to occupy habitats on shale soils and, on the most fertile of these, occurs at the edge of rainforest, while *Choricarpia leptopetala* also occurs at the edge of rainforest, as does *Backhousia myrtifolia* often close to creeks or rivers, as do *Tristaniopsis laurina* and *Tristania neriifolia*. Several species of *Melaleuca* and *Callistemon* inhabit soils that are periodically waterlogged, as do some species of

*Leptospermum*. In heaths on the most infertile soils, eucalypts are often lacking or have a very low cover, but other Leptospermoideae are almost always present, such as species of *Leptospermum*, *Kunzea*, *Baeckea*, *Micromyrtus*, *Darwinia*, and *Calytrix*.

In the Sydney region, the diversity of Myrtaceae appears to increase, both at the generic and specific levels, as soil fertility decreases. This aligns well with the suggestion of Beadle (1981a) and Johnson and Briggs (1981) that differentiation of scleromorphic taxa on soils of low fertility has a long history, and with the suggestion that the climate of the Sydney region, and, indeed, that of the rest of the Australian eastern seaboard in general, has changed less than that of the continent as a whole during the late Tertiary and Quaternary. Further evidence for the long history of differentiation of scleromorphic taxa on soils of low fertility in the Sydney region is the high degree of local endemism seen among species in habitats with such soils (for several such species in Myrtaceae, all in Leptospermoideae, see Table 3, pp. 484–5, of Benson (1986); Table 4, p. 140, of Keith and Benson (1988); Table 4, p. 332, of Benson and Keith (1990); p. 576, *Micromyrtus minutiflora*, in Benson (1992); Table 5, pp. 775–6, of Benson & Howell (1994); Table 4, pp. 102–9, of James and Kodela (1994b); Table 4, pp. 185–6, of Fisher et al. (1995); and Table 4, p. 463, of Ryan et al. (1996)).

The high diversity and much local endemism of the scleromorphic flora of sandstones and Tertiary alluvial deposits in the Sydney region are shared by areas also with low soil fertility in south-western Australia whose climate has also changed less through the Tertiary and Quaternary than that of the continent as a whole (Beadle 1981a). Such areas in the south-western tip of Western Australia and in the Sydney region deserve special consideration in conservation. In the Sydney region, this is well recognised in the many and extensive national parks over sandstone areas, and in the recent move to recognise an extensive part of the Blue Mountains and surrounding plateaus in which 132 taxa of eucalypts, 16% of the global total, occur (James & Kodela 1994a), as World Heritage. The actual area nominated for World Heritage is smaller than this, though still containing 90 eucalypt taxa (NSW National Parks & Wildlife Service 1998). Perhaps less well conserved than areas of vegetation on sandstone in the region are areas of native vegetation on Tertiary alluvial deposits.

It is clear that patterns of distribution arise and survive through various processes. Processes range in scale from individual metabolic reactions in tissues, to capture of resources, light and inorganic nutrients necessary for growth, to replication of genetic material and cell division, to initiation, growth and death of individual organs such as roots, leaves, and flowers and fruits, to transfer of gametes and development of embryos, to establishment of seedlings, growth, successful reproduction of individuals, and to survival of a pool of interbreeding individuals from one generation to the next. For survival and continued evolution of species in a flora, all these component processes have to be completed under prevailing environmental variation. This variation includes not only day-to-day changes of weather, effects of other organisms, plants, micro-organisms and animals, but events such as extreme weather conditions and fire. Effects of these things are likely to interact and to vary with site-specific characteristics such as soil fertility, to whose variation between sites, patterns of distribution among the region's Myrtaceae have so marked a relationship. In short, ecological processes in Myrtaceae of the Sydney region can be expected to have patterns correlated with those seen in their distributions.

## Ecological processes in Myrtaceae of the Sydney region

Across the range of soil fertility occupied by Myrtaceae in the Sydney region, the following processes may be expected to show particular patterns of variation: the acquisition, conservation and cycling of resources by plants; interactions between plants and micro-organisms, including formation of mycorrhizas, incidence of diseases, and decomposition of litter; interactions between plants and animals, including folivores, sap-suckers, nectar and pollen-feeders including effective pollinators, and frugivores including effective dispersers; interactions between plants including competitors of the different or the same species, and, in the same species, mates within a breeding system; and interactions between plants and fire.

