Ecology of Proteaceae with special reference to the Sydney region

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In Australia, the Proteaceae are a diverse group of plants. They inhabit a wide range of environments, many of which are low in plant resources. They support a wide range of animals and other organisms, and show distinctive patterns of distribution in relation to soils, climate and geological history. These patterns of distribution, relationships with nutrients and other resources, interactions with animals and other organisms and dynamics of populations in Proteaceae are addressed in this review, particularly for the Sydney region.

The Sydney region, with its wide range of environments, offers great opportunities for testing general questions in the ecology of the Proteaceae. For instance, its climate is not mediterranean, unlike the Cape region of South Africa, south-western and southern Australia, where much of the research on plants of Proteaceae growing in infertile habitats has been done.

The diversity and abundance of Proteaceae vary in the Sydney region inversely with fertility of habitats. In the region's rainforest there are few Proteaceae and their populations are sparse, whereas in heaths in the region, Proteaceae are often diverse and may dominate the canopy. Research in the region has led to an understanding of their various responses to fire, dynamics of their populations in fire-prone landscapes, interactions with animals in pollination and dispersal, and of their breeding systems. This review examines results of this research and shows that ecological research has been uneven in Australian Proteaceae, with little work done on rainforest and alpine Proteaceae.

The review reveals an enormous range of interesting features of the Proteaceae of the Sydney region. It also identifies a large number of questions about ecological and evolutionary processes that are at the cutting edge of our current knowledge. The diversity of taxa of Proteaceae, the range of habitat, soil and climatic zones they occupy, the variety of life-histories (even among populations within species), fire responses, floral morphologies, pollinator types and breeding systems combine to make this family in the region a rich 'test bed' for many of these questions.

Proteaceae and Australian ecology

Distribution and diversity

Australia has the world's greatest diversity of Proteaceae, a family of woody evergreen plants ranging from tall trees, small trees, to shrubs — some of which are prostrate. It is the only continent in which all five of the subfamilies recognised by Johnson and Briggs (1975) are represented, and confined to it are two new subfamilies recognised since 1975 (CSIRO 1995). Africa including Madagascar has representatives from only the Proteoideae and Grevilleoideae, while South and Central America have representatives from only the Grevilleoideae (Johnson & Briggs 1975). Even within Australasia, the Western Pacific and East Asia, the Sphalmioideae and Carnarvonioideae occur only in Australia (Johnson & Briggs 1975) as do the recently recognised Bellendenoideae and Eidotheoideae (CSIRO 1995). Of the tribes recognised in the family by Johnson and Briggs (1975), the only one lacking in Australia is the Proteeae, which is endemic to Africa. Johnson and Briggs (1975) identified 51 of the world's 75 genera then recognised in the Proteaceae as endemic to their super-region of Australasia, the Western Pacific and East Asia. More recently, of 80 genera recognised in the family, 46 occur in Australia with 37 entirely endemic to it, while of 1769 species in the family, 1093 occur in Australia with 1088 of them endemic to it (George 1998). In a careful analysis of species diversity of Proteaceae in areas of the Cape Floristic Region of South Africa and Western Australia's South West Botanical Province, comparable in climate and their range of habitats, Cowling and Lamont (1998) found greater diversity of species in the latter. In short, at all taxonomic levels, and on various criteria of comparison, Australia has a greater diversity of Proteaceae than elsewhere (Table 1).

In Australia, Proteaceae occur in a much wider range of habitats than in other continents. The rainforests of the wet tropics in north-eastern Queensland are remarkable in containing trees of several genera in the family, many of them with high endemism in this area at the levels of tribes and subfamilies (Johnson & Briggs 1975, 1981, Beadle 1981a, Specht 1981a, Webb & Tracey 1981, Carpenter 1994). Subtropical and warm temperate rainforests of eastern Australia have trees and shrubs of Proteaceae while cool temperate rainforest has shrubs of the family including two Tasmanian endemic monotypic genera *Agastachys* and *Cenarrhenes* (Specht et al. 1974, Johnson & Briggs 1975, 1981, Beadle 1981a). Shrubs of Proteaceae occur in alpine areas of eastern Australia, including, in Tasmania, the monotypic *Bellendena montana* (Specht et al. 1974, Johnson & Briggs 1975, Beadle 1981a), now in its own subfamily (Weston 1995b). Beyond the rainforests and alpine areas, Proteaceae extend across the continent in almost every major formation of vegetation as small trees and shrubs; Proteaceae occur in 12 of the 13 major vegetation formations recognised by Specht (1981a), apparently lacking only from chenopod low shrubland, as they are from saline coastal areas. Though they occur in monsoonal northern Australia, and in the arid and semi-arid Eremean region where they are represented almost entirely by species of *Grevillea* and *Hakea*, Proteaceae are particularly abundant as species in the sclerophyllous forests, woodlands and heaths of eastern and south-western Australia (Johnson & Briggs 1975, Beadle 1981a), particularly in south-western Australia (Johnson & Briggs 1975, Beadle 1981a, Cowling & Lamont 1998).

Table 1. Comparison of the representation of the Proteaceae in the Sydney region with Australia and other regions of the world [modified from Weston & Crisp (1996)].

	Sydney Region	Australia	Africa	Madagascar	Mainland Asia	Indonesia Philippines	New Guinea	Pacific	South America
Eidotheoideae									
Eidothea		✓							
Proteoideae									
Consopermum	✓	✓							
Synaphea		✓							
Petrophile	✓	✓							
Isopogon	✓	✓							
Stirlingia		✓							
Cenarrhenes		✓							
Beauprea								✓	
Beaupreopsis								✓	
Agastachys		✓							
Symphionema	✓	✓							
Dilobeia				✓					
Franklandia		✓							
Adenanthos		✓							
Protea			✓						
Faurea			✓	✓					
Leucospermum			✓						
Vexatorella			✓						
Diastella			✓						
Spatalla			✓						
Sorocephalus			✓						
Mimetes			✓						
Orothamnus			✓						
Paranomus			✓						
Serruria			✓						
Aulax			✓						

Table 1 cont.	**Sydney Region**	**Australia**	**Africa**	**Madagascar**	**Mainland Asia**	**Indonesia Philippines**	**New Guinea**	**Pacific**	**South America**
Proteoideae cont.									
Leucadendron			✓						
Bellendenoideae									
Bellendena		✓							
Persoonioideae									
Persoonia	✓	✓							
Acidonia		✓							
Garnieria								✓	
Toronia								✓	
Placospermum		✓							
Sphalmioideae									
Sphalmium		✓							
Carnarvonioideae									
Carnarvonia		✓							
Grevilleoideae									
Orites		✓							✓
Neorites		✓							
Megahertzia		✓							
Knightia								✓	
Eucarpha								✓	
Darlingia		✓							
Cardwellia		✓							
Embothrium									✓
Oreocallis									✓
Alloxylon		✓					✓		
Telopea	✓	✓							
Lomatia	✓	✓							✓
Stenocarpus	✓	✓					✓	✓	
Strangea		✓							

	Sydney Region	Australia	Africa	Madagascar	Mainland Asia	Indonesia Philippines	New Guinea	Pacific	South America
Grevilleoideae cont.									
Buckinghamia		✓							
Opisthiolepis		✓							
Grevillea	✓	✓					✓	✓	
Hakea	✓	✓							
Finschia							✓	✓	
Helicia	✓	✓			✓	✓	✓	✓	
Xylomelum	✓	✓							
Triunia		✓							
Hollandaea		✓							
Macadamia		✓				✓			
Panopsis									✓
Brabejum			✓						
Hicksbeachia		✓							
Athertonia		✓							
Heliciopsis					✓	✓			
Virotia								✓	
Catalepidia		✓							
Malagasia				✓					
Gevuina		✓					✓		✓
Turrillia								✓	
Sleumerodendron								✓	
Kermadecia								✓	
Euplassa									✓
Roupala									✓
Floydia		✓							
Lambertia	✓	✓							
Banksia	✓	✓					✓		
Dryandra		✓							
Musgravea		✓							
Austromuellera		✓							

Interactions with other organisms

Plants in the Proteaceae in Australia support a wide range of other species. Many species of invertebrates and vertebrates in Australia draw food and other resources from plants of the family. In some, galls are formed by various insects, including leaf-pit galls by some hemipterans, *Cecidopsylla putealis* in *Banksia* and by a species of *Aacanthocnema* in *Hakea* (CSIRO 1991), while an endemic species of wasp, *Mesostoa kerri*, causes stem galls in *Banksia marginata* (Austin & Dangerfield 1998). Australian aleyrodids (white flies) colonise plants of Proteaceae and other families (CSIRO 1991). Beetles of the genus *Idaethina* are found in seeds of Proteaceae (CSIRO 1991). In some *Banksia* species, curculionid (weevil) and lepidopteran larvae consume seeds (Scott 1982). Leaves are mined between the upper and lower epidermis by some lepidopteran larvae, while other lepidopteran larvae tunnel in woody stems and fruits, and yet others feed while exposed on foliage (CSIRO 1991). Black cockatoos break open woody infructescences of some species of *Banksia* apparently in search of insect larvae tunnelling within them (Scott & Black 1981). Flowers, occurring in many Proteaceae in showy inflorescences, are visited by birds, fruit bats and blossom bats, sugar gliders and feather-tailed gliders, honey and pygmy possums, antechinuses, native rats, and a range of insects including moths, beetles, and bees, many feeding on the often abundant nectar, and some acting as effective pollinators (Maynard 1995). Many forage widely, but some are specific; colletid bees of the subgenus *Cladocerapis* of *Leioproctus* forage only on the flowers of *Persoonia* (Michener & Houston 1991). Moreover, most *Persoonia* species are pollinated by a limited range of native bee visitors. In a survey of pollen loads of all insects caught on flowers of 21 *Persoonia* taxa, Bernhardt & Weston (1996) found that over 50% of insects were carrying pollen only of the *Persoonia* species on which they were caught.

Some Proteaceae have succulent fruits, some of which are taken by mammals, including fruit bats, and by birds (Douglas 1995). Thus, Proteaceae are not only important components themselves of Australia's biodiversity but may be key components in supporting the life of various species of its animals, and probably also species of its fungi, bacteria and other micro-organisms.

Nutrient uptake and allocation

Many plants in the Proteaceae have a remarkable capacity for uptake of scarce nutrients, moving them between various plant organs, and storing them in high amounts in seeds and organs such as lignotubers from which growth may be renewed. Effective uptake of scarce inorganic nutrients by most plants in the family growing on impoverished soils appears to be related to the production and function of clusters of fine roots, the so-called proteoid roots, particularly just below the surface of the soil (Purnell 1960, Jeffrey 1967, Lamont 1972a & b, 1976, 1981, 1982, 1984, Pate 1994, Jeschle & Pate 1995, Pate et al. 1998), though proteoid roots are absent in the subfamily Persoonioideae (Weston 1995a) and also in *Symphionema* and *Agastachys* (Lee 1978).

Translocation and storage of inorganic nutrients in plants of Proteaceae may be in part related to the large and more complex rays and plentiful parenchyma associated with vessels shown by Chattaway (1948) to occur in their wood. She examined the wood of a wide range of species in the family and found large rays in all except some in the Persoonioideae which had small rays, but, even among the Persoonioidae, some species in all genera studied had some very large rays in their wood (Chattaway 1948). With such a structure, the wood of Proteaceae can be expected to be of low density, as Boas (1947) reported in *Cardwellia sublimis*, *Grevillea robusta* and *Orites excelsa* and Beadle (1966) in *Banksia serrata*.

Storage of polyphosphate was shown by Jeffrey (1964, 1968) in the roots of some heathland species of Proteaceae. Translocation of phosphorus was shown by Beadle (1968) in the wood of *Orites excelsa*; it was the only species among the rainforest species he examined that was Proteaceae and in which considerable amounts of phosphorus were withdrawn from the xylem as it matured into heartwood. Translocation of inorganic nutrients, particularly of phosphate, occurs in a marked way in the differentiation and senescence of leaves in many plants of the family. Significant translocation of nutrients must occur during the differentiation of the high amount of sclerenchyma and other non-living tissues that are laid down during the maturation of leaves of many plants in the family.

Many Proteaceae are sclerophyllous, having mature leaves with much lignin in sclerenchyma, cutin in thick cuticles, or silica present, especially in epidermal cell walls, the three characteristics occurring together in several Proteaceae (Beadle 1966). Sclerophyllous plants occur particularly on infertile soils (Beadle 1954, 1962, 1966), but several rainforest Proteaceae are also at least somewhat sclerophyllous (Beadle 1966, Johnson & Briggs 1975, Carpenter 1994). A consequence of differentiating sclerophyllous leaves is often slower growth than in plants with soft, mesomorphic leaves (Beadle 1968), but a much higher production of dry matter per unit weight of phosphorus absorbed by the plant (Grundon 1972), lower proportions of phosphorus in the dry mass of the leaves (Beadle 1954), and often long-lived leaves, up to ten years in one species of *Banksia* (Witkowski et al. 1992).

During the senescence of leaves of sclerophyllous Proteaceae, significant translocation of nutrients occurs, especially in the withdrawal of phosphorus from the leaves (Beadle 1968, Specht 1981b, Pate & Dell 1984). Perhaps the most spectacular transfer of nutrients in the Proteaceae is in the provisioning of embryos in seeds. No starch is stored in them, but a very high proportion of their dry mass is protein with oil abundant in the seeds of most species (Kuo et al. 1982, Pate et al. 1986) and very high amounts of phosphorus (Grundon 1972, Pate et al. 1986, Lamont & Groom 1998). The amounts of the plant's phosphorus and nitrogen allocated to seeds in many plants in the Proteaceae may be disproportionately very high compared to carbon allocated to them; this was certainly shown to be so in one species of *Banksia* by Witkowski and Lamont (1996). In short, provisioning of their embryos and other aspects of the nutrition indicate that plants in the Proteaceae as a whole tend to fall into Grime's (1974) category of stress-tolerators, inhabiting environments where at least one resource for growth is in low supply.

In Australia, the Proteaceae are a diverse group of plants. They inhabit a wide range of environments, many of which are low in plant resources. They support a wide range of animals and other organisms, and show distinctive patterns of distribution in relation to soils, climate and geological history. These patterns of distribution, relationships with nutrients and other resources, interactions with animals and other organisms and dynamics of populations in Proteaceae are addressed in this review, particularly in the Sydney region.

Patterns of distribution in the Proteaceae

Patterns of distribution in the Proteaceae in Australia are related to variation in soils and climate. Modern climatic patterns and patterns of distribution of Proteaceae in Australia are related to its geological history.

In the early Tertiary, though Gondwana had broken up in the Cretaceous with Africa and India drifting northward, the southern edge of Australia was broadly attached to Antarctica, while South America was narrowly connected (Barlow 1981). Though Australia was then in relatively high southern latitudes, with sea temperatures much warmer than now at such latitudes, its climate was generally warm and wet with rainforests in Central Australia and what are now arid or semi-arid areas in south-eastern Australia (Martin 1998). At such high latitudes, the seasonal variation in light available for photosynthesis is great with long days in summer and very short days in winter. The fossil record indicates a continuous presence of Proteaceae in Australia since the Cretaceous (Johnson & Briggs, 1981, Hill et al. 1995, Hill et al. 1999), and, with such a long history under so seasonal a light regime, it is perhaps no surprise that the capacity for uptake, storage and translocation of resources is so well developed in many Australian Proteaceae. Seasonal separation between uptake and use of resources occurs in some Australian Proteaceae, for example in *Banksia prionotes* (Pate et al. 1998).