### Growth and resources

Across the gradient of fertility from rainforest to heath the availability of plant resources clearly varies. Under the relatively fertile conditions of rainforest, light is probably the resource most usually limiting establishment of seedlings, whilst in heaths, in phases in which seedling establishment occurs, particularly after fire, light often remains abundant for some time, but soil nutrients, after an initial flush immediately following fire (see, for instance, Siddiqi et al. (1976)), are in short supply. At the two extremes of the fertility range, more massive seeds may be expected than in the middle of the range, (a) where light is in short supply on the rainforest floor, supplying the seedling with initial energy requirements, and, (b) where inorganic nutrients are in short supply in heath soils, supplying it with its initial requirements for these nutrients. Apart from *Austromyrtus*, Myrtoideae in the Sydney region have fruits each with few seeds to one seed in the case of *Acmena*. In the Leptospermoideae, *Backhousia* and *Choricarpia* (genera normally found in or at the edge of rainforest) also have few-seeded fruit. At the other end of fertility range, fruit of some heath genera are few-seeded and even one-seeded as, for instance, in *Calytrix*, while the dry indehiscent fruits of *Darwinia* and *Micromyrtus* are usually also one-seeded. This may reflect a need to provision embryos with sufficient mineral nutrients for establishment of seedlings in soils in which their supply is chronically low. Once established and growing, plants take up inorganic nutrients from the soil. Most other members of the Leptospermoideae have many-seeded capsules and usually a large production of light-weight seeds, requiring open, well-lit habitats for establishment of seedlings. As soil fertility decreases, seed size appears to increase across a comparable series of species, as, for instance in *Angophora* species — *Angophora subvelutina*, occurring on deep fertile alluvial soils, has a smaller seed than *Angophora floribunda*, on soils of intermediate fertility, while *Angophora hispida*, occurring in heaths on very infertile soils, has the largest seeds (Mowatt & Myerscough 1983).

As Beadle (1954, 1966, 1966, 1968) and Loveless (1961) showed, plants occupying infertile soils, in particular phosphate-poor soils, are more sclerophyllous and show other xeromorphic characteristics; leaves are harder, have higher proportions by weight of lignified tissue and lower amounts of phosphorus per unit weight, and are often more long-lived, than leaves of plants growing on more fertile soils. This generalisation is likely to apply across members of the Myrtaceae over the range of

soil fertility they inhabit in the Sydney region, but it requires systematic testing before it can be taken as conclusive. A comparison of specific leaf area in laboratory-grown seedlings of four species of *Angophora* showed *Angophora hispida*, a heath species, to be most sclerophyllous and *Angophora floribunda*, the species growing on the most fertile soils of the four species, the least sclerophyllous (Mowatt & Myerscough 1983).

Beadle (1968) showed that some rainforest plants withdraw a smaller proportion of phosphorus from their leaves as these senesce than do plants with sclerophyllous leaves from infertile habitats. He also compared the phosphorus content of the trunks of trees in four rainforest species with that in three species of eucalypts that are characteristic of tall open forests. He showed that the phosphorus content per unit weight was much lower in the wood of the eucalypts and that the fall in phosphorus content of the tissues from the cambium to the wood deeper in the tree was much greater in the eucalypts than in the rainforest trees; indeed, in three of the four species of rainforest tree there was no detectable decrease in phosphorus content from the cambium to the wood. These preliminary data of Beadle (1968) suggest that internal cycling of the key nutrient phosphorus, as seen in its withdrawal from senescing and from maturing lignified tissues, is much more efficient in non-rainforest plants than in rainforest plants. In the Sydney region, there is excellent opportunity to test whether this applies across members of the Myrtaceae from a wide range of soil fertility over which they occur from rainforest to heath. Ashton and Frankenberg (1976) showed that in their sample of leaves of *Acmena smithii* 54% of the phosphorus was withdrawn before leaf fall, while about 70% was withdrawn from leaves before their fall in *Eucalyptus obliqua* (Attiwill et al. 1978). Given that sclerophyllous leaves have a lower phosphorus content in the live state and may have a higher proportion of that phosphorus withdrawn before leaf fall than mesomorphic leaves in rainforest, it would be expected that rainforest litter is richer in nutrients and much more rapidly broken down by micro-organisms and the soil fauna than sclerophyllous litter.

#### Questions for research:

1. What patterns in seed mass occur in the family, and taxa within it, across gradients of fertility?
2. What patterns occur in specific leaf area in the family across gradients of fertility?
3. Does the phosphorus content of leaves in the family show a continuous decrease from fertile to infertile sites?
4. Do plants in the family that grow on infertile soils withdraw a greater proportion of phosphorus from leaves before they fall than those that grow on fertile soils?
5. In differentiation of wood in stems, is a larger proportion of phosphorus withdrawn from tissues in plants of the family growing on infertile than in those that grow on fertile soils?

## Decomposition of litter

Fallen sclerophyllous leaves are broken down more slowly than fallen leaves of rainforest species, and this holds for the limited number of Myrtaceous samples examined. Ashton & Frankenberg (1976) found that, at Wilsons Promontory, freshly fallen leaves of *Acmena smithii* decayed and disintegrated in 6–8 months. In moist *Eucalyptus regnans* forest in Victoria, Ashton (1975) found that, due to action of soil fauna, fallen leaves of *Eucalyptus regnans* were largely chewed and incorporated into the mineral soil within six months, while in *Corymbia maculata* forest McColl (1966) found that 60–70% of the dry weight of fallen leaves remained after one year. Again, in the Sydney region, there is opportunity for comparing rates of breakdown of fallen leaves, as well as other dead plant parts, including perhaps roots, among members of Myrtaceae across the range of soil fertility they occupy. The expectation is that rates decrease along the gradient of fertility from rainforest to heath.

### Question for research:

1. Is there a decrease in rate of decomposition of fallen leaves in the family from fertile to infertile sites?

## Mycorrhizas and micro-organisms

It is generally observed that mycorrhizas are more abundant in soils of low-nutrient availability than in those with higher availability (Harley 1959, Keith 1997). However, in their survey of mycorrhizas in the Myrtaceae, Stevens et al. (in prep.) find that mycorrhizas occur in rainforest and heath species and in species inhabiting soils of intermediate fertility, and that variation in the types of mycorrhizas observed across the family is not related to this gradient in fertility. It should be emphasized that their survey looked at the presence of mycorrhizas, not at their abundance. With saprophytic and parasitic micro-organisms associated with the Myrtaceae, there is at present probably insufficient known of them to attempt to discern whether trends may exist across habitats differing in soil fertility.

### Question for research:

1. Do parasitic and saprophytic micro-organisms associated with the Myrtaceae vary from fertile to infertile sites?

## Plant-animal interactions

Variation in the diversity of animals, both invertebrates and vertebrates, in eucalypt forests is at least partly related to availability of nutrients to plants (Woinarski et al. 1997, Landsberg & Cork 1997). It seems impossible at this stage to suggest what trends might be expected in patterns of animals attacking various vegetative parts of Myrtaceous plants across the fertility range of their occurrence in the Sydney region; it will take careful further observation to find whether such patterns exist.

Some patterns related to fertility of habitats do exist in animals that visit flowers and fruits in the Myrtaceae. As Johnson & Briggs (1981) pointed out, flowers of the Myrtaceae, almost invariably protandrous, are attractive to animals, being showy and in some taxa massed in inflorescences of various configurations, with petals conspicuous in some genera and stamens in others and even conspicuous bracts in a few, and almost all of them have copious nectar. Many Myrtaceae have relatively non-specialised flowers (Beardsell et al. 1993b) and are visited by a range of animals from insects, birds, such as the brush-tongued lorikeets and honeyeaters, to mammals, such as possums, blossom bats (Law 1994) and flying foxes (Eby 1995). Eby (1996) observed flying foxes foraging throughout the year in the Sydney region on nectar of Myrtaceae. She observed that they used 29 species of eucalypts and *Melaleuca quinquenervia*. Nine of the thirty species had their greatest nectar flow in spring; nine in summer; one in late summer or early autumn, depending on location; seven in autumn; and four in winter. Of the thirty species, only two, *Eucalyptus robusta* and *Melaleuca quinquenervia*, both with peak nectar flows in winter in the Sydney region, are reliable sources of nectar for grey-headed flying foxes *Pteropus poliocephalus* every year.

Some members of the Leptospermoideae have somewhat more specialised flowers, for instance the brush inflorescences of *Callistemon*, which are primarily bird-pollinated. In the Sydney region, the most specialised inflorescences and flowers are in *Darwinia*, a genus confined, in the Sydney region, to infertile soils. In *Darwinia*, pollen presentation is secondary, with the pollen presented on subterminal ring of hairs below the top of the style (Howell et al. 1993), with the length of the fully elongated style appropriate to pollination by spinebills (Briggs 1964).