Johnson and Briggs (1975) argued that some patterns of distribution in Australian Proteaceae directly relate to distributions of Proteaceae in the early Tertiary. Among these patterns is the occurrence of *Orites*, *Lomatia* and *Gevuina* in Australia shared with South America; at the subtribal level, the Embothriinae is represented in Australia and South America and the Macadamiinae has representatives in them both and in South Africa. Another of these patterns is the occurrence of the strictly rainforest genera of diverse lineages within Proteaceae that are endemic to the wet tropics of north-east Queensland. Another may be the occurrence of the Tasmanian endemic monotypic genera *Agastachys*, *Cenarrhenes* and *Bellendena*, the first two closely associated with cool temperate rainforest and the third an alpine species. These Tasmanian genera and the endemic genera of north-eastern Queensland have probably remained in the same sort of habitats as they occupied in the early Tertiary. In these places, they have escaped the general drying of the continent as it detached from Antarctica and drifted north into lower latitudes during the Tertiary (Martin 1998).

Differentiation of highly sclerophyllous plants in Proteaceae onto infertile soils and less sclerophyllous ones onto more fertile soils is of long standing in Australia (Johnson & Briggs 1975). Beadle (1981b) suggested that such xeromorphic plants on infertile soils in moist climates were most widely distributed during wet periods in the Miocene, and, then, as the modern arid zone formed, contracted into two main assemblages, one in the east on Triassic sandstones centred on Sydney and the other in south-western Western Australia. These sclerophyllous Proteaceae include a great many species, particularly in the south-west, and have five genera that are endemic to the south-west and two almost so, with only one genus endemic to the east (Johnson & Briggs 1975), and only slight evidence of recent interchange between west and east (Nelson 1981), presumably along sand dunes in the Bight during periods of low sea levels in the Quaternary. Despite their obviously high species diversity, particularly in the south-west (Cowling & Lamont 1998), they do not show the same degree of generic diversity at high taxonomic levels as the Proteaceae of the north-eastern rainforest of the Queensland wet tropics (Johnson & Briggs 1975, 1981), and, unlike some Proteaceae on the east coast, those in the south-west show no connections with extra-Australian taxa in the Proteaceae.

Though most Proteaceae appear to have become more restricted in their distribution by the onset of aridity during the late Tertiary, some species of two genera, *Grevillea* and *Hakea*, survive in the Australian arid zone (Johnson & Briggs 1975). Both *Grevillea* and *Hakea* are particularly rich in species; indeed ranking third and fourth respectively behind *Acacia* and *Eucalyptus* (sensu lato) in genera with the most species in the Australian flora (Beadle 1981b). *Grevillea* and *Hakea* have the widest ecological range of any genera in the Proteaceae in Australia, occurring in rainforest, monsoonal woodlands of the north, through the great variety of temperate sclerophyll forests and woodlands, to open shrubland and low woodlands of the arid zone. Nevertheless, the vast majority of their species are in the sclerophyllous communities of infertile soils in mediterranean climates of south-western and southern Australia and moist climates of eastern Australia. Like the arid zone, the monsoonal region of northern Australia has a climate of recent origin, and is relatively poor in Proteaceae, both in species and genera, with five other genera beside *Grevillea* and *Hakea,* most of them with many more species elsewhere in Australia (Johnson & Briggs 1975).

In summary, the current distribution of Australian Proteaceae seems to reflect ancient patterns of distribution with most taxa associated with rainforests or with infertile soils under climates of relatively high non-seasonal or winter rainfall. Sclerophyllous taxa are particularly numerous on infertile soils in winter-rainfall areas of south-western Australia. Early Australian Proteaceae would have existed under a highly seasonal climate, in terms of light at least. Only a few taxa survive in the arid zone of Central Australia and monsoonal regions of northern Australia, whose present climates have both originated in relatively recent geological times.

The Sydney region, like much of the rest of eastern Australia, would not have had as great a change of climate through the Tertiary as most of the rest of Australia (Martin 1998). It possesses a large area with infertile soils and thus is rich in species of sclerophyllous Proteaceae. There are some soils of moderate fertility over basalt, shales and some alluvia, and there is some variation in climate across the region, and the distribution of its Proteaceae can be related to variation in soils and climate.

Ecological distribution of Proteaceae in the Sydney region

Climate and soils each vary across the Sydney region and variations in the regional vegetation have been related to them and other features of its landscape (Pidgeon 1937, 1941, Burrough et al. 1977, Benson & Howell 1990). The relative importance of Proteaceae in the vegetation shows a marked inverse relationship to soil fertility; the poorer the fertility of a site the greater the probability of a high number of species and abundance and cover of plants of Proteaceae in its vegetation. This trend appears to hold irrespectively of variation across the region in rainfall and temperatures.

Rainforest Proteaceae

In the region's rainforests, which occur on patchily distributed sites of at least moderate fertility, as indicated by Beadle (1954, 1962), there are few Proteaceae; some patches lack them completely. *Helicia glabriflora* occurs in southern rainforests, on fertile soils near Robertson and Minnamurra (Floyd 1989). In rainforest on the basalt cap of Mount Wilson, a few *Banksia integrifolia* subsp. *monticola* occur (Brough et al. 1924). *Lomatia myricoides* occurs on Mount Wilson, in the tall eucalypt forest at the junction of the basalt and underlying sandstone and in rainforest on sandstone on sheltered south-eastern slopes (McLuckie & Petrie 1926). *Lomatia myricoides* also occurs in remnant gallery rainforest along the banks of some creeks in northern parts of the region (Benson 1986), while, in central coastal parts of the region, it occurs together with *Stenocarpus salignus* along creek lines on sandstone in gallery rainforest of small trees and shrubs (Benson & Howell 1990, 1994), whereas along the Ettrema creeks and gorges and gullies, the most frequently observed rainforest species were *Livistona australis*, *Synoum glandulosum*, *Diospyros australis* and *Stenocarpus salignus* (D. Black, pers. obs.).

Proteaceae of other habitats

From the rainforests, the importance of Proteaceae increases in the region's eucalypt forests and woodlands. However, the forests and woodlands on shale soils have few Proteaceae; *Grevillea juniperina* occurs on Wianamatta shales (Beadle et al. 1972), and *Persoonia laurina*, *Persoonia linearis* and *Hakea sericea* occur on both shale and sandstone soils (Beadle et al. 1972, P.H. Weston, pers. comm.). A few species appear to be most abundant on the sandstone-shale interface, for example *Persoonia nutans*, *Persoonia bargoensis* and *Grevillea parviflora* (P.H. Weston pers. comm.). It is on the region's sandstone soils that most of its Proteaceae occur, though many also occur on dune sands and lateritic surfaces. Beside eucalypt forests and woodlands, sandstone areas also carry sclerophyllous scrub and heathlands where Proteaceae may dominate the canopy. For instance, there is a marked contrast between the single species of Proteaceae, *Banksia integrifolia*, in rainforest on the basalt summit of Mount Wilson (Brough et al. 1924) and the nineteen species of Proteaceae, covering nine genera, Petrie (1925) mentioned in data from the surrounding sandstone vegetation. Though most of the region's Proteaceae occur in habitats on Triassic sandstones, some species extend into habitats over other rocks. In data of Benson and Keith (1990), given on the reverse side of their map of the vegetation of the Wallerawang area, *Persoonia linearis* and *Hakea dactyloides* are recorded as widespread extending well beyond areas of Triassic sandstone; this is also evident in data from the Burragorang area where *Banksia spinulosa* subsp. *spinulosa* is also widespread (see Appendix A of Fisher et al. 1995).

Local endemism

The high diversity of Proteaceae in infertile sites indicates a long history of their occupation of such sites in the region, as suggested by Beadle (1981b) and Johnson and Briggs (1975, 1981). Another aspect of their long history is the high degree of local endemism among Proteaceae in such sites, see p. 97 of Benson & Fallding (1981); Table 3, p. 485, of Benson (1986); Table 4, pp. 140–141, of Keith & Benson (1988); Table 4, pp. 332–333, of Benson & Keith (1990); Table 14, p. 590, of Benson (1992); Table 5, p. 776, of Benson & Howell (1994); and Table 4, p. 186, of Fisher et al. (1995). The grevilleas with 'tooth brush' inflorescences in the Sydney region, for example, include a number of similar species which occupy highly specific habitats, and many of which are rare, with restricted ranges (e.g. *Grevillea macleayana*, *Grevillea longifolia*, *Grevillea caleyi*, *Grevillea acanthifolia*, *Grevillea rivularis* and *Grevillea aspleniifolia*) (McGillivray 1993, Pickup 1999, T. Llorens pers comm.)

The Sydney region has a high degree of diversity and local endemism in its Proteaceae in infertile sites, perhaps higher for such scleromorphic Proteaceae than elsewhere in eastern Australia, but not as high as south-western Australia, where infertile habitats have particularly high degrees of diversity of Proteaceae (Cowling & Lamont 1998). Though the Sydney region shares with the south-western Australia the occurrence of genera such as *Banksia*, *Conospermum*, *Grevillea*, *Hakea*, *Isopogon*, *Lambertia*, *Persoonia*, *Petrophile* and *Xylomelum*, the two regions have no species in common. The genera *Helicia*, *Lomatia*, *Stenocarpus*, *Symphionema* and *Telopea* occur in the Sydney region but not in south-western Australia, while *Acidonia*, *Adenanthos*, *Dryandra*, *Franklandia*, *Stirlingia*, *Strangea* and *Synaphea* occur in south-western Australia but not in the Sydney region. *Strangea* occurs elsewhere in New South Wales and Queensland, and *Adenanthos* occurs in South Australia and Victoria though most of its species are endemic to south-western Australia, while the genera *Acidonia, Dryandra*, *Franklandia*, *Stirlingia*, and *Synaphea* are endemic to south-western Australia. The Sydney region is poor in rainforest Proteaceae with only *Helicia glabriflora* and the rainforest sub-species of *Banksia integrifolia* which are each at the southern edges of their distributions in the region, and *Stenocarpus salignus* and *Lomatia myricoides*. It lacks any alpine Proteaceae.

Thus, although the Sydney region does not give a fully representative sample of Australian Proteaceae, lacking alpine and being poor in rainforest Proteaceae, it has a good representation of sclerophyllous Proteaceae of infertile soils. They cover the same three subfamilies represented in south-western Australia, Persoonioideae, Proteoideae and Grevilleoideae. Proteaceae of the Sydney region's infertile soils display a similar range of fruits and infructescences to those in Proteaceae of south-western Australia. There are fleshy drupes in *Persoonia*. There are achenes, which in *Conospermum* and *Symphionema* are shed on maturity, but in *Isopogon* and *Petrophile* are held in the scales of bradysporous cone-like infructescences. There are follicles in all the Sydney region's Grevilleoideae except *Helicia* which is confined to rainforest and has a fleshy, one-seeded fruit. The follicles in *Grevillea*, *Lomatia*, *Stenocarpus* and *Telopea* open at maturity, while the follicles of *Banksia*, *Hakea*, *Lambertia* and *Xylomelum* are woody and, in most species, are bradysporous with their opening delayed after they mature, in some cases until stems bearing them die or are killed by fire or drought. In *Banksia*, the follicles are in cone-like, woody infructesences. In the Sydney region, Grevilleoideae with follicles have winged seeds, although seeds of nearly all species of *Grevillea* in the region have, according to Makinson (2000), short, apical wings or, in most of the species, apical elaiosomes, though a few lack even these, for instance *Grevillea caleyi* and *Grevillea longifolia* (see Auld & Denham 1999).

The diversity of fruit and the mode and timing of dispersal of seeds indicate that, in the Sydney region, as in south-western Australia, Proteaceae in infertile sites have a diversity of responses to environmental events and conditions, at least at this phase of the life cycle. Responses of plants across their life cycles to these environmental conditions and events constitute the processes underlying patterns of distribution. It is only through understanding these processes and how they result in survival and reproduction of populations of interbreeding individuals that patterns of distribution and abundance can be interpreted and predicted. This is not only of scientific interest, but required for managing such populations, particularly, in the context of the Sydney region, in relation to events such as fire.

Ecological processes in Proteaceae of the Sydney region

In the Sydney region, processes affecting survival and reproduction in populations of Proteaceae may be expected to vary both across various types of habitat and within particular habitats. It is convenient to review processes across various phases of life cycles of various Proteaceae in the region, thence how populations are constrained in different ways in them and how various patterns in their distribution and abundance may arise and vary in time and space across the landscape. To survive and reproduce, a plant must acquire resources and grow (Fig. 1).

Growth and resources

Seed reserves

Resources are not only acquired by plants during their growing phase, they are also passed on to them in seed reserves from their maternal parent. After germinating from the seed, resources in short supply to seedlings may include light, inorganic nutrients and water. Water is taken up by seeds from soil; indeed, it is necessary for their germination. Inorganic nutrients are in short supply in heath soils, though there may be an initial flush after fire, as Siddiqi et al. (1976) found, but light is generally abundant for seedlings, particularly after fire. In rainforest, light may be limiting to seedlings, while nutrients in the soil may be sufficient for growth. In alpine areas, due to active weathering of the soil and open conditions, both nutrients and light may be sufficient for seedling growth. In their survey of nutrient reserves in seeds of Proteaceae, Pate et al. (1986) showed that particularly high levels of nitrogen, phosphorus and magnesium are generally in those seeds that had high levels of

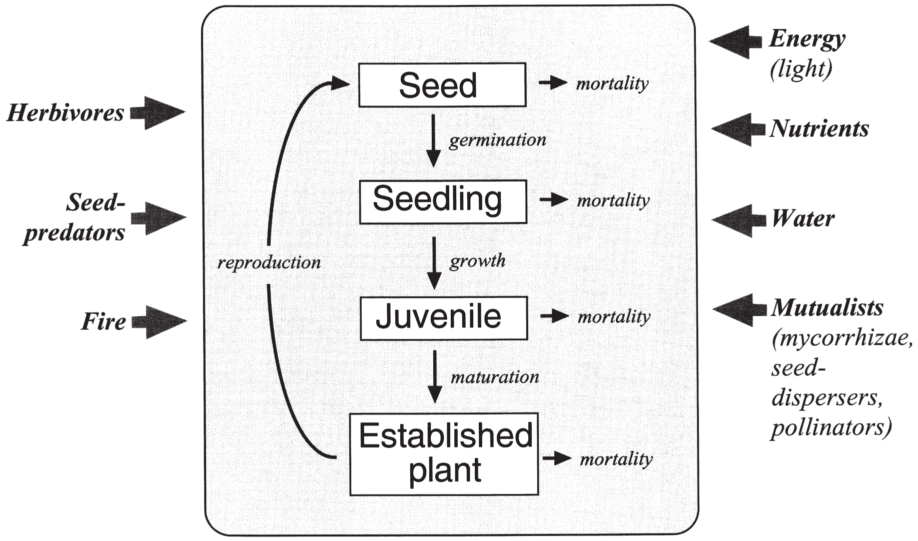

Fig. 1. Diagram indicating processes affecting survival and reproduction across various phases of life cycles of Proteaceae.

protein, and that oil was abundant in seeds of most species with starch being universally absent. Species with relatively low levels of inorganic nutrients included the Tasmanian alpine endemic *Bellendena montana* and rainforest species *Macadamia integrifolia* and the Chilean *Gevuinia avellana.* Embryos of *Macadamia integrifolia* are high in lipid and low in protein, compared to other species of Proteaceae, most of them from infertile soils, in data reviewed by Lamont and Groom (1998). This aligns with the suggestion of Pate et al. (1986) that large energy reserves have high survival value to seedlings under rainforest canopies on fertile soils, where light but not inorganic nutrients may be in short supply.