As already noted, the fleshy-fruited Myrtoideae are largely confined to rainforest, and fruits of the most common of them in the Sydney Region, *Acmena smithii*, are taken by parrots, currawongs and pigeons (Floyd 1989), brushtail possums (T.D. Auld, personal observation) and by the widespread grey-headed flying fox *Pteropus poliocephalus* (Eby 1995). From Eby's (1995) description of the handling of fruit and the seeds they contain and movements of *Pteropus poliocephalus*, it appears that these mammals would be very effective dispersers of viable seed of *Acmena smithii* over some distances, the seeds being of the size that the animals would not ingest and yet carry and later eject from their cheek pouches. From the porous nature of the endocarp of the fruit of *Acmena smithii* (Ashton & Frankenberg 1976), it would seem likely that seeds so ejected from the mouth would be viable rather than any swallowed and voided in the faeces. Such wide animal dispersal of seeds would only be a regular feature of the Myrtoideae, and not the Leptospermoideae whose dry seeds or, in some genera, indehiscent fruits would be dispersed initially primarily by gravity and wind, though some secondary dispersal might occur by ants as well as wind and water. Ants remove and eat seeds of some Leptospermoideae (see, for instance, Andersen & Ashton (1985)), but they may also disperse them. Ants are, for instance, major dispersal agents of indehiscent fruits of *Darwinia* (T.D. Auld, unpublished data). The ants are attracted to the old petal parts that adhere to the fruit, with the larger species of ants able to drag the fruits away to their nests, though the fate then of such fruits is currently unknown. Indehiscent fruits of *Calytrix*, shed with the hypanthium and papery calyx attached, could be expected to be dispersed

some distance in strong winds. Most seeds of eucalypts are dispersed short distances. Cremer (1965) showed that even from isolated trees of *Eucalyptus regnans* most of the seed falls within the canopy height's distance of the foot of the tree. Cremer et al. (1990) state, as a general rule, that beyond a circle one and a half times the height of an isolated eucalypt tree, seed dispersed from it is inadequate for seedling establishment. It is generally accepted that rings of saplings sometimes seen around isolated eucalypt trees (see, for instance, Fig. 17, p. 182, of Fisher et al. (1995)) relate to the short distances seed is dispersed from parental trees.

#### Questions for research:

1. Are patterns present in types and effects of animals attacking vegetative organs of Myrtaceae in the Sydney region, particularly in relation to gradients in soil fertility?
2. How far and to what habitats are seeds of fleshy-fruited Myrtoideae dispersed?
3. How effective is wind in dispersing fruits of *Calytrix*?
4. What role do ants play in effective dispersal of fruits or seeds of Myrtaceae in heathland?

### Reproductive biology

The breeding systems of most eucalypts studied show significant levels of outcrossing (House 1997), and it is probable that most members of Myrtaceae in the Sydney region are outbreeding. In the region's rainforests, *Acmena smithii* may be in a single breeding population by virtue of wide dispersal of its seeds by agents such as flying foxes, assuming that some widely dispersed seeds give rise to mature breeding trees. At the other end of the fertility gradient, in infertile habitats, there are some inbreeding members of the family, as Briggs (1964) showed in short-styled, autogamous species of *Darwinia*, *D. leptantha*, *D. taxifolia* subspecies *taxifolia*, *D. biflora* and *D. diminuta*. Also in infertile soils there are some Myrtaceous plants, usually of rare or local species, that seem to breed successfully very rarely and subsist vegetatively as clones apparently originating from lignotubers whose centres have rotted or burnt away; this seems to be so in some populations of *Melaleuca deanei* observed in areas near Holsworthy by Travers-Morgan (1990) and Virtue (1991), and in Garrigal National Park (L. McDougall, personal communication).

#### Questions for research:

1. Do effective breeding populations of fleshy-fruited trees in the Myrtoideae extend over a greater area than those of dry-fruited trees in the Leptospermoideae?
2. Is the proportion of inbreeding populations of plants in the Leptospermoideae greater in heaths than in more fertile habitats?

## Seed dormancy and bradyspory

Seed dormancy varies in members of the Myrtaceae in the Sydney region and shows some relationship to habitat. Beardsell et al. (1993b) note that few species of Myrtaceae have been found to have dormant seeds. For example, Ashton & Frankenberg (1976) showed that, though germination of seed of *Acmena smithii* was delayed until the fleshy pulp of the fruit had either dried out, been eaten or decayed, it had no dormancy. Dormancy occurs in seeds of some eucalypts that grow in cool areas (Bell & Williams 1997), for example high-altitude populations of *Eucalyptus pauciflora* whose seeds after dry storage required cold treatment before they would germinate (Beardsell & Mullett 1984). In genera of Leptospermoideae whose seeds are dispersed in indehiscent fruit, such as *Calytrix*, *Darwinia* and *Micromyrtus* in the Sydney region, seeds often fail to germinate under usually favourable conditions (Turnbull & Doran 1987). Roche et al. (1997) showed that smoke increased germination in *Calytrix tetragona*. In *Thryptomene calycina*, a species in the Leptospermoideae with indehiscent fruit, Beardsell et al. (1993a) showed that no seed germinated from freshly fallen fruit held at 20°C for 200 days, that seed excised from fresh fruits were partially dormant but that 100% germination occurred once the seed coats were torn. They also found in *Thryptomene calycina* that fruits weathered for over two years in the field held viable seeds. Most species of these genera of Leptospermoideae with indehiscent fruit occur in infertile, fire-prone habitats.

In other Leptospermoideae occurring in these habitats, the fruits open and seeds are dispersed onto the soil. In some of these species, the fruits are bradysporous; that is the opening of the mature fruit held on the plant is normally delayed for some time, often years, before it is heated usually by fire or extremely hot weather, or the stem bearing it senesces, and the fruit opens and seeds are shed. Bradysporous fruits are usually fairly tough and woody. Many eucalypts are bradysporous, including all species of *Eucalyptus* and *Corymbia* in the Sydney region, but not the region's species of *Angophora*. *Leptospermum* has both non-bradysporous species, whose fruits open shortly after they mature, and bradysporous species.

In infertile, fire-prone areas of the Sydney region, there are both bradysporous species of *Leptospermum*, such as *Leptospermum polygalifolium* and *Leptospermum squarrosum*, and non-bradysporous species, such as *Leptospermum trinervium*. In such habitats, it would be expected that the seed of the bradysporous species would have no dormancy once shed from the fruit, but that the seed of the non-bradysporous species would have some form of dormancy in the soil, with this dormancy being broken by some aspect of the passage of fire through the habitat. Thus, for Leptospermoideae in infertile, fire-prone habitats, it would be expected that fire would ready seeds for germination by either triggering release of non-dormant seeds from bradysporous fruits, or by breaking dormancy of naked seeds already shed into the soil from non-bradysporous fruits or contained within indehiscent fruits in the soil. In Myrtoideae on fertile rainforest soils, as exemplified by *Acmena smithii*, it would be expected that fire would have none of these effects in readying seeds for germination. In short, the dynamics of recruitment of seedlings from seeds are different at the two extremes of the fertility range in the Myrtaceae over which the family occurs in the Sydney region.

**Questions for research:**

1. Does the proportion of species with seed dormancy increase as soil fertility decreases?
2. What maintains dormancy of seeds in those species of the family that have it?
3. Do seeds of non-bradysporous species of *Leptospermum* have some form of dormancy and those of bradysporous species lack it?
4. In species with seed dormancy, does fire break that dormancy, and, if so, how does it do so?

**Fire and responses to it**

As fertility decreases across habitats, so the flammability of plant litter tends to increase. The flammability of litter of a given dryness appears to depend in part on its nutrient content. Litter with high nutrient content, particularly phosphorus content, such as usually occurs in rainforest, is less flammable than that, for instance in heath, with low nutrient content. Furthermore, as already noted, rates of decomposition would be higher in nutrient-rich litter than in nutrient-poor litter. Whilst the amounts of litter present depend on the amounts being deposited as well as their rates of decay, it is clear that, across the range of habitats occupied by Myrtaceae in the Sydney region from rainforest to heath, the incidence and effects of fire can be expected to vary.

Fires in Australian vegetation have a long history in the geological record (Martin 1996), and can be expected to have influenced the survival and distribution of members of the Myrtaceae in the Sydney region. Beyond influences on seed shedding and the possible breaking of dormancy of seeds in the soil, either as naked seed or within indehiscent fruit, already mentioned, fire may influence other critical phases of the plant life cycle, (Keith 1996). In rainforest, because of the relatively low flammability of litter and standing vegetation, and low amounts of litter to carry fire at ground level, fires are less frequent and, when they do occur, less intense than in eucalypt forests that normally abut them. Ashton & Frankenberg (1976) showed on Wilsons Promontory that, in *Acmena smithii*, fires confined to ground level die out on the rainforest margins, humus fires would kill trees that are growing on humus-rich soils, and crown fires from surrounding vegetation burn into the rainforest and kill the above-ground tissue of the trees, though after the fire, most of them coppice, growing from the base of the trunk. They found that well-grown seedlings begin to form lignotubers in their second year. As already indicated, in *Acmena smithii*, dispersal and germination of seed and establishment of seedlings are not triggered by fire. Fire obviously interrupts the production of fruit from mature trees and there is some period, as yet unrecorded, before trees coppicing after fire resume flowering and fruit production. Nor is it known how long it takes seedlings to reach reproductive maturity or to become capable of surviving through fire.