In the Sydney region, certain trends in seed reserves of Proteaceae may be expected across the range of habitats occupied by them. It may be expected that higher levels of inorganic nutrients occur in the embryos in seeds of species occurring in heaths than in those in rainforest and other fertile sites, and, conversely, that those in rainforest have a higher proportion of their seed reserves as lipid than those occurring elsewhere. It would be instructive to test this expectation within genera. This could be done in *Banksia*, along the range of fertility its species occupy, with *Banksia integrifolia* at the most fertile end with subspecies *monticola* on basalt in montane rainforest and subspecies *integrifolia* on recently deposited dune sands, some of which have significant amounts of shell, and, at the infertile end, *Banksia serrata*, on sandstone ridges and podsolised dunes and *Banksia aemula*, on highly podsolised sands. In the region, three species of *Lomatia* occur over a range of fertility; *Lomatia myricoides* occurs in moist, reasonably fertile sites, while *Lomatia silaifolia* occurs on infertile, dry sandstone soils.

Amongst Proteaceae occurring in infertile sites in the Sydney region, there is opportunity to test the suggestion of Pate et al. (1986) that small-seeded species tend to have higher proportions of inorganic nutrients in embryos than the larger-seeded species. It would be instructive to make such comparisons both within and between species whose fruit is a achene and those in which the fruit is a follicle, as well as between them and species of *Persoonia* which has drupes.

Beyond the Sydney region, it would be interesting to examine the seed reserves of rainforest, alpine and arid-zone Proteaceae, particularly the relative proportions of inorganic nutrients, proteins and lipid in their embryos and to make such studies across and within genera. Studies within *Grevillea* across representative species from various habitats within the wide ecological range of the genus would be particularly interesting.

Acquisition and conservation of resources

Resources that plants acquire during growth are energy from light, carbon dioxide, water and inorganic nutrients. Acquisition of inorganic nutrients and water by Proteaceae from infertile soils and their use in plant growth have received critical attention, particularly under mediterranean climates in Australia [e.g. Specht et al. (1958), Jeschke & Pate (1995) and Pate et al. (1998)]. Acquisition of sufficient light for photosynthesis is unlikely to be a problem for heath plants, particularly in the early phases of growth after fire, but may be critical in seedling growth in Proteaceae in rainforest. This seems to have received not even preliminary study.

Establishment in rainforest

Successful acquisition and use of available light by rainforest seedlings and saplings have to be assessed in relation to dynamics of the canopy above them. Seedlings of some species can survive and grow into the canopy only if there is a large gap above them, others may be able to survive below an intact mature canopy and make signifcant growth when small gaps in the canopy arise above them, while others may survive and make slow growth sufficient to complete their life cycle below an intact canopy. These and other possibilities are identified among species of trees in tropical rainforest by Whitmore (1975) and Swaine and Whitmore (1988), together with some of the events that create gaps in the canopy, including branch and tree falls, damage to the canopy by hail, severe winds, or lightning strikes. Observations are required on where and how seedlings of Proteaceae in Australian rainforest arise and survive and the circumstances that allow them to progress to saplings and beyond to mature reproducing adults. Observations in Appendix 1, p. 164, of Connell et al. (1984) indicate that, in a sample plot in north-eastern Queensland, seedlings of *Cardwellia sublimis*, a *Carnarvonia* species, presumably *Carnarvonia araliifolia* var. *montana* (Hyland 1995), *Darlingia darlingiana* and *Gevuina bleasdalei* became established between 1965 and 1981 under a rainforest canopy that included adults of the same species, as did seedlings of *Orites excelsa* in the same period below a rainforest canopy containing its adults in a plot in Lamington National Park in southern Queensland. In contrast, seedlings of *Grevillea robusta* do not occur below the canopy of their own species and colonise habitats such as the margins of rainforest, levees of streams in rainforest and areas disturbed by roading or past cultivation (Webb et al. 1967). Clearly, to gain understanding of populations of rainforest species of Proteaceae, studies are required of their seed dispersal, germination, survival and growth of seedlings and saplings in relation to dynamics of light mediated by the canopy above them. This includes species in the family in and around rainforests in the Sydney region. Is *Helicia glabriflora* a gap- or a shade-regenerator; does it require a gap in the canopy for ongoing growth? Are *Banksia integrifolia*, *Lomatia myricoides* and *Stenocarpus salignus* species of the well-lit edges of rainforests with which they are associated? For establishment of seedlings and their onward growth, are large, relatively long-lasting gaps required, such as might arise by fire at the edge of rainforest?

Proteoid roots and nutrient uptake

In the Sydney region, soils that are less fertile than those that normally support rainforest are widespread. In these soils, as Beadle (1954, 1962, 1966, 1968) showed, inorganic nutrients, especially phosphorus, are normally in short supply, particularly in heath and scrub on podsolised sands and sandstone. Proteoid roots, possessed by all Proteaceae except the Persoonioideae, *Symphionema* and *Agastachys*, are regarded as being important in the uptake of inorganic nutrients (Purnell 1960, Jeffrey 1967, Lamont 1972a & b, 1981, 1982, 1984, Malajczuk & Bowen 1974, Pate 1994, Jeschke & Pate 1995, Pate et al. 1998), a view supported by data from three *Banksia* species from heathland in the Sydney region (Siddiqi & Carolin 1976). Observations of Grierson and Attiwill (1989) suggested that the proteoid root mat of *Banksia integrifolia* enhances uptake of nutrients by chemically modifying the soil environment. In artificial media, the production of proteoid roots in seedlings of *Telopea speciosissima* was found to vary with level of phosphate supplied (Grose 1989), and in those of *Banksia ericifolia* with levels of phosphate and iron supplied (Handreck 1991). In the mediterraean climate of south-western Australia, the production and activity of proteoid roots are limited to the wet season (Lamont 1976, Pate et al. 1998). Whether the production and activity of proteoid roots are seasonal in the Sydney region is yet to be assessed, though, since the climate is not nearly so predictably seasonal, such seasonal production and activity are not likely.

Once acquired, inorganic nutrients, especially phosphorus, are sparingly used and highly conserved in the growth of Proteaceae on infertile soils. One manifestation of this is the production of sclerophyllous leaves (Beadle 1954, 1962, 1966, 1968, Loveless 1961). Over the range of soil fertility that Proteaceae occupy in the Sydney region, and more generally in eastern Australia, it could be expected that leaves from fertile sites would have more phosphorus per unit weight and would be less lignified and generally have less hardened tissue than leaves of plants from infertile sites. Whether this is so requires testing both in the Sydney region, and more generally in eastern Australia, across taxa within the family and also within those genera, such as *Banksia* in the Sydney region and *Grevillea* in eastern Australia, whose species are distributed over a wide range of soil fertility.

As already noted, seeds of Proteaceae tend to be lavishly provisioned with resources that seedlings establishing in their habitat will find scarce. Resources of inorganic nutrients available from the maternal parent for provisioning seed may limit seed set in some Proteaceae from infertile soils (Stock et al. 1989, Lamont & Groom 1998); this should be considered with other factors controlling seed set in these plants (Ayre & Whelan 1989). Are Proteaceae on infertile soils in the Sydney region limited in their seed set by resources available in the maternal plant? This was certainly inferred to be so in a population of *Banksia ericifolia* in the Sydney region from studies of pollination by Paton & Turner (1985), and was raised as a possibility in *Banksia spinulosa* in Victoria by Wallace and O'Dowd (1989) who found that fruit set per infructescence was increased after applying both insecticide and inorganic nutrients.

Questions for research:

1. Are the proportions of inorganic nutrients in embryos in seeds of Proteaceae inversely related to fertility of sites and is their lipid content inversely related to availability of light for seedlings in the sites?
2. In infertile sites, is the proportion of inorganic nutrients in embryos in seeds of Proteaceae inversely related to seed size?
3. In Australia, are the proportions of various forms of seed reserves in the Proteaceae related to habitat?
4. In the Sydney region, and in eastern Australia generally, under what range of light conditions do seedlings of various species of rainforest Proteaceae arise, survive and grow to maturity?
5. Do the Persoonioideae, *Symphionema* and *Agastachys* (Proteoideae) have systems of uptake of soil nutrients that are as effective as those of the proteoid roots of other Proteaceae?
6. Are the production and activity of proteoid roots seasonal?
7. Does phosphorus per unit dry mass of leaf show a positive relationship, and does degree of sclerophylly, measured as specific leaf area, show an inverse relationship to fertility of site, in Proteaceae of the Sydney region and, more generally, in eastern Australia?
8. Is resource limitation a major factor in controlling seed set in Proteaceae on infertile soils?

Decomposition of litter

It is expected that rates of decomposition of litter will be faster under fertile than infertile conditions along gradients of soil fertility that exist in the Sydney region and elsewhere in eastern Australia. This could be tested for litter of plants of Proteaceae in the Sydney region from rainforest to heath sites.

Preliminary data of Specht and Rayson (1957) from South Australia indicate that, in Dark Island Heath, leaves shed by *Banksia marginata* and *Banksia ornata* take between 18 and 30 months to be completely decomposed. Further work by Specht (1981b) confirmed that, in layers of dead leaves deposited under bushes of *Banksia ornata*, the fallen leaves were almost completely decayed after two years. Specht (1981b) found that leaves falling in summer-autumn showed an initial rapid loss of dry matter up to June, no loss for the next 10 to 12 months, but then, after they were blanketed by newly shed leaves, a steady loss in dry matter until their complete decay. In contrast, phosphorus in the layer of fallen leaves did not begin to disappear until the second summer, but, following the layer's colonisation by fine rootlets, then disappeared rapidly in the final 4 to 6 of the 30 months of observations.

Questions for research:

1. Does the rate of decomposition of litter of plants of Proteaceae vary with soil fertility?
2. Are particular sets of micro-organisms involved in decomposition of litter of plants of Proteaceae?

Mycorrhizae and micro-organisms

Although fungi may be associated with roots of many Proteaceae, no symbiotic mycorrhizae appear to be formed in Proteaceae with proteoid roots. Malajczuk and Bowen (1974) showed that, in seedlings of *Banksia grandis* grown in sterile cultures, the formation of proteoid roots was induced by inoculating the cultures with washings from fresh proteoid roots growing in a nutrient-poor soil. They concluded that micro-organisms were involved in inducing proteoid roots, though, in the absence of a control of an inoculum of sterilised washings, the possible influence of chemical agents in the washings cannot be ruled out. Lamont and McComb (1974) compared seedlings of *Hakea prostrata* grown in autoclaved and non-autoclaved sand, and showed that micro-organisms were probably involved in the formation of proteoid roots, though they could not dismiss the possibility that autoclaving the sand either released nutrients or a substance that inhibited the initiation of proteoid roots. Proteoid roots appear to function in similar ways to mycorrhizae in other plants, increasing the area for absorption of water and inorganic nutrients from the soil (Malajczuk & Bowen 1974, Lamont 1984).

Endophytic fungi occur in Proteaceae of the Sydney region; Macarthur & McGee (MS submitted to *Australian Mycologist*) have isolated eleven unidentified species of fungi from coastal populations of *Banksia integrifolia* from Sydney, the central and northern coasts of New South Wales. Bellgard (1991) observed arbuscular mycorrhizae in roots of *Conospermum longifolium*, *Conospermum taxifolium* and *Telopea speciosissima*, but observed hyphae with vesicles but no arbuscules in roots of *Persoonia levis*, *Persoonia pinifolia*, *Hakea dactyloides*, *Grevillea buxifolia*, *Grevillea oleoides* and *Grevillea sphacelata*, as had McGee (1986) in *Grevillea ilicifolia*. Hyphae, typical of fungi that form arbuscular mycorrhizae, were observed by Pattinson (2000) in roots of seedlings of *Banksia ericifolia* and *Banksia serrata* collected from the field in the Sydney region. In experimentally raised seedlings of *Banksia ericifolia*, he showed that infection of roots by a *Glomus* species resulted in the production of hyphal vesicles but not arbuscles and infected seedlings tended to have less growth than uninfected seedlings. In short, in his work and in other work to date, there is no evidence of a functional symbiosis in mycorrhizae in Proteaceae.

The possibility that bacteria associated with the roots of local Proteaceae may assist in uptake of phosphate from the soil has been raised by the work of Wenzel et al. (1994). They showed that bacteria isolated from the proteoid and non-proteoid lateral roots of field-grown seedlings of *Telopea speciosissima* solubilised calcium phosphates in cultures when nitrogen was supplied as NH_4^+ but not when it was supplied as NO_3^-. Whether the bacteria render insoluble phosphates in soils soluble and make them available for uptake by roots of seedlings in the field is as yet unknown.

Fungal diseases, and some of the fungi causing them, are known among local Proteaceae, particularly among those of horticultural interest such as *Telopea speciosissima*. In *Telopea speciosissima*, the identity of several fungi entering plants through the root in horticultural conditions is known (Summerell et al. 1992), and so is the identity of the fungus causing crown and stem canker (Summerell et al. 1990) and of fungi that are leaf pathogens (Crous et al. 2000). *Phytophthora cinnamoni* has been isolated from Royal National Park (Keith McDougall pers. comm.). In eastern Australia, some Proteaceae (e.g. *Telopea speciosissima*) seem to be susceptible to this pathogen, but not to the same extent as the wide range of susceptible Proteaceae in Western Australia. Leaf spot occurs among wild populations in Proteaceae in the Sydney region, as in *Hakea dactyloides*, but what pathogens are in such populations and whether there are patterns in the association of particular parasitic micro-organisms with Proteaceae in the region are unknown.

Questions for research:

1. Do bacteria associated with roots of Proteaceae assist in uptake of phosphates by the plants?
2. Is the initiation of proteoid roots stimulated by micro-organisms in Proteaceae?
3. What pathogens occur in wild populations of Proteaceae?
4. Do patterns occur in micro-organisms parasitic on Proteaceae in relation to soil fertility?
5. To what extent are eastern Australian Proteaceae susceptible to and infected by *Phytophthora cinnamoni*?

Plant-animal interactions

Animals take food from plants. This is often a tax on the flow of resources to the next plant generation. In Proteaceae, with their relatively lavish investment of protein, phosphate and lipid in seed resources, the most serious and potentially damaging form of herbivory is eating of seeds. Least damaging is the taking of nectar, particularly in nutrient-poor habitats where light is often abundant and plants, though poorly supplied with inorganic nutrients, have abundant energy to expend in surplus carbohydrate. It is perhaps not surprising that the most spectacular floral displays with heavy flows of often concentrated nectar are among Proteaceae on infertile soils, both in Australia and in southern Africa.

Herbivory

Leaves and stems of Proteaceae are attacked by insects of various sorts and in various ways (CSIRO 1991). Proteaceae of the Sydney region rarely display extensive insect damage, such as seen occasionally in the almost complete defoliation of some eucalypts. Such defoliation is hardly to be expected in plants most of which are highly sclerophyllous and in a family many of whose taxa contain poisons (Swenson et al. 1989, CSIRO 1995). Cyanogenic glycosides occur in several species, including *Xylomelum pyriforme*, while positive tests for cyanide have been obtained in young leaves of *Hakea dactyloides*, flowers of *Hakea saligna*, parts of flowers and fruits of *Lomatia silaifolia*, and in *Lambertia formosa* (based on the Everist's (1974) summary of the work of various authors). In *Grevillea macleayana* (previously *Grevillea barklyana*), Edwards (1990) also got positive tests for cyanide in about 25% of seed coats obtained following germination of soil-stored seed.

Significant leaf damage is sometimes evident, as in *Banksia oblongifolia*, perhaps less so in leaf canopies formed during the first year after fire than in the leaves two or more years after fire (P.J.M. pers. obs. Myall Lakes). Zammit (1988) recorded damage in *Banksia oblongifolia* by stem-boring insects of a few shoots among those regrown 18 months after fire. Whether there are spatial or temporal patterns to be found in insect damage of vegetative parts of Proteaceae in the region, or whether such damage is critical in controlling either the distribution or abundance of any Proteaceae in the region, is currently unknown. Vertebrate damage of vegetative parts of Proteaceae in the region appears to be even less common than damage by insects, though in young shoots of *Petrophile pulchella* some appear to have been bitten off by mammalian incisors, while Zammit (1988) suspected Swamp Wallabies (*Wallabia bicolor*) of grazing young shoots of *Banksia oblongifolia*.

Inflorescences and infructescences of Proteaceae may be attacked by animals. For instance, in *Lomatia silaifolia*, flowering and fruiting branches were heavily browsed, with 69% of exposed branches of inflorescences destroyed, probably by Swamp Wallabies (*Wallabia bicolor*) (Denham & Whelan 2000). In species of *Banksia*, inflorescences and infructescences are attacked by insects (Scott 1982) and infructescences by cockatoos as they search for insects within them (Scott & Black 1981, Witkowski et al. 1991). Zammit and Hood (1986) showed that insecticide treatment of inflorescences of *Banksia ericifolia* from before anthesis through to flowering and on to maturation of fruits decreased the number of barren infructescences, prevented damage of the rachis by boring insects and, in fertile infructescences, prevented damage of seeds and increased the number of seeds matured. In *Banksia spinulosa*, Wallace and O'Dowd (1989) found that the number of follicles per inflorescence was increased when both insecticide and additional inorganic nutrients were applied to the shrubs, while, in *Banksia spinulosa* var. *neoanglica*, Vaughton (1990a) showed that application of insecticide increased number of seeds produced per inflorescence and per plant.

Seed predation

Losses of seed from the follicles before dispersal, due to predation by insects, was shown by Zammit and Westoby (1988) to be 20–30% in populations of *Banksia oblongifolia* and *Banksia ericifolia*, though in one population of *Banksia ericifolia* there were no such losses. Similar levels of predation were found in *Banksia ericifolia*, *Banksia serrata* and *Petrophile pulchella* by Bradstock (1985) though he measured much higher levels of predation (e.g. > 50%) in old (> 5years old) compared with young (circa 5 % — one year old) cones. Auld and Scott (1997) found that in populations of *Grevillea caleyi*, 20–31%, and in a population of *Grevillea shiressii*, 57% of seeds were lost before dispersal. In *Grevillea shiressii*, significant losses of seeds were to a wasp, *Eurytoma* sp., and in *Grevillea caleyi* to a weevil, *Cydmaea dorsalis* (Auld & Scott 1997). Weevils of this species also feed on seeds of *Grevillea buxifolia*, *Grevillea linearifolia*, *Grevillea sericea* and *Grevillea speciosa* (Auld et al. 1993). French (unpublished data) found a diversity of levels of predation of seeds of *Grevillea* species before dispersal. Only 4% of seeds were lost in *Grevillea oleoides*, but between 40 to 50% of seeds were taken in *Grevillea sphacelata*, *Grevillea linearifolia* and *Grevillea mucronulata*. Vertebrates and invertebrates took seeds, and levels of predation varied spatially and temporally. Auld and Denham (in press a) found that larvae of *Cydmaea* were the major consumers of seeds before dispersal in *Grevillea caleyi* and *Grevillea buxifolia*, while, in smaller-seeded species *Grevillea shiressii* and *Grevillea linearifolia*, the wasp *Eurytoma* sp. was the major consumer. In their survey of five species of *Grevillea*, Auld and Denham (in press a) found that, although pre-dispersal losses of seed were appreciable, they were not as high as post-dispersal losses, with the exception of *Grevillea shiressii*, where they observed the highest loss of developing seeds (46%). Parrots take immature seeds from follicles of *Grevillea* spp. In populations of *Grevillea macleayana*, Vaughton (1998) showed that 9–40% seeds are taken before dispersal by Crimson Rosellas (*Platycercus elegans*), while Eastern Rosellas (*Platycerus eximius*) fed heavily on seeds in follicles of garden-grown *Grevillea caleyi* (P.J.M. pers. obs.). In *Grevillea macleayana*, there was loss of seeds before dispersal to insects but this was not as great as that to parrots (Vaughton 1998).

Seeds may be attacked by animals after dispersing from their parental fruits. In populations of *Grevillea caleyi*, *Grevillea longifolia* and in a population of *Grevillea shiressii*, 82–92%, 92–93% and 60% of dispersed seeds were lost to predation by animals (Auld & Scott 1997). In populations of *Grevillea macleayana*, 78–100% of dispersed seeds were taken (Vaughton 1998). In these species, most of the seeds lying on the soil are consumed by mammals, in *Grevillea macleayana* by rodents (Vaughton 1998) and in the *Grevillea* species studied by Auld and Scott (1997) and by Auld and Denham (1999) by Swamp Wallabies (*Wallabia bicolor*) and Bush Rats (*Rattus fuscipes*). In *Grevillea caleyi*, Auld and Denham (in press b) observed that, in the first two fruiting seasons after a wildfire, virtually all seeds dispersed (99–100%) were lost to rats and wallabies, exceeding estimated losses before the fire and those in a population not burnt for ten years.

A consequence of bradyspory in the Proteaceae is that large numbers of seeds are typically released en masse soon after a fire. It is possible that the rate of post-dispersal seed predation will be lowest at this time, if granivores have been temporarily eliminated by the fire or if they are satiated by the mass of seeds released at one time. O'Dowd and Gill (1984) showed that predation by ants of *Eucalyptus* seeds was least in the couple of weeks immediately after fire. In a manipulative experiment involving a chronosequence of stands of *Hakea teretifolia* of differing age, Turner (1990) found that high proportions of seeds placed on the soil surface (> 50%) were consumed or damaged in uncaged treatments in coastal stands that had been unburnt for more than 10 years. In stands that had burned less than 10 years previously, levels of predation of unenclosed seeds were relatively low (< 20 %). Turner (1990) found a similar pattern in populations in the upper Blue Mountains, but in that case high levels of predation were restricted to sites of longer time since fire (> 20 years). In *Banksia ericifolia*, *Banksia serrata*, *Isopogon anemonifolius* and *Petrophile pulchella*, Bradstock (1991) reported almost total destruction of early germinants from seeds placed in experimental meshed and unmeshed enclosures in an unburnt area, whereas no losses were recorded in a burnt area. In both studies, small vertebrates (probably rodents) were considered as being responsible for these effects, based on patterns of damage to seeds and other circumstantal evidence. Post-fire predation of seeds and seedlings of other bradysporous Proteaceae species requires investigation in the Sydney region. If post-dispersal predation is significant, then factors which affect the predators will determine seed losses. Area or patchiness of the fire is one potentially important factor which needs to be tested (see Whelan 1995).

Whether losses of seed by animal predation both before and after dispersal are critical in overall dynamics of populations was assessed in populations of *Grevillea caleyi* (Auld et al. 1993, Auld 1995, Auld & Scott 1997, Auld & Denham in press b), *Grevillea longifolia* and *Grevillea shiressii* (Auld et al. 1993, Auld & Scott 1997), *Grevillea speciosa* (Auld 1995) and *Grevillea macleayana* (Vaughton 1998). It can be concluded that post-dispersal predation of seeds might be particularly critical in survival of populations under particular regimes of fire. In *Grevillea caleyi,* Auld and Denham (in press b) suggested that, due to the very high losses of seeds to rats and wallabies, particularly in the first two fruiting seasons, relatively long inter-fire intervals, at least three times the juvenile period of the plant, are required to ensure survival of populations. Clearly, similar analyses of seed predation are required in assessing survival of populations of other Proteaceae in the Sydney region.

Floral visitors and pollination

Flowers of Proteaceae in the Sydney region are visited by animals, and all available evidence indicates that they are effectively pollinated by animals, though, for most species, the identities of their specific pollinators are currently unknown.

All the region's Proteaceae have hermaphrodite flowers, though in the inflorescences of some there may be some male flowers, lacking functional ovaries ['andromonoecy' — Goldingay & Carthew (1998)]. Ladd & Connell (1994) reported clear andromonoecy in both *Stirlingia* and *Xylomelum* in Western Australia. In the hermaphrodite flowers, the stigma appears to become receptive after the pollen is shed. It is not clear whether this is an invariable rule (see Goldingay 2000) or how it contributes to the breeding system, for instance in inflorescences in which some flowers are in the male phase while other adjacent flowers are in the female phase.

Pollen is presented in three ways in flowers of the region's Proteaceae. The first, in *Persoonia*, is directly from the dehisced anthers; flowers of *Persoonia* are predominantly visited by insects, some colletid bees foraging only on flowers of *Persoonia* (Michener & Houston 1991, Bernhardt & Weston 1996), and insects are probably their effective pollinators in south-western Australia (Collins & Rebelo 1987). The second is in its explosive release from the anthers triggered by probing of the flower, probing insects being dusted in pollen. This occurs through one mechanism in *Symphionema* (Carolin 1961) and through another in *Conospermum* (Carolin 1961, Morrison et al. 1994). In flowers of *Conospermum*, the explosion of pollen can be released by touching the triggers with a straw (Holm 1978). Collins and Rebelo (1987) suggested that insects are the effective pollinators in *Conospermum* in south-western Australia. *Leioproctus* bees forage on *Conospermum* in south-western Australia (Houston 1989). The third way in which pollen is presented in flowers of the region's Proteaceae is on a specialised area of the style, the pollen presenter, on which pollen is deposited from the anthers before the flower opens. In *Isopogon* and *Petrophile*, the pollen presenter is a region around the style below its top; the pollen deposited thus on the sides of the style would seem to be easily removed by insects of appropriate form, size and behaviour as they probe the flowers for nectar. In south-western Australia, Collins and Rebelo (1987) suggested that *Isopogon* and *Petrophile* are pollinated by insects. The identity of insects visiting and acting as effective pollinators of species of *Isopogon* and *Petrophile* awaits research in the Sydney region. In the region's genera of the subfamily Grevilleoidae, the pollen presenter is at the tip of the style which is thickened in most genera, though, in *Lambertia*, the tip is not thickened and the pollen is presented subapically on the sides of the style. Several of the region's Gevilleoidae have robust flowers, many of them in showy inflorescences with copious nectar, that are visited by vertebrates as well as by insects. Thus, in the region's Proteaceae, floral visitors, and probably effective pollinators, are in part related to subfamilies; flowers of *Persoonia*, sole presentative of the Persoonioidae in the region being visited by insects, those of the region's Proteoidae, *Symphionema*, *Conospermum*, *Isopogon* and *Petrophile*, also by insects; while those of its Grevilleoidae are visited by vertebrates and/or insects — for instance, flowers of *Grevillea sphacelata* are visited by insects while those of *Grevillea mucronulata* are visited by birds and honeybees (Richardson et al. 2000).

A fourth form of pollen presentation has been described by McFarland (1985) and Ramsey (1988). In some *Banksia* species, florets appear to remain closed for some time after they have matured and anthesis has resulted in the deposition of pollen on the pollen presenter. Contact by a large flower visitor is sufficient to trigger flower opening and expose the style tip, but contact by insects is not. Ramsey (1988) suggested that this may be an adaptation which minimises pollen theft by non-pollinating insects such as staphylinid beetles. It may also provide some protection against pollen theft by honeybees; this is worth further investigation. Stimulated floret-opening occurs in some of the straight-styled *Banksia* species of the Sydney region, such as *Banksia integrifolia, Banksia paludosa, Banksia oblongifolia, Banksia serrata* and *Banksia robur,* but not in the hooked-styled species such as *Banksia ericifolia* and *Banksia spinulosa* (R.J.W. pers. obs.).

Most of the work on pollinators and pollination of Proteaceae in the Sydney region has been done in the subfamily Grevilleoidae, much of it in *Banksia*, mostly in heath or sclerophyll woodland. Outside the Grevilleoidae, Krauss (1994a) looked at aspects of pollination in the *Persoonia mollis* complex, Bernhardt and Weston (1996) in several species of *Persoonia*, and Morrison et al. (1994) touched on pollination in four species of *Conospermum*. Within the Grevilleoidae, some genera, *Helicia*, *Lomatia* and *Xylomelum*, would seem to have inflorescences and flowers more likely to be visited and effectively pollinated by insects than by vertebrates; Denham and Whelan (2000) observed only insects visiting inflorescences of *Lomatia silaifolia*. Other genera in the Grevilleoidae, *Banksia*, *Lambertia* and *Telopea*, have robust, showy inflorescences and flowers, often with copious nectar, and forms and shapes suitable to visits by vertebrates. It is, however, only within *Stenocarpus* and the two closely related, species-rich, genera of *Grevillea* and *Hakea* that some species are almost certainly predominantly insect-pollinated while others have inflorescences and flowers suitable to visits by vertebrates. Vertebrates that visit inflorescences of the region's Proteaceae have attracted much research, involving some study of production of nectar and pollen and pollination in *Telopea speciosissima* (Pyke 1981, Whelan & Goldingay 1989, Goldingay et al. 1991a), *Lambertia formosa* (Pyke 1982a, Pyke & O'Connor 1993), *Grevillea speciosa* (Pyke 1983a, 1988, Armstrong 1991), *Grevillea macleayana* (Harriss & Whelan 1993, Vaughton 1996, England et al. in press), *Grevillea mucronulata* (Richardson et al. 2000, Whelan et al. 2000), *Grevillea caleyi* (Whelan et al. 2000), and, above all, in species of *Banksia*.

Mammal visitors

In species of *Banksia* on the eastern coast of Australia, vertebrates that visit inflorescences include flying foxes, *Pteropus alecto*, *Pteropus poliocephalus* and *Pteropus scapulatus*, which visit *Banksia integrifolia* and *Banksia serrata* (Eby 1995), and the common blossom-bat, *Syconycteris australis*, which feeds on both nectar and pollen of *Banksia integrifolia* (Law 1994). The Grey-headed Flying Fox *Pteropus poliocephalus* occurs in the Sydney region, often with high numbers present in summer, as recorded for the Gordon roost (Pallin 2000), but the blossom-bat does not extend as far south as Sydney (Law 1994). Carpenter (1978) suggested that non-flying mammals in visiting species of *Banksia* in the Sydney region might act as pollinators, a suggestion confirmed in the work of Goldingay et al. (1987, 1991a) and Carthew (1993a, 1994), who showed that small marsupials, a dunart, *Antechinus stuartii*, Sugar Glider, *Petaurus breviceps* and Eastern Pygmy-possum, *Cercartetus nanus*, and native rats, *Rattus fuscipes* and *Rattus lutreolus* visit inflorescences of species of *Banksia*, including *Banksia spinulosa*, *Banksia ericifolia*, *Banksia serrata*, *Banksia robur*, *Banksia oblongifolia* and *Banksia integrifolia*, as well as *Telopea speciosissima* (Goldingay et al. 1991a). All these visits by mammals, both flying and non-flying, are nocturnal, but more obvious are the diurnal visits to *Banksia* inflorescences made by honeyeaters (Meliphagidae) and by day-flying insects, including the introduced honeybee.