Mature trees of most of the region's species of eucalypts survive through crown fires often of high intensity, with their crowns regrowing from epicormic buds below fire-resistant bark following fire (Jacobs 1955). In the case of mallee eucalypts, which in the Sydney region are confined to infertile soils, their stems above ground are killed but fresh ones sprout after fire from their lignotubers in the ground. Some

lignotubers appear to be particularly long-lived and massive, as in mallee forms of *Corymbia gummifera* (Mullette 1978). In Sydney region's eucalypts, very soon after passage of a crown fire, seeds are shed, often *en masse*, from the bradysporous, woody capsules, most of which survive such fires, and it is after fire that seedling recruitment mostly occurs in these species. However, as Gill (1997) points out, not all seedling recruitment in eucalypts occurs in this way following fire, but, almost invariably, it occurs following some event, for instance flooding or drought, that has produced significant areas of bare ground and gaps free of shade. For instance, Benson (1985) showed how recruitment from seed in *Eucalyptus benthamii* was related to episodic floods. Where eucalypt recruitment not related to fire seems most likely to occur in the Sydney region is in the Cumberland Plain woodlands of Benson & Howell (1990) and Benson (1994), but this needs testing by appropriate field observation.

In some species of eucalypts, mature trees are killed by fire, of which the most closely studied is *Eucalyptus regnans* (Ashton 1976). Since the trees are killed, regeneration is solely from seedlings establishing from seed shed after fire. With obligate-seeders, as such seed-only-regenerating species are often termed, there is a particularly critical period between the seedling stage and the stage when young trees carry their first crops of bradysporous fruits. Occurrence of a crown fire in this period often causes local extinction of populations of the species, simply due to lack of any means of regeneration (Keith 1996). There are few species of obligate-seeding eucalypts in the Sydney region, but *Eucalyptus oreades*, which occurs on sheltered south-eastern slopes in the Upper Blue Mountains, is such a species, and its critical period between the seedling stage and trees bearing first crops of seed-containing capsules appears to be about 25 years (Glasby et al. 1988). Across the eucalypts, the extent to which crowns of trees are damaged, or individuals killed, varies with the nature of the fire. In crown fires of high intensity, crowns of trees, particularly in ashes such as *Eucalyptus sieberi*, are sometimes killed and the trees only shoot again from the base or are killed outright.

The greatest diversity of responses to fire among Myrtaceae in any type of habitat over the range of soil fertility in the Sydney region is found in infertile habitats. In them, there are bradysporous and non-bradysporous species, species that are obligate-seeders and species whose mature individuals survive fires of high intensity, resprouting species that shoot after fire from underground organs such as lignotubers and those that shoot from epicormic buds below bark on burnt trunks or branches, species with viable dormant seed in the soil and species that have no soil seedbank, and species in which fire stimulates flowering and those in which fire does not act as a stimulus to flower. As Auld (1987) showed, nearly all mature shrubs or dwarf trees of *Angophora hispida* survive fire, and after fire sprout fresh shoots from lignotubers or from epicormic buds which then flower most profusely in their first summer and less profusely in succeeding ones after a fire. Its non-bradysporous capsules open at maturity, and the seeds are shed in late summer. They have no dormancy and germinate following sufficient rainfall. Their growth is slow, but, after eight years, surviving seedlings had lignotubers, and Auld (1990) showed that, at this stage, some of the seedlings survived fire, with survival increasing with depth of burial and size of the lignotuber. Other species also have no soil seedbank. These include mallee ash eucalypts of infertile habitats in the Sydney region. Some of them, *Eucalyptus obstans*, *Eucalyptus luehmanniana*, *Eucalyptus burgessiana* and *Eucalyptus rupicola*, have been found by Auld et al. (1993) also to require 7–10 years before seedlings survive fire, and, as in *Angophora hispida*, this is related to sufficient

development of a lignotuber. Furthermore, in these mallee species, about ten years is also required after fire for stems regrown from lignotubers of mature individuals to have flowered and bear a crop of seeds in bradysporous capsules (Auld et al. 1993). A fire before this time, because of lack of seed, allows no episode of recruitment from seedlings following it.

Several species of *Leptospermum* have bradysporous capsules and mature shrubs that, after fire, sprout fresh shoots from lignotubers. Their seeds once shed probably have no dormancy, though this requires testing, and their seedlings will have critical periods after establishment before they can survive fire, but these periods and other details of recruitment from seed in these species are yet to be observed. Many of these bradysporous species of *Leptospermum* appear to flower and carry seed sooner after fire than do the species of mallee studied by Auld et al. (1993). Indeed, some species, for instance, *Leptospermum juniperinum*, flower within a year of being burnt. Other bradysporous species of *Leptospermum* are obligate-seeders, such as *Leptospermum squarrosum*, which occurs in infertile habitats on sandstone. Mature individuals of these species may bear particularly heavy crops of seed often in markedly woody capsules. It seems likely that, once shed onto the soil, their seeds have no dormancy but all germinate once rainfall is sufficient. If so, they would be eliminated from a habitat if one fire followed another within the critical period between seedling establishment and young plants bearing their first crops of seeds. This critical period may be quite short in these species. Burrell (1981) found that *Leptospermum laevigatum* would be eliminated from a habitat if it were burnt twice within five years. As argued earlier, seed of non-bradysporous species of *Leptospermum* may have some form of dormancy within the soil, but it is also possible that it has no dormancy in species such as *Leptospermum trinervium*, whose mature plants survive fire and strongly sprout from epicormic buds and lignotubers and flower within a year of being burnt.