Bird visitors

Visits of honeyeaters to *Banksia* inflorescences can be readily observed, and it is well known that an important part of the diet of several species of honeyeaters is nectar from *Banksia* and other Grevilleoidae with showy, robust inflorescences. Tongues of honeyeaters, unlike those of nectarivorous birds of other parts of the world, are finely divided into a brush tip, which appears to be particularly well suited to rapid collection of nectar spread over large surface areas as it often is on rachises of *Banksia* inflorescences (Paton & Collins 1989). Whereas in south-western Australia, there is some nectar from species of *Banksia* throughout the year, in eastern Australia, the availability of nectar from *Banksia* is seasonal (see Collins & Rebelo 1987, Copland & Whelan 1989) and the activity of honeyeaters on *Banksia* infloresecences is correspondingly seasonal. As Collins and Rebelo (1987) indicated, in eastern Australia no species of *Banksia* is in flower between September and December, but flowering starts in January when somewhat under 40% of the species of *Banksia* flower and reaches a maximum in April, May and June when 80% are in flower, with successive decreases in July and August. In the Sydney region, in many heaths and sclerophyllous scrubs and woodlands, *Banksia* nectar becomes available from January due to flowering of species such as *Banksia serrata*, *Banksia oblongifolia*, and, in coastal areas, *Banksia integrifolia*, but reaches its maximum availability in April to June when species such as *Banksia marginata*, *Banksia spinulosa* and *Banksia ericifolia* are in flower. In some heaths and scrubs, *Banksia ericifolia* may completely dominate patches of the canopy, and thus be a source of abundant nectar (Recher 1977, Pyke 1988).

Pyke et al. (1993) showed that, in one such heathland, nesting of honeyeaters resident there was mostly during the period in which nectar production reached its peak. In the same area, Armstrong (1991) showed that, although honeyeaters significantly depleted nectar in uncaged inflorescences of *Banksia serrata* and *Banksia aspleniifolia* earlier in the year, later in the year they did not do so in those of *Banksia ericifolia*; he suggested that *Banksia ericifolia* produced far more nectar than the birds could consume. In New England National Park at 1400 m (McFarland 1986a & b), the only consistent source of nectar was from two species of *Banksia*. Nectar from them was unavailable in spring and early summer, but became available in March when *Banksia integrifolia* subsp. *monticola* started to flower and was most plentiful in mid winter, after *Banksia integrifolia* had ceased to flower but when *Banksia spinulosa* var. *neoanglica* was at its peak of nectar production. Numbers of honeyeaters present were closely related to amounts of nectar available, and, though the daily production of nectar occasionally fell below the daily energy requirements of the honeyeaters in the habitat, the overall production of nectar exceeded their energy needs during the time they were in the habitat (McFarland 1986a) and the amounts of their abdominal fat reserves increased (McFarland 1986b). Studies in these two areas, one at low altitude and the other at high altitude, in eastern New South Wales, both demonstrate the importance of the midwinter flow of nectar from *Banksia* species to populations of honeyeaters.

The concentration of flowering of many nectar-rich Proteaceae in winter and spring, and a dearth of nectar at some other times of year, in the Sydney region perhaps explains why no mammals have evolved to be nectar-specialists. This contrasts with the situation in coastal heaths and woodlands of south-western Australia, where sequential flowering of *Banksia* species occurs throughout the year (see Whelan & Burbidge 1980). These plant communities support populations of honey possum (*Tarsipes rostratus*), which is a nectar-and-pollen specialist.

Pollen and animal diets

Pollen of eastern Australian Proteaceae is sticky and, if contacted, adheres to animals visiting the flowers (see, for instance, Collins & Rebelo 1987). Some insects may collect pollen directly from the pollen-presenting organs of plants, as, for instance, sometimes, worker bees of *Apis mellifera* (Butler 1954), but most insects and other animals visiting flowers of Proteaceae collect firstly nectar and then clean pollen adhering to their bodies. In some, the pollen cleaned off their bodies is collected and forms part of their diet. Pollen may be the chief source of proteins in their diet, as it is in bees, Apoidae, (Michener & Houston 1991), and the blossom-bat *Syconycteris australis* (Law 1992, 1994). In one group of bees, the pollen in their diet appears to be derived solely from Proteaceae, bees of the subgenus *Cladocerapis* of *Leioproctus* (Colletidae) that gather pollen only from *Persoonia* (Michener & Houston 1991). Pollen from Proteaceae is one source of protein in the diet of some small marsupials, *Cercartetus nanus*, *Petaurus breviceps* and *Antechinus stuartii*, and the rat *Rattus fuscipes* (van Tets & Whelan 1997). Though some honeyeaters ingest pollen of Proteaceae (Recher 1977), there is no evidence that that they digest it; indeed, evidence in the New Holland Honeyeater indicated that it was not digested (Paton 1981). It is clear, however, that pollen from Proteaceae is important, and in some cases, absolutely essential in sustaining populations of some animals.

Effective pollination

Transport of pollen from one flower and its deposition on receptive stigmas are two essential steps of pollination. Not all animals visiting flowers of Proteaceae for nectar contact organs bearing exposed pollen, as Richardson et al. (2000) showed for honeybees visiting inflorescences of *Grevillea mucronulata.* Such animals obviously fail as effective pollinators as they do not transport sufficient pollen. Many animals visiting flowers of Proteaceae have been shown to have pollen adhering parts of their bodies with which they would be expected to contact receptive stigmas, but in relatively few cases has it been shown that pollen is deposited from them onto receptive stigmas [see, for instance, Collins & Rebelo (1987)]. Detection of which animals or group of animals may be acting as effective pollinators may be difficult or fairly straightforward. For *Banksia spinulosa* var. *neoanglica*, at 1400 m in New England National Park, the effective pollinators appear to be honeyeaters, chiefly Eastern Spinebills *Acanthorhynchus tenuirostris*, simply because removal of pollen is mostly diurnal and honeyeaters are the only animals visiting the inflorescences, except for insects late in the flowering season (Vaughton 1990b). In a population of *Banksia ericifolia* at Manly-Warringah, pollination was shown to be diurnal (Paton & Turner 1985). Insects, principally *Apis mellifera*, and honeyeaters visited inflorescences, but experiments excluding different groups of visiting animals indicated that, though both groups of animals produced higher fruit set than wholly bagged inflorescences, honeyeater visits tended to produce greater fruit set than insect visits (Paton & Turner 1985). Nocturnal and diurnal animals were shown by automated photography to visit inflorescences in a population of *Banksia spinulosa* (Carthew 1993a) at the Barren Grounds Nature Reserve. Nocturnal small mammals visiting the inflorescences carried pollen on their fur (Goldingay et al. 1987), and the three species of marsupial among them foraged widely through the *Banksia* population with most of the movements they made between inflorescences being between different plants rather than different inflorescences on the same plant (Carthew 1994). A careful study by Carthew (1993a) of the behaviour of animals visiting inflorescences, the pollen loads they removed and carried, the relative amount of pollination effected by diurnal and nocturnal visitors assessed by observing growth of pollen tubes in styles, indicated that both diurnal and nocturnal visitors were effective pollinators, and that, within each group, the vertebrates, honeyeaters by day, chiefly Eastern Spinebills, and small marsupials by night, were probably more effective pollinators than insects, bees by day and moths by night. These three examples, all from populations of hooked-styled *Banksia* species in eastern Australia, serve to illustrate that, in the Proteaceae, simply because there is particular form of flowers or inflorescences, no single group of animals acts as effective pollinators, nor do effective pollinators remain the same from place to place.

A film called *A Curious and Diverse Flora* was made by Dr Peter Valder for the International Botanical Congress in Sydney in 1981. While this film was designed to be a '... description of flora of Botany Bay as Banks would have seen it', virtually every close-up of a native plant included *Apis mellifera*, the introduced honeybee! The possibility that the introduced honeybee *Apis mellifera* may reduce pollination was suggested by Taylor and Whelan (1988) for *Grevillea X gaudichaudii* and investigated in detail by Vaughton (1996) in *Grevillea macleayana*. Vaughton found that the bees may remove pollen without effecting pollination and may even prevent self-pollination in this species by removing all the pollen from a pollen presenter before the stigma becomes receptive. The extent to which this may reduce seed set in a population will depend on the relative abundance and activity of honeybees and animals that are effective pollinators. Honeybees are certainly active on Proteaceae in the region. The extent to which their activity may reduce seed set and degree of outcrossing in populations of Proteaceae has yet to be established. In *Telopea speciosissima*, Goldingay (2000) found that stigmas were receptive immediately on anthesis, and that removal of self pollen from flowers resulted in lower levels of fruit initiation but no change in fruit maturation, suggesting that self pollen on pollen presenters caused fertilisation but subsequent abortion. Perhaps this explains the vast numbers of flowers — to produce maximal fruit set while tolerating and expunging self pollination.

Pollination may not proceed to the extent of all the receptive stigmas receiving pollen needed to achieve maximum fruit set. The extent to which the degree of pollination may be limiting fruit set has been tested in some populations of Proteaceae in the Sydney region, as has the extent to which out-cross pollen may increase fruit set over selfed pollen. Artificial pollination by hand of supplementary out-cross pollen to open-pollinated inflorescences has produced increased fruit set in some populations, as it did in *Banksia paludosa* (Whelan & Goldingay 1986), *Banksia spinulosa*, *Banksia ericifolia* (Copland & Whelan 1989), *Banksia aemula* (Dalgleish 1999), and *Telopea speciosissima* (Whelan & Goldingay 1989), but not in others, *Telopea speciosissima* (Pyke 1982b), *Lambertia formosa* (Pyke 1982a), *Banksia ericifolia* (Paton & Turner 1985), and *Banksia spinulosa* (Whelan & Goldingay 1986). As shown in *Telopea speciosissima* and *Banksia ericifolia*, pollen limitation may be evident in some years but not in others (Copland & Whelan 1989, Goldingay 2000). In *Persoonia mollis*, Krauss (1994a) showed that fruit set resulted predominantly from cross pollen, even though most pollen received by stigmas was from their immediate neighbourhood; in an experiment in one population using bagged flowers, Krauss (1994b) found that fruit set was much greater from cross than self pollen. While autogamy occurs readily in *Banksia spinulosa* var. *neoanglica* in New England (Vaughton 1988) and, closer to Sydney, in *Grevillea macleayana* (Harriss & Whelan 1993, Vaughton 1995), cross pollen in populations of *Banksia* studied in the Sydney region results in more fruit set than self pollen; *Banksia spinulosa* and *Banksia paludosa* (Whelan & Goldingay 1986, Goldingay & Whelan 1990), *Banksia ericifolia* (Goldingay et al. 1991b), and *Banksia spinulosa* and *Banksia ericifolia* (Carthew et al. 1996).

While variability in degree of pollination achieved in populations is one component underlying spatial and temporal variation in fruit set, another is variation in production of inflorescences. Copland and Whelan (1989), for example, found that flowering intensities, at peak flowering, of four *Banksia* species in the vicinity of Barren Grounds Nature Reserve varied by nearly an order of magnitude over four years (1983–86 inclusive) of censusing. Mean numbers of inflorescences per plant at peak flowering of *Banksia ericifolia*, for example, ranged from a low of 1.63 in 1986 to a high of 12.43 in 1985, but percent of inflorescences producing fruits was lowest in this year of greatest flowering. Carthew (1993b) found similar variation in flowering and fruit set over three years in a *Banksia spinulosa* population (Fig. 2).

In interaction of animals and plants of Proteaceae in the collection of nectar and pollen and in pollination, some patterns of mutual dependence are beginning to be understood, especially in some populations of *Banksia*. In most of the Proteaceae of the Sydney region, there is, however, little such understanding. This is so in nearly all members of the subfamily Proteoidae, for instance, in *Petrophile* and *Isopogon*, in nearly all Proteaceae associated with more fertile habitats, such as *Helicia glabriflora*, *Stenocarpus salignus*, *Lomatia myricoides*, and in two woody-fruited genera *Hakea* and *Xylomelum*.

Animals and dispersal of fruit and seed

The role of animals in dispersal of fruits and seeds of Proteaceae in the Sydney region is known in only the most preliminary way. Fleshy fruits of *Helicia glabriflora* perhaps form part of the diet of pigeons or fruit bats, and may be dispersed by these animals. The fleshy fruit of *Persoonia pinifolia* are recorded as being taken by Pied Currawong, Satin and Regent Bowerbirds, Olive-backed Oriole and Lewin's Honeyeater (Barker & Vestjens 1990), though to what extent they act as effective agents of dispersal is unknown. In the *Persoonia mollis* complex (Krauss 1994a), wide dispersal of fruits

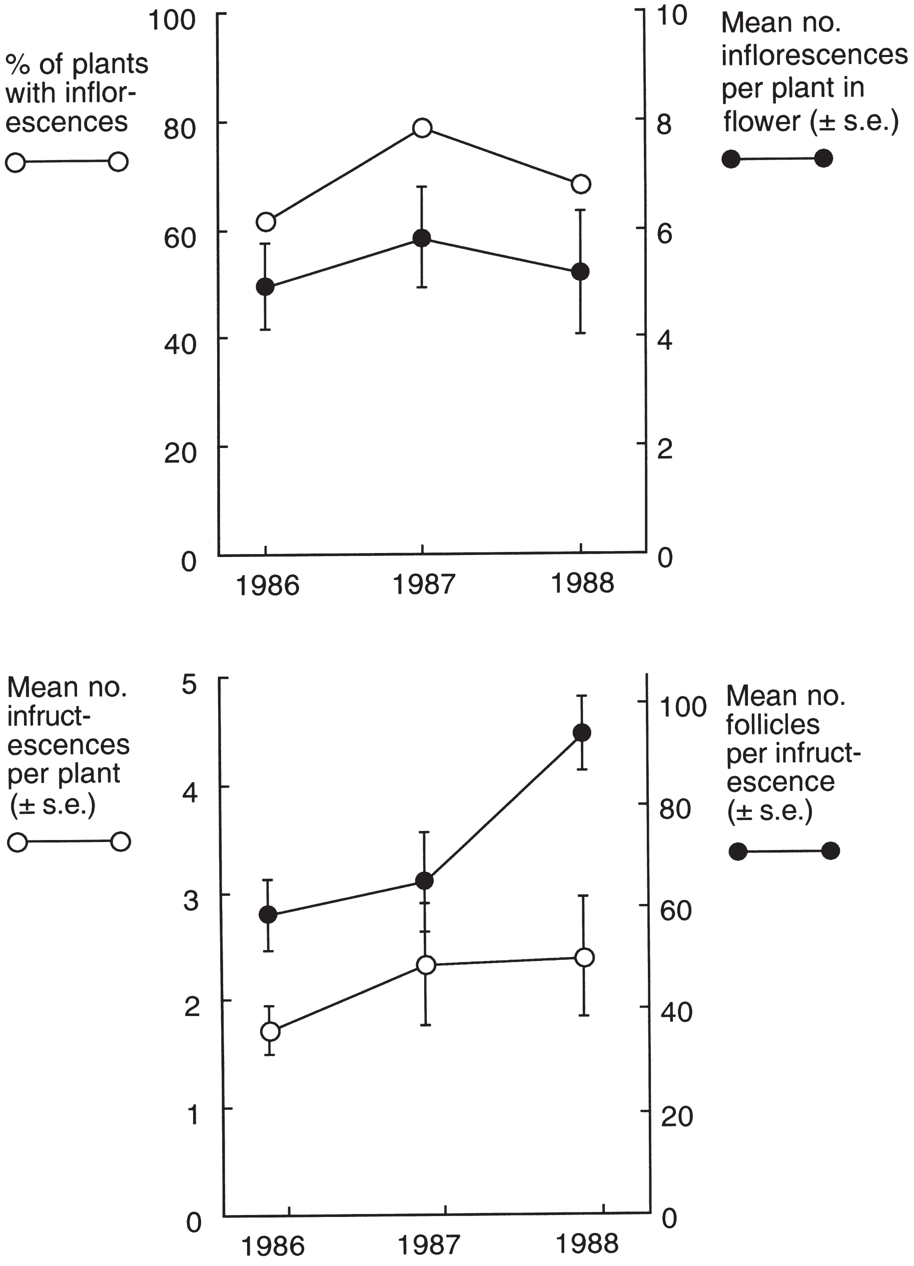

Fig. 2. Variation in flowering and fruit set in a population of *Banksia spinulosa* (data from Carthew 1993b).

followed by establishment of seedlings appears to be very infrequent. Ants are known to take seeds of some Proteaceae, for instance, those of *Grevillea buxifolia*, *Grevillea speciosa* and *Grevillea sericea* (Rice & Westoby 1981). There is an attached lipid body (elaiosome) in *Grevillea buxifolia Grevillea speciosa* and *Grevillea linearifolia* (Auld 1995, Auld & Denham 1999), and in *Grevillea shiressii* (Auld & Scott 1997, Auld & Denham 1999), while *Grevillea caleyi* and *Grevillea longifolia* have no such lipid body and are not dispersed by ants (Auld & Scott 1997, Auld & Denham 1999). Auld and Denham (1999) showed that, while a range of ants were attracted to the elaiosomes of *Grevillea buxifolia Grevillea speciosa* , *Grevillea linearifolia* and *Grevillea shiressii*, smaller ants moved the seeds very little but bit off the elaiosomes, while larger ants, gripping seeds by their elaiosomes, moved them some distance. Though Auld and Denham (1999) did not follow fates of seeds moved, they may be effectively dispersed by larger ants, though larger ants were only involved in 0–24% of seed-ant interactions observed by Auld and Denham (1999) in these species of *Grevillea*. In *Grevillea macleayana*, Edwards and Whelan (1995) found no evidence of dispersal of seeds with no seeds collected from soil cores away from adult plants but with a mean ranging from 4.3 to 15.2 seeds per m^2 estimated from soil cores under canopies.

Questions for research:

1. Do spatial or temporal patterns exist in insect damage of vegetative parts of Proteaceae?
2. Is insect damage of vegetative parts critical in controlling distribution or abundance of any Proteaceae?
3. Is mammalian herbivory on Proteaceae substantial or important?
4. How critical in the dynamics of populations of species of Proteaceae is animal predation on flowers and seeds?
5. Does the area or patchiness of fire affect levels of post-fire predation of seeds and seedlings in bradysporous Proteaceae?
6. What patterns occur in nectar and pollen collection by animals and in pollination in the subfamily Proteoidae, in Proteaceae of relatively fertile habitats, and in the woody-fruited genera *Xylomelum* and *Hakea*?
7. Do activities of *Apis mellifera* alter fruit set and/or extent of out-crossing in populations of Proteaceae?
8. Are animals effective in the dispersal of seeds of Proteaceae, including the rainforest species *Helicia glabriflora*?

Breeding systems and genetic variation in populations

Work on breeding and mating systems of Australian Proteaceae was critically reviewed by Goldingay and Carthew (1998). Their review showed the unevenness of the work done, with much in *Banksia* and much less in other genera. The Sydney region is well represented in the work done, and work in the region has covered a broader range of subfamilies than elsewhere in Australia. In the Sydney region, breeding and mating systems have been investigated not only in the Grevilleoidae, but also in the Persoonioidae in the work of Krauss (1994a & b) in the *Persoonia mollis* complex, and in the Proteoidae in the work of Morrison et al. (1994) in four closely related species of *Conospermum*.

Breeding systems observed range from from those with no autogamy evident in the *Conospermum* species studied by Morrison et al. (1994) to full self-compatibility in *Grevillea macleayana* without a higher rate of abortion of self than cross fruit (Harriss & Whelan 1993, Vaughton 1995). In *Banksia spinulosa* var. *neoanglica* in New England, a high degree of autogamy occurs (Vaughton 1988), but there are higher rates of fruit abortion in self than in cross-pollinated inflorescences (Vaughton & Carthew 1993). In other species of Proteaceae studied in the Sydney region, it appears that, though self-fertilisation is possible, there are effectively high levels of outcrossing; *Banksia ericifolia* (Paton & Turner 1985, Goldingay et al. 1991b, Carthew et al. 1996), *Banksia paludosa* (Goldingay & Whelan 1990), *Banksia spinulosa* var. *spinulosa* (Goldingay & Whelan 1990, Carthew et al. 1996), *Persoonia mollis* (Krauss 1994b), *Telopea speciosissima* (Whelan & Goldingay 1989, Goldingay & Whelan 1993), *Lomatia silaifolia* (Denham & Whelan 2000), *Grevillea linearifolia*, *Grevillea longifolia*, *Grevillea mucronulata*, *Grevillea oleoides* and *Grevillea sphacelata* (Hermanutz et al. 1998). In the species of *Grevillea* investigated by Hermanutz et al. (1998), there are degrees of self-compatibility with *Grevillea linearifolia* almost completely self-incompatible and *Grevillea longifolia* fairly highly self-compatible. Interestingly, variation also occurs within species. Hermanutz et al. (1998) found that *Grevillea oleoides* was highly self-compatible in one population but more self-incompatible in another. Ayre et al. (1994) found high levels of outcrossing in one population of *Grevillea macleayana* in a site at Jervis Bay but very high selfing in three other populations.

In the Sydney region, and indeed elsewhere in Australia [see Goldingay & Carthew (1998)], breeding and mating systems in Proteaceae have mainly been studied in species from relatively infertile, fire-prone habitats. It would be interesting to know to what extent similar patterns occur in breeding and mating systems of Proteaceae in more fertile habitats.

Variation within and among populations has been explored in some species of Proteaceae in the Sydney region. In the *Persoonia mollis* complex, this has been studied by Krauss and Johnson (1991) and Krauss (1994a & b, 1996, 1997 & 1998). Among populations, the variation extends across the region and is a mosiac of morphologically distinct allopatric or parapatric populations (Krauss 1996) with nine subspecies recognised in it by Krauss and Johnson (1991). An analysis by Krauss (1998) of allozyme variation among populations is consistent with a recent southerly expansion of the complex. Within populations, variation is maintained by outcrossing (Krauss 1994b), though genetic diversity is lower across the complex than would be expected, with a significant deficit of heterozygotes in 11 loci studied by Krauss (1997). Krauss (1997) suggested that the low genetic diversity of *Persoonia mollis*, a species of fire-sensitive shrubs whose individuals usually only regenerate after fire from seed, may be related to relatively frequent localised extinction and subsequent recolonisation of its populations. If this suggestion is correct and applies generally, then genetic diversity might be expected to differ between those species whose individuals regenerate only from seed after fire (obligate seeders) and those in which some plants survive through fire and sprout again after it (resprouters). Given the large number of congeneric resprouters and obligate seeders in the Proteaceae of the Sydney region, this would be an appropriate region in which to test this expectation.

Within some species of Proteaceae in the Sydney region, the mode of regeneration after fire varies among populations. There are obligate-seeding populations and resprouting populations in a number of species; *Hakea teretifolia* (Auld & Morrison 1992, Barker et al. 1999), which is obligate-seeding in Bouddi National Park (Siddiqi et al. 1976) and resprouting in Myall Lakes National Park (Myerscough et al. 1995); *Banksia ericifolia*, which resprouts at Governor's Head (Jervis Bay) and is an obligate seeder elsewhere (Ingwersen unpublished data, Whelan 1995); and *Banksia marginata* (George 1981, 1999). The pattern of resprouting in some habitats and obligate-seeding in others may relate to variation between habitats in typical fuel loads (determining fire intensity) and/or intervals between fires. There is potentially opportunity to test this by relating resprouting in these species to fire histories of the habitats in which the two forms of their populations occur. Variation among populations in the degree to which seeds are retained in woody infructescences after they mature (bradyspory) has, in *Banksia serrata*, been related to variation between habitats in intervals between fires, with less bradysporous infructescences tending to be in those habitats where intervals between fires are longer (Whelan et al. 1998).

Within some species of Proteaceae in the Sydney region, variation among populations in growth form appears to be related to their habitats. Auld and Morrison (1992) found that, in *Banksia ericifolia* and *Hakea teretifolia*, populations on coastal headlands had a genetically determined prostrate growth form rather than the more erect form found in more inland habitats. The extent to which genetically determined variation that relates to such physical environmental variation occurs in other species of Proteaceae in the Sydney region is currently unknown.

Hybrids between some species of Proteaceae occur in the Sydney region. In *Persoonia*, interspecific hybrids appear to be quite common (Weston 1995a, Bernhardt & Weston 1996). Hybrids between *Conospermum taxifolium* and *Conospermum ericifolium* and between *Conospermum taxifolium* and *Conospermum ellipticum* (Mackay & Morrison 1989) occur in habitats intermediate between those of the parental species but there is no evidence that they back-cross with them (Morrison et al. 1994). Hybrid swarms between *Banksia oblongifolia* and *Banksia robur* also occur in habitats intermediate between those of the parental species near Kariong in the Gosford area and in O'Hares Creek catchment (Elphinstone 1980, Schibeci 1994). Schibeci (1994) had evidence of more back-crossing in one direction than the other. *Banksia robur* reaches the southern limit of its distribution in the Sydney region where it occurs in swamps in valleys over sandstone (Buchanan 1980, Keith & Myerscough 1993, Keith 1994). Further north, there appear to be fewer obvious hybrids between it and *Banksia oblongifolia*, even though they occur in habitats along similar gradients in relation to water table, as on leached sand ridges in Myall Lakes National Park and in other locations on the north coast (Myerscough & Carolin 1986). *Banksia aemula* also reaches the southern limit of its range in the Sydney region. One of its larger populations in the region on leached sands of Bombi Moors in Bouddi National Park (McRae 1990) shows variation in leaf characteristics (P.J.M. pers. obs.) that may indicate high genetic diversity within it, and possibly introgression from *Banksia serrata*; this could be tested. The four species of *Banksia* just mentioned are each resprouters, and, following the obverse of Krauss' (1997) argument for an obligate-seeding species, survival of some adults, along with episodic recruitment and subsequent survival of seedlings under various conditions through time, may allow accumulation of a wide range of genotypes, including interspecific hybrids, over a long period. Using allozyme electrophoresis, Henderson (1991) detected hybrids between obligate-seeding *Banksia ericifolia* and resprouting *Banksia spinulosa* subsp. *spinulosa* at Barren Grounds.

Questions for research:

1. Are patterns in breeding and mating systems of Proteaceae in fertile habitats similar to those that have been observed among species of Proteaceae from relatively infertile, fire-prone habitats?
2. Are species of obligate seeders less genetically diverse than congeneric species of resprouters among Proteaceae of fire-prone habitats?
3. Is variation between obligate-seeding and resprouting populations within some species of Proteaceae in the Sydney region related to variation between their habitats in intervals between fires?
4. Is genecological variation that is readily related to physical environmental variation common among species of Proteaceae in the Sydney region?
5. Do *Banksia robur* and *Banksia aemula* have more surviving interspecific hybrids, *Banksia robur* with *Banksia oblongifolia*, and *Banksia aemula* with *Banksia serrata*, in the Sydney region, where they are at the southern edge of their distribution, than further north?

Seed dormancy, bradyspory & timing of germination

Timing of germination

Timing of germination can enhance survival of seedlings when seeds germinate in periods when resources for establishment and growth are high and when abundances of potential predator and disease organisms are low. In Proteaceae of the Sydney region, it is not obvious what mechanisms may time germination of seeds of those species in more fertile, less fire-prone habitats, but, in many species in fire-prone, infertile habitats, it is apparent that germination is timed in various ways to fall largely within a period of 1–3 years, rather than in later years, after a fire.

In these fire-prone habitats, timing of germination in the region's Proteaceae appears to be controlled in three ways. Firstly, mature, non-dormant seeds may be retained on parental plants in fruits that open and disperse the seeds usually only after the plants have been burnt (bradyspory). Secondly, seeds are shed on maturity, with some seeds at least in a dormant state, onto the soil, and with the dormancy of some of the seeds in the soil subsequently broken by the passage of a fire (dormant soil seed bank). Thirdly, plants that survive fire are stimulated to flower, when they resprout after the fire, produce non-dormant seeds that are shed on maturity (fire-stimulated flowering and seed production).

Fire-stimulated flowering of resprouting plants with subsequent production of non-dormant seeds occurs in *Lomatia silaifolia* (Denham & Whelan 2000) and in *Telopea speciosissima* (Pyke 1983b, Bradstock 1995, Denham & Auld 1999). In each case, seed production appears to reach a maximum in the second summer after fire (Denham & Whelan 2000, Bradstock 1995), and, presumably, then the highest number of seedlings might be expected in the following autumn and winter. This mode of timing of germination seems to be the rarest of the three modes in the region's Proteaceae in fire-prone habitats. It also appears to be rare in other families of dicotyledons, but does occur in *Angophora hispida* (Myrtaceae) (Auld 1987b), though it is common in many species of *Xanthorrhoea* (Gill 1981) and in other monocotyledons [see Table 5 of Keith (1996)].

Seed dormancy

Dormancy of seeds is common among several Proteaceae that flower freely and shed seeds or fruits through the intervals between successive fires in the region's fire-prone habitats. Fruits of *Persoonia*, which are shed at maturity, maintain seeds in a dormant state, which is hard to break artificially and is not well understood (Wrigley & Fagg 1989, Ketelhohn et al. 1996), though seedlings of species of *Persoonia* readily appear after fire [e.g. *Persoonia lanceolata* on podsolised sands in the Myall Lakes area (Myerscough & Skelton pers. obs.)]. The small, one-seeded achenes of *Symphionema* and *Conospermum* shed on maturity would be expected to show some form of dormancy. Although Morrison et al. (1994) apparently obtained seedlings of four species of *Conospermum* in the laboratory from freshly collected seed without any form of treatment, viable seeds of *Conospermum taxifolium* collected by Auld et al (in press) were found to be all dormant. After fire, seedlings of *Conospermum* are evident in some habitats at least, with some aspect of fire presumably having broken dormancy of seeds allowing them to germinate. In three Western Australian species of *Conospermum*, treating achenes with smoke has been shown to enhance germination of seeds: *Conospermum huegellii* (Dixon et al. 1995), *Conospermum incurvum* (Dixon et al. 1995, Roche et al. 1997) and *Conospermum triplinervium* (Roche et al. 1997).