The genera of Myrtaceae in which dormancy of seed is found in the soil, or very likely to be found in species yet to be examined, are those in which indehiscent fruits are dispersed. In obligate-seeding species of *Darwinia*, *D. biflora*, *D. diminuta*, *D. glaucophylla* and *D. procera*, Auld et al. (1993) and Auld and Scott (1995) showed that dormant seed was present in the soil in populations of all of the species, but that its proportion and persistence in the soil seedbank varied between species and populations within them. They also showed that seedling recruitment follows fire in species they observed and that heat broke dormancy of some seeds. In established seedlings, fruit production was low until they were five years old. To maintain numbers of seeds in the soil seedbanks for significant recruitment, Auld et al. (1993) recommend that populations should have fire-free periods of between 5 and 10 years. To generate sufficient heat to break dormancy of seeds in the soil for significant germination after fires, Auld et al. (1993) recommend that fires when they occur consume high levels of fuel. In short, to conserve the high diversity of Myrtaceae in habitats of low fertility, the habitats not only have to be set aside, but, as far as possible, fires have to be managed to take account of the diversity of responses to fire of these plants. As indicated above, much still remains to be learnt of responses of species of *Leptospermum*. This also applies to species of *Baeckea*, *Calytrix*, *Kunzea* and *Micromyrtus*, as well as to species of *Callistemon* and *Melaleuca*, looking, as Keith (1996) indicates, for particularly critical phases in their life cycles.

As seen above, fire provides opportunity for recruitment in many species of Myrtaceae in the Sydney region, but lack of it may bring about the local extinction of some species while allowing others to continue to occupy a habitat. This situation is seen in relationships between rainforest that includes *Acmena smithii* and tall quick-growing species of eucalypts such as *Eucalyptus saligna* and *Eucalyptus pilularis* in fertile areas near the coast and *Eucalyptus blaxlandii* on basalt soils in the Blue Mountains. These eucalypts recruit in well lit gaps such as are produced occasionally in rainforest canopies by crown fires or other damaging events. If the gaps remain long enough, eucalypt seedlings survive and grow above regenerating rainforest canopy, but if no further large gap arises the eucalypts do not regenerate and when they reach the end of their lifespan they are lost from what is then an entirely rainforest canopy. Such colonisation of rainforest by eucalypts and then replacement of eucalypts by entirely rainforest canopies are modelled in schemes of Noble & Slatyer (1977, 1980). The small seeds of the eucalypts contrast with the large seeds of *Acmena smithii*, and thus requirements of their seedlings for establishment differ. Also, the structure of the mature canopies of eucalypts with their discontinuous crowns (Jacobs 1955), approximating to multilayered canopies in Horn's (1971) models, differs from the more continuous crown of *Acmena smithii*, approximating to the monolayered canopy of Horn (1971). As Horn argues, while the monolayered canopy is more productive in shade than the multilayered, the multilayered is far more productive in full sunlight than the monolayered canopy. In addition, the eucalypts may be expected to grow more quickly in full sunlight than *Acmena smithii* due to their leaf stance. In mature canopies of the eucalypts, the leaves hang down with the flattened surfaces held vertically while in *Acmena smithii* the leaves are predominantly held horizontally. Under moist, well lit conditions, canopies of vertically held leaves are more productive than those of horizontally held leaves (Larcher 1980), but, under shade, the horizontally held leaves are more productive. Thus, *Acmena smithii*, along with most other members of the Myrtoidae, perhaps represents the original way of life in Gondwanan rainforest with a relatively large seedling able to tolerate and grow in shade, while these species of tall quick-growing eucalypts represent a newer way of life, which arose in the Tertiary, exploiting large gaps in forest canopies with small shade-intolerant seedlings that can grow very rapidly in full sunlight. That such slow-growing tree species of Myrtoidae and tall, quick-growing eucalypts of the Leptospermoidae coexist in some habitats in eastern Australia is probably largely due to occurrence of intense fires. If this is correct, to maintain such coexistence in the Sydney region over millennia, such intense fires should occur at least once during the lifespans of trees of *Eucalyptus saligna*, *Eucalyptus pilularis* and *Eucalyptus blaxlandii*. That some patches of rainforest exist in the Sydney region without an overstorey of eucalypts may suggest that some areas at least have escaped such intense fires for longer than this.