Species of *Grevillea* also shed seeds onto the soil surface as they mature. In many species, seedlings are evident after fire, as in *Grevillea buxifolia* and *Grevillea speciosa* (Auld & Tozer 1995). Auld and Tozer (1995) showed that heat was not involved in breaking the dormancy of seeds of these two species, nor of seeds of *Grevillea caleyi*, *Grevillea linearifolia*, *Grevillea longifolia* and *Grevillea shiressii*. They suggested that some other aspect of fire broke their dormancy. In seeds retrieved from soil under bushes of *Grevillea macleayana*, Edwards and Whelan (1995) showed that heat treatment broke the dormancy of some of them, but simply nicking them with a sharp blade allowed an even greater percentage to germinate. Morris (2000) found that smoke enhanced germination of seed in seven species of *Grevillea* from the Sydney region (cf. Roche et al. (1997) for some Western Australian species of *Grevillea*). He also found that a short exposure of seed to heat alone increased germination in *Grevillea buxifolia*, *Grevillea diffusa*, *Grevillea juniperina* and *Grevillea linearifolia*, but did not increase it in *Grevillea mucronulata*, *Grevillea sericea* or *Grevillea speciosa*. After seeds had been exposed to both heat and smoke, higher germination was found in *Grevillea buxifolia*, *Grevillea diffusa*, *Grevillea juniperina*, *Grevillea linearifolia* and *Grevillea speciosa* than when exposed to either separately (Morris 2000). Kenny (1999) did factorial experiments with seeds of *Grevillea sericea* and *Grevillea speciosa*, exposing them to heat briefly and smoke before setting them to germinate with or without charcoal. She showed that smoke accelerated germination, that heat and smoke each increased levels of germination attained in each species and that, in *Grevillea speciosa*, smoke with or without other factors brought about maximum germination observed. In *Grevillea sericea*, smoke and heat were additive in their effects on level of germination attained. Morris et al. (2000) showed that, in *Grevillea linearifolia*, the seed coat controls the dormancy of the seed, its removal allowing complete germination of viable seeds. In contrast, dormancy of seeds of the Western Australian *Grevillea wilsonii* is in part controlled by the embryo as well as the seed coat (Morris et al. 2000). From work so far, it is clear that, in this group of Proteaceae with seeds or fruits whose dormancy in the soil may be broken by fire, much remains to be discovered about the nature of the dormancy and how it is broken by fire, especially in species of *Conospermum*, *Symphionema* and *Persoonia*.

Bradysporous fruits

Bradysporous fruits among Proteaceae of the Sydney region are of two types. Firstly, there are fruits with seeds within woody follicles in some genera of the Grevilleoidae, *Banksia*, *Hakea*, *Lambertia* and *Xylomelum*. Secondly, in *Petrophile* and *Isopogon* of the Proteoidae, the small one-seeded achenes are held between persistent bracts that are tightly clustered in oval or globular heads. After fire, the bracts in the heads of *Petrophile* and *Isopogon* open up releasing the achenes, and, similarly, the woody follicles of *Banksia*, *Hakea*, *Lambertia* and *Xylomelum* open and release their seeds after fire. The seeds of *Banksia*, *Hakea*, *Lambertia* and *Xylomelum* appear to have no dormancy and germinate once available moisture is sufficient, though optimum temperatures for germination may vary among species, as Sonia and Heslehurst (1978) showed in *Banksia integrifolia*, *Banksia aemula* and *Banksia serrata*. Bradstock (1985) and Bradstock and Bedward (1992) found a strong effect of ambient temperature on germination of *Banksia ericifolia*, *Banksia serrata*, *Isopogon anemonifolius* and *Petrophile pulchella.* Diurnal cycles of high temperatures typical of summer conditions imposed secondary dormancy on seeds irrespective of moisture availability, whereas germination levels were maximal under cool conditions typical of winter when moisture was non-limiting. Such effects are broadly similar to those found in other bradysporous species from mediterranean environments in southern Australia (Lamont & Groom 1998).

The degree of bradyspory also varies among and within species of *Banksia* in the Sydney region (e.g. Whelan et al. 1998) as it does in Western Australia (e.g. Cowling & Lamont 1985b). Lamont and Cowling (1984) suggested that in species of Western Australian *Banksia*, the persistence of dead florets is related to bradyspory and that their flaming off in fire assists with heating necessary for opening of follicle after fire. In eastern Australia, *Banksia integrifolia* is hardly bradysporous at all, releasing most seeds as they mature, while bradyspory in *Banksia serrata* varies among populations (Whelan et al. 1998). The release of seeds from follicles in *Banksia* after fire may depend on the season and intensity of the fire (Bradstock & Myerscough 1981) and on wetting and drying cycles in subsequent weather [cf. Cowling & Lamont (1985a) for Western

Australian *Banksia* species]. Dunlop (1996) found, in the laboratory, that effects of cycles of wetting and drying on seed release from bradysporous fruits varied among species of Proteaceae of the Sydney region; being obligatory for seed release in *Banksia ericifolia* and *Banksia marginata*; very important in *Banksia oblongifolia* and *Petrophile pulchella*; and having no effect in *Banksia serrata*, *Hakea teretifolia* and *Isopogon anethifolius*.

Survival of seeds in bradysporous fruits through fire varies among species and is related to the degree of insulation from heat afforded to the seeds in the fruits or infructescences. Bradstock et al. (1994) showed that survival of seeds in follicles subjected to standard regimes of heating was better in the larger-fruited species of *Hakea constablei*, *Hakea gibbosa* and *Hakea propinqua* than in smaller-fruited *Hakea dactyloides*, *Hakea sericea* and *Hakea teretifolia*.

Seed dormancy in bradysporous fruits

Although it is highly probable that there is no seed dormancy amongst bradysporous members of Grevilleoidae, it is possible that some dormancy occurs in the one-seeded achenes among species of *Petrophile* and *Isopogon*. The evidence for such dormancy is currently tenuous. Firstly, it can be argued that, at high fire intensities, the bracts in the heads may not afford sufficient heat insulation to maintain viability in the one-seeded achenes they hold, and, thus, survival of populations through such fires could only be ensured by dormant seeds in the soil. In *Petrophile pulchella*, however, Bradstock (1991) found similar levels of germination in achenes taken from cones burnt in a fire of moderately high intensity and in those from unburnt cones. Secondly, dormancy is perhaps suggested by the low germination Whelan and York (1998) observed from achenes of *Petrophile sessilis* sown in field plots compared from that observed from seeds of *Hakea sericea* in the same experiments. Thirdly, and even more tenuous, is the occurrence of *Petrophile pulchella* on leached sand dunes ridges in the Eurunderee system in Myall Lakes National Park, the only obligate-seeding bradysporous species to occur there [see Appendix II of Myerscough et al. (1995)]. If the frequency of fire there is, during some periods, very high [as hypothesised by Myerscough and Carolin (1986)], then the only means by which such an obligate-seeding bradysporous species would avoid local extinction would be through maintaining some dormant seeds in the soil, or by dispersing large distances. Though Bradstock (1985) found no evidence of dormancy among achenes of *Isopogon anemonifolius* and *Petrophile pulchella*, based on germination in the laboratory of wetted achenes and tetrazolium tests for viable embryos, it is possible that achenes dispersed in the field may develop secondary dormancy in the soil. Whether such dormant seeds of *Isopogon* and *Petrophile* occur in soil requires investigation.

Whether dormancy of seeds exists in Proteaceae that occur in rainforest and other moderately fertile habitats in the Sydney region requires investigation, as do the spatial and temporal patterns of germination of such seeds in the field. Currently, such matters seem to be completely unknown.

Questions for research:

1. What temporal and spatial patterns occur in the germination of seeds of Proteaceae in fertile habitats, and what dormancy mechanisms, if any, do these seeds have?
2. Do species of *Petrophile* and *Isopogon* have dormant seeds in the soil?
3. Do species of *Conospermum* and *Symphionema* have dormant seeds in the soil, and, if so, how is that dormancy broken?
4. How is recruitment from the soil seed bank in species of *Persoonia* triggered?
5. Are some seeds in populations of all *Grevillea* species dormant? Does seed dormancy vary among species of *Grevillea* with fertility or proneness to drought of their habitats? Do triggers in breaking dormancy in the species vary with their habitat?

Seedlings & their establishment

Seedlings can only arise in sites where seeds have lodged after dispersal and in which germination has occurred. In Proteaceae of the Sydney region, little is known about sites to which seeds are dispersed and those from which seedlings successfully establish, and, importantly, how closely related they are. In two species of *Banksia* and two species of *Hakea* in Western Australian fire-prone shrubland, Lamont et al. (1993) found that sites to which most seeds were dispersed were not necessarily those most favourable for establishment of seedlings. In five species of *Banksia*, also in Western Australian fire-prone habitats, Enright and Lamont (1989) showed that seeds that became buried after dispersal survived better and had a higher probability of giving rise to seedlings than those that remain unburied. In the Sydney region, in four species of Proteaceae, Bradstock (1991) found that conditions of the soil surface were important in establishment of seedlings, with differences between the species. In *Banksia ericifolia* and *Banksia serrata*, Bradstock (1991) showed that establishment of seedlings was unaffected by whether the soil surface on which the seeds were placed had been heated or not, or by the nature of surface, whether it was litter, ash or bare, but, in *Petrophile pulchella*, less seedlings became established on litter than on a surface of pure ash, while, in *Isopogon anemonifolius*, more seedlings established on litter or litter with ash than on other surfaces, except on soils whose surface had only been heated lightly, where the nature of the surface had no effect.

These experiments indicate that, at least in several species, there is no requirement for burnt substrates for early seedling establishment. Bradstock (1985) estimated that annual rates of spontaneous leakage of seeds from bradysporous storages in the interval between fires (unburnt conditions) exceeds replacement of parent plants, beyond ten years after fire. A similar conclusion was reached for *Hakea teretifolia* by Turner (1990). Bradstock (1985) observed the existence of cohorts of *Petrophile pulchella* and *Banksia ericifolia* seedlings in long unburnt stands (> 20 years) but short-term mortality of these was high and was circumstantially linked to predation. In combination with experimental evidence (Turner 1990, Bradstock 1991) these observations indicate that predation of seedlings seems to play a major role in constraining successful establishment to the immediate post-fire period in these species. Nonetheless the role of other dynamic factors such as shrub cover in influencing establishment and survival in unburnt conditions requires further work (see Bradstock 1991). In particular, the fate of seeds beyond postulated senescence in bradysporous obligate seeders within the region remains totally speculative.

Dunlop (1996) tested the effect of microsite on seedling survival in *Banksia ericifolia*, *Banksia oblongifolia*, *Banksia serrata*, *Hakea teretifolia*, *Petrophile pulchella* and *Allocasuarina littoralis* by planting seedlings of these species and broadcasting their seeds and those of *Isopogon anethifolius* into a recently burned site at Colo Vale. He located all the seedlings, recorded their survival into the second year, and classified the microsite of each seedling. He found that, in contrast to the work of Enright and Lamont (1989), microsite did not explain much of the variation in survival and that aspect and the presence of neighbouring shrubs had a much greater influence on their survival.

Differences in habitat occupied by species of Proteaceae may be related to sites to which seeds are dispersed and sites in which seedlings successfully establish. In the Myall Lakes area, in heath on leached sand, the segregation of habitats between two species of *Banksia*, with *Banksia aemula* in drier habitats on ridges and *Banksia oblongifolia* on slopes in habitats with shallower water tables, was related to patterns in dispersal of seeds and sites available for successful establishment and survival of seedlings (Myerscough et al. 1996, Clarke et al. 1996). After fire, seeds of *Banksia aemula* were not found in control sites on plots studied by Myerscough et al. (1996) on the moister habitats on slopes, but occurred in the drier habitats on ridges, where they tend to lodge in holes made in the loose sand surface by foraging bandicoots; such holes were largely absent in the more consolidated peaty surface on the slopes. Seedlings of *Banksia aemula* were found to establish on slopes if seeds were buried or sown onto artificially disturbed soil surfaces (Clarke et al. 1996). Seeds of *Banksia oblongifolia* were shown to be present after fire in control sites on plots of Myerscough et al. (1996) both on ridges and slopes, and their seedlings occurred in each habitat but did not survive in drier habitats of the ridges. Myerscough et al. (1996) showed that, under glasshouse conditions, the tap roots of seedlings of *Banksia oblongifolia* were shorter than those of *Banksia aemula* when the water table was low. Thus, in these habitats, the data of Myerscough et al. (1996) and Clarke et al. (1996) are consistent with the restriction of *Banksia aemula* to drier habitats being due to lack of sites suitable for dispersed seed to lodge and seedlings to establish in moister habitats on slopes, and with the restriction of *Banksia oblongifolia* to moister sites due to inability of their seedlings to survive in drier habitats in periods when water tables are low. This differs from competition between *Banksia aemula* and *Banksia oblongifolia* invoked by Siddiqi and Carolin (1975) to explain in part the segregation of habitats occupied by these species in heath at Mourawaring Point in Bouddi National Park. The extent to which segregation of habitats between species of Proteaceae in the Sydney region may be related to differences among species in patterns of dispersal and sites in which their seedlings may establish and survive needs investigation.

The abundance of seedlings, and thereafter adults, in populations of Proteaceae may be restricted by availability of seeds. By adding seeds to sites, it is possible to demonstrate whether recruitment of seedlings is limited by the availability of seeds. For instance, in the Myall Lakes area, after fire in heath on leached sand, Myerscough et al. (1996) showed that addition of seed of *Banksia aemula* and *Banksia oblongifolia.*

increased numbers of their seedlings establishing on otherwise untreated sites. It is probable that low availability of seeds restricts the density of seedlings in many populations of Proteaceae in the Sydney Region. Certainly, the availability of seeds is a key component in understanding fluctuations in populations between fires of certain Proteaceae, such as *Banksia ericifolia*, as is discussed below in considering responses of Proteaceae in the Sydney region to fire.

There is an obvious flush of seedlings after fire that is often commented upon and interpreted as adaptive, given that post-fire conditions seem likely to maximise water, nutrient and light availability to seedlings and minimise competition and herbivory. However, Whelan & Tait (1995) found that not all seeds of *Hakea sericea* and *Banksia spinulosa* released immediately after fire germinated immediately, with new seedlings appearing as much as 15 months after fire. Whelan & York (1998) found a similar pattern for *Hakea sericea* and *Petrophile sessilis*. In some sites, the first seedlings did not appear for over six months after fire. These findings show that post-fire germination is related to rainfall events and that, in the Sydney region, there is not strong seasonality of rainfall and, hence, the timing of the first opportunity for germination after fire is quite unpredictable (Bradstock & Bedward 1992). Seeds that have been lying on the ground for many months (at least > 12 months; Whelan & York unpublished data) still germinate readily when conditions are appropriate. Bradstock (1985) found that, in *Banksia serrata*, *Banksia ericifolia*, *Isopogon anemonifolius* and *Petrophile pulchella*, seedlings emerge up to 700 days after fire, though the extent to which this is attributable to delayed germination or to delayed release of seeds is not known.

Questions for research:

1. How do sites for germination and seedling establishment vary across the region's Proteaceae, and how are these sites related to those in which their dispersed seed lodge?
2. To what extent is segregation of habitats between species of Proteaceae related to differences among species in patterns of dispersal and sites in which their seedlings may establish and survive?
3. To what extent, and under what conditions, is seedling establishment limited by the availability of seeds in populations of Proteaceae in the Sydney region?

Fire and responses to it

Fire burns vegetation in the Sydney region. No habitat in the region is immune from it. There is abundant fossil evidence of fires in the past in various types of vegetation, including rainforest (Martin 1996). Though burning is a variable and stochastic process in the region's vegetation, there are some trends in its variation. Vegetation in fertile habitats appears to burn less often and less intensely than that in infertile habitats. This may be due to various factors related to sheltered positions, greater moisture in these habitats, the disposition of litter, stems and leaves, or higher mineral content of plant material. More mineral-rich plant material burns less easily than less mineral-rich, particularly if the mineral-rich material contains appreciable amounts of phosphate (King & Vines 1963, Cheney 1981). Fertile habitats in the Sydney region often occur where ancient rivers have cut through the Hawkesbury Sandstone cap, exposing more fertile strata below in sheltered, moist sites, though some occur on basalt caps, as at Mount Wilson (Brough et al. 1924, Keith & Benson 1988), exposed on high plateaux.

As already noted, the diversity and abundance of Proteaceae increase from fertile to infertile habitats. Indeed it is only in infertile scrubs and heaths in the region that Proteaceae may completely dominate the canopy. Occasionally, in such habitats in the region, a single species of Proteaceae, *Banksia ericifolia*, may form the entire uppermost canopy, and the density and size of its individuals be such that continued growth only occurs as some individuals die off; that is self-thinning populations form (see Morris & Myerscough 1983, 1988).

It is in the region's infertile habitats, where Proteaceae are both abundant and diverse, that responses of some of their populations to fire have been relatively well studied and are now reasonably well understood. In fertile habitats, however, where populations of Proteaceae are both low in diversity and in abundance, little is known of their responses to fire. For instance, much less is known of the responses to fire of populations of *Helicia glabriflora*, *Stenocarpus salignus* and *Lomatia myricoides* than of those of many other species of Proteaceae in the region.

Among the Proteaceae of infertile habitats in the region, responses to fire are diverse. The outcome of such responses, in terms of elimination or ongoing persistence of populations, varies between species and, to some extent, between populations.

Fire also varies in space and time, and it is convenient to talk of the term 'fire regime' to describe the pattern of fires a habitat has experienced in time to the present. A fire regime has a number of components: intervals between fires (sometimes termed fire frequency, though frequency should not be taken to imply uniform intervals); the nature of the events of the fires themselves (their intensities, relating to amounts of heat released per unit time per unit length of the fire fronts as they traversed the habitat); the seasons in which they occurred; type of fire, surface, including canopy fires, or subsurface, peat or humus fires [for discussion of fire regimes — see Gill (1975), Whelan (1995), Keith (1996), Bond & van Wilgen (1996)]. It is important to emphasise that a habitat's fire regime is an analytical sketch of what it has experienced, its fire history. Though fire regimes can never be precisely predicted for habitats, they can provide useful goals in their management. For instance, Bradstock et al. (1995) define the domain of fire regimes acceptable for conservation in sclerophyll shrublands and woodlands of the Sydney region in which Proteaceae are major components. Conroy (1996) gives ranges in some components of fire regimes experienced in recent times in such vegetation in Ku-ring-gai National Park; frequency 2–25 years; intensity 250–30 000 kW/m; season, any, but strongly biased toward spring and early summer [see also data of McLoughlin (1998)].

The setting of goals in managing plant populations in fire-prone habitats is logical because, although fire regimes can not be predicted, responses of plant populations, with sufficient knowledge, can be. The responses allowing plant survival under particular fire regimes occur over all stages of the life cycle, and vary in the region's Proteaceae. Variation at two stages of the life cycle in particular can be used to classify their responses to fire (Table 2). This classification is based on more general

Table 2. Responses to fire of Proteaceae in fire-prone habitats of the Sydney region.

Regeneration of adults	Seed bank	Diaspore	Taxa
A. Obligate seeders	(i) Soil	(a) Seeds (b) Fleshy fruit (c) Achene	*Grevillea* spp. *Persoonia* spp. *Conospermum* *?Symphionema*
	(ii) Bradysporous	(a) Achene (b) Seeds	*Petrophile* *Banksia* spp. *Hakea* spp.
B. Resprouters	(i) Non-dormant	(a) Seeds	*Telopea* *Lomatia silaifolia*
	(ii) Soil	(a) Seeds (b) Fleshy fruit (c) Achene	*Grevillea* spp. *Persoonia* spp. ?Symphionema
	(iii) Bradysporous	(a) Achene (b) Seeds	*Isopogon* *Banksia* spp. *Hakea* spp. *Lambertia* *Xylomelum*

classifications of responses of plants to fire (e.g. Gill 1981, Gill & Bradstock 1992, Keith et al. in press a, Whelan et al. in press), but also uses details of seed banks and diaspores, dispersal units, specific to the region's Proteaceae from fire-prone habitats with sclerophyllous vegetation.

The distinction between those populations in which some adults survive fire (resprouters), and those in which all adults are killed by it and thus re-establish only through seed (obligate seeders) is important in understanding responses to particular fire regimes. One component of fire regime, fire intensity, may determine whether a particular population is resprouting (after fires of low intensity) or obligate-seeding (after fires of high intensity) (Morrison 1995, Morrison & Renwick 2000), though some populations may be obligate-seeding even under low intensities, as Morrison (1995) and Morrison and Renwick (2000) found in *Hakea sericea*.

The following sections of this review consider responses of Proteaceae in infertile habitats in the Sydney region according to their characteristics in resprouting and seed storage.

Bradysporous obligate-seeders

Bradysporous obligate-seeding populations with seed stored in the canopy are liable to local extinction (Gill & Bradstock 1995) when intervals between successive fires are less than the 'juvenile period'. This is defined as the time taken for adult plants bearing mature seeds to have grown from those seeds that were shed after the previous fire. The relationship between short interval between fires and absence of species of bradysporous obligate-seeders from otherwise suitable habitat in the Sydney region is known for *Banksia ericifolia* (Siddiqi et al. 1976, Nieuwenhuis 1987, Bradstock & O'Connell 1988, Morrison et al. 1995, Bradstock et al. 1997), *Hakea sericea*

(Nieuwenhuis 1987, Morrison 1995, Morrison et al. 1995, Morrison & Renwick 2000), *Hakea teretifolia* (Siddiqi et al. 1976, Nieuwenhuis 1987, Morrison et al. 1995) and *Petrophile pulchella* (Bradstock & O'Connell 1988, Morrison et al. 1995). Among obligate-seeding populations in bradysporous species, juvenile periods vary between places (Benson 1985) and between soils of differing depths (Bradstock & O'Connell 1988). Notwithstanding such variation, it is clear that once the interval between fires is very short, less than six years, populations of obligate-seeding, bradysporous Proteaceae in shrub/heathlands within the region may be expected to decline (Bradstock et al. 1995, Williams and Bradstock 2000). Extinction may be expected should such a short-interval fire regime persist without interruption. Typical juvenile periods for common species are as follows: *Banksia ericifolia* 6 (Bradstock & O'Connell 1988, Morris & Myerscough 1988) to 7–8 years (Benson 1985), *Hakea teretifolia* 6–7 (Benson 1985) and *Petrophile pulchella* 5 (Bradstock & O'Connell 1988) to 6–9 years (Benson 1985).

Beyond the juvenile period, fires change densities of populations. As Bradstock and O'Connell (1988) showed, in populations of *Banksia ericifolia* and *Petrophile pulchella*, changes that occur in density between one generation of plants and the next depend on the season and intensity of the previous fire, and the time and weather since it. Seed release is maximised by fires of high intensity in late summer or autumn, germination and seedling establishment are maximised by an ensuing wet winter and, beyond the juvenile period, seeds accumulate in the canopy at least until 30 years after the previous fire (Bradstock & O'Connell 1988). Based on observations of populations in the field and rainfall records for the Sydney region, Bradstock & O'Connell (1988) modelled relative changes in densities expected under optimal conditions of the previous fire and ensuing rainfall and under the least favourable conditions that could be expected. Under optimal conditions in populations of both *Banksia ericifolia* and *Petrophile pulchella*, population densities could increase even at the smallest possible interval between fires of 6 years, while under least favourable circumstances Bradstock and O'Connell (1988) predicted a minimum interval of 13 years between fires would be required just for populations to replace themselves at their previous densities.

Bradstock and O'Connell (1988) also considered the possible effects of having very long intervals between fires in populations of *Banksia ericifolia* and *Petrophile pulchella*. Their modelling suggests that, despite senescence of individuals, available seed would be sufficient for replacement of populations for up to 45 years after a fire in *Banksia ericifolia* and 90 years in *Petrophile pulchella*. They pointed out, however, that it is difficult to test these suggestions in heathland and shrublands in the Sydney region, as there is a lack of long-unburnt stands (e.g. > 25 years without fire). Of all groups of Proteaceae in fire-prone habitats of the Sydney region, the ecology of bradysporous obligate-seeders is perhaps the best understood. Yet, even in this group, many aspects of their ecology in relation to fire remain unknown. As already raised, there is the possibility that the achenes of *Petrophile pulchella*, though held in bradysporous infructescences, may also have a proportion that retain some dormancy in the soil. Also, as noted, juvenile periods vary with habitat, and it is possible that, in the Blue Mountains, populations of *Banksia ericifolia*, *Petrophile pulchella* and other bradysporous obligate-seeders may have slower dynamics (slower growth, rates of maturation and longer juvenile periods) and require longer intervals between fires to persist than on the coast. Conversely, in the South African Cape region, where some of the obligate-seeding bradysporous Proteaceae from the Sydney region are weeds in fynbos, their population dynamics may be faster and their populations may survive under shorter intervals between fires. For instance, in Cape fynbos, Richardson et al. (1992) found that two years was the juvenile period of *Hakea sericea* and of *Hakea gibbosa*, far shorter than juvenile periods recorded for populations of bradysporous obligate-seeders of Proteaceae in fire-prone habitats near the coast in the Sydney region.

Obligate-seeders with soil seed banks

Among the region's Proteaceae in fire-prone habitats, the dynamics of populations of obligate-seeders with soil seed banks are less well known than those of bradysporous obligate-seeders. This can be related to the increased difficulty of studying seed banks in the soil, rather than canopy-held seed banks. Soil seed banks have, nevertheless, been studied in *Grevillea caleyi* (Auld 1994, 1995, Auld & Scott 1997, Auld et al. in press), *Grevillea longifolia* (Auld 1994, 1995, Auld & Scott 1997), *Grevillea speciosa* (Auld 1995, Auld et al in press) and *Grevillea macleayana* (Edwards & Whelan 1995, Vaughton 1998). Longevity of seed in seed banks has been assessed in *Grevillea caleyi* and *Grevillea speciosa*, and in *Conospermum taxifolium*, *Grevillea linearifolia* and *Persoonia pinifolia* (Auld et al. in press). Not assessed, however, are fates of seeds buried at various depths in the soil, especially during the passage of fires of various intensities [cf. study of *Acacia suaveolens* by Auld (1986a & b, 1987a)].

Fates of seeds of *Grevillea* at various depths in soil can not readily assessed in relation to the passage of fires of particular intensities. This is largely because the breaking of dormancy in seeds of most species of *Grevillea* studied to date is related to smoke, and patterns of penetration of dormancy-breaking smoke to seeds in soil is currently unknown. Such an assessment, using the methods of Auld (1986 a & b, 1987a), may be feasible in *Grevillea macleayana* in which heat does appear to break dormancy of seeds (Edwards & Whelan 1995). In the flush of seedlings after a fire, it is possible, by looking at lengths of the portions of their hypocotyls that were buried, to assess the depths of the seeds in the soil from which recruitment of seedlings occurred (Auld 1986b). Recruitment of seedlings after fire from seeds in the soil is readily observed, as reported in *Grevillea caleyi*, *Grevillea longifolia*, *Grevillea buxifolia* and *Grevillea speciosa* by Auld and Tozer (1995) and in *Grevillea macleayana* by Vaughton (1998).

Among the region's Proteaceae in fire-prone habitats, the juvenile period appears to be shorter in obligate-seeders with soil seed banks than in bradysporous obligate-seeders. It ranges from 2–3 years in *Grevillea macleayana* (Vaughton 1998), 2–4 in *Grevillea speciosa* (Benson 1985, Auld 1995), 2.5–5.0 in *Grevillea caleyi* and 3–5 years in *Grevillea longifolia* (Auld 1994, 1995, Auld & Scott 1997), 4 years in *Conospermum taxifolium* and *Grevillea sericea* (Benson 1985), to 8 years in *Grevillea buxifolia* (Benson 1985). Once the plants become reproductive, the size of the seed bank can be expected to rise in the soil. In populations of *Grevillea caleyi*, however, Auld and Denham (in press b) showed that virtually all seeds shed in the first two reproductive years were taken by rats and wallabies, and that a period approximately 3 times the length of the juvenile period, 8–12 years, is required between successive fires for the seed bank to be sufficient to sustain the populations. In populations of *Grevillea macleayana*, Vaughton (1998) showed that there were more seeds in the soil beneath a population of 16-year-old bushes than beneath younger or older populations. In older populations, she found high proportions of senescent and dead shrubs, no longer producing seed. Auld (1995) modelled variation of abundance of seed in seed banks of *Grevillea caleyi*, *Grevillea longifolia* and *Grevillea speciosa*. Based on observations of reproductive output of adults, losses of seeds pre- and post-dispersal, and seed longevity in the soil, his models indicated an expected peak in abundances of seed in *Grevillea caleyi* and *Grevillea speciosa* at about ten years, and that in *Grevillea longifolia* seed may be held at maximum abundance over a period of 25 to 50 years after the last fire.

In infrequently burnt vegetation, Nieuwenhuis (1987) reported that *Conospermum taxifolium*, *Grevillea speciosa* and *Grevillea buxifolia* were absent whereas they were present in more frequently burned sites, while Morrison et al. (1995) found that *Grevillea sericea* was among a group of obligate-seeders with soil seed banks from several families whose abundance declined in vegetation with time-since-fire. These observations raise questions about longevity of soil seed banks of this group of plants and the minimum and maximum times between fires that can elapse without endangering the continued survival of the populations. As Auld (1994) pointed out, these questions are crucial in understanding management of much fire-prone vegetation, and the population dynamics of these obligate-seeding plants with soil seed banks. In obligate-seeders with soil seedbanks, the type of analysis and modelling that Bradstock and O'Connell (1988) did for populations of two species of bradysporous obligate-seeders are difficult to do, though they should be attempted. Such an attempt would stimulate study of how soil seedbanks function and how effective they may be in sustaining populations both through short and long intervals between fires. Also, in the region's Proteaceae, study of populations of obligate-seeders with soil seed banks should be extended to include species of *Conospermum* and *Persoonia.*

The susceptibility of obligate seeders to frequent or intense fire may be reflected in their distributions. Gill and Bradstock (1995) introduced the notion of a 'fire shadow', which is a part of the landscape in which fire frequency, and perhaps intensity, is typically lower than surrounding areas. There is some evidence that, in the sandstone plateaux of the Sydney region where fire return times have been shorter since European settlement and the modal season of fires has changed (Clark & McLoughlin 1986, McLoughlin 1998), obligate seeders such as *Grevillea rivularis* (Pickup 1999) are restricted to areas such as stream sides because they have experienced less frequent fires, not because of any preference for edaphic or other features of the riverine environment. Similarly, many of the rare *Persoonia* species of the Sydney region, most of which are obligate seeders, appear to occur in greatest numbers near roads and tracks (P. Weston pers. comm.), again perhaps because of the reduced fire frequencies in this part of the landscape.

Non-bradysporous resprouters with non-dormant seed

Resprouters with non-dormant seed and without bradysporous fruit are the smallest group of Proteaceae in fire-prone habitats in the Sydney region, but the group includes *Telopea speciosissima*. In *Telopea speciosissima*, Bradstock (1995) has shown that, in dynamics of populations, seed production, recruitment of seedlings, their survival and growth to maturity are key processes between fires and that, through fires, survival of plants is also critical. Although more data are required, it appears that, in *Telopea speciosissima*, 8–10 years after fire, less than 25% of juveniles in the population are fire-tolerant, and that, for populations to increase in density, intervals between fires of greater than ten years are required (Bradstock 1995).

Flowering in *Telopea speciosissima*, though stimulated by fire, may