As with much of the above written on processes operating in the ecology of plants of the Myrtaceae, this coexistence of eucalypts and rainforest species is largely based on surmise, and requires properly designed experimental work to test hypotheses that are components of the surmise. Only then will more understanding be gained of the processes that underlie the patterns observed.

**Questions for research:**

1. Does the flammability of litter produced by members of the Myrtaceae change across gradients of fertility, and, if so, is this related to its nutrient content?
2. In resprouting species in the family, is the time required for seedlings to become fire-resistant related to habitat?
3. In resprouting species in the family, does the time required after fire for surviving mature individuals to flower and set viable seed change across gradients of fertility?
4. In which habitats in the Sydney region does seedling establishment occur in eucalypt populations that is not related to fire?
5. Of the great diversity of responses to fire among Myrtaceae in infertile sites, do some give greater change in populations with variation in fire regimes than others? If so, what are the particularly critical phases in the life cycles involved in each form of response?
6. Are current models of invasion of eucalypts into local rainforest, and how they may be retained or eliminated from it, correct?

**Concluding remarks**

Most of the major patterns in the vegetation of the Sydney region arise from processes that are clearly important in the distribution of members of the Myrtaceae. Indeed, members of the Myrtaceae are important components of these patterns. Distribution of members of the Myrtaceae is differentiated along gradients of soil fertility, with this differentiation appearing to have originated at the latest in the early Tertiary. It is the infertile end of the variation that is of particular interest with its high diversity of xeromorphic Leptospermoidae, high level of local endemism, some specialised pollination mechanisms, occurrence of some inbreeding systems, existence of seed dormancy in some taxa, and wide range of responses to fire. The Sydney region is similar to parts of south-western Western Australia in having this diversity of xeromorphic Leptospermoidae in infertile habitats, but is dissimilar in also having rainforest with Myrtoideae. The Sydney region is thus particularly appropriate for research into the ecology of Myrtaceae.

Many of the questions for ecological research in the Myrtaceae of the Sydney region can be usefully posed in relation to the gradient of fertility over which various members of the family are distributed. These range from specific to general ones. General ones include whether there is an ever-increasing degree of sclerophylly in the family along the gradient from the Myrtoideae in rainforest to the specialised Leptospermoidae in heath, or whether a particular plateau is reached in conditions of low but intermediate fertility; more specific ones include whether patterns of distribution and abundance in Leptospermoidae associated with rainforest edges, such as *Choricarpia leptopetala* or *Backhousia myrtifolia*, are controlled in particular ways, or how strictly the features of the ecology of *Acmena smithii* revealed in the study of Ashton & Frankenberg (1976) apply to populations of the species in the Sydney region. In view of the local endemism and general diversity of Leptospermoidae in

infertile, fire-prone habitats, it is appropriate that recent work has concentrated on them, as in Auld et al. (1993), but, in time, research into the ecology of the Myrtaceae should be more evenly spread across the full range of habitats members of the family occupy in the region.

Whilst many environmental variables may differentiate habitats in the region, it is suggested that gradients of fertility are particularly important and are a good basis for general investigation of the ecology of the Myrtaceae in the Sydney region. Certainly, this proved to be so in an investigation of characteristics of seed dispersal among samples of the region's flowering plants by Westoby et al. (1990). The recent scheme of Westoby (1998) might be useful in organizing the collection of data and their interpretation in any general investigation of the family in the region. It uses plant height at maturity, specific leaf area and seed mass to place taxa in the scheme. As indicated above, plant height would be expected to be least among taxa from the least fertile habitats, and specific leaf area to be least also among those taxa, reflecting the general increase in sclerophylly expected with decreasing habitat fertility, while seed mass would be greatest in the Myrtoideae in rainforest but within the Leptospermoideae might tend to increase with decreasing fertility, particularly in those with indehiscent fruits.

#### **Questions for research:**

1. Is soil fertility alone a sufficient environmental basis on which to base a general investigation of the ecology of the Myrtaceae in the Sydney region? If so, how is it to be specified and measured?
2. Do the Leptospermoideae of south-western Western Australia show similar patterns of distribution and responses to environmental variation to the Leptospermoideae of the Sydney region?
3. Where should detailed demographic work be directed in understanding the ecology of the Myrtaceae in the Sydney region?
4. Will the scheme of Westoby (1998) be an appropriate framework for organising a general investigation of the ecology of the Myrtaceae in the Sydney region and beyond?

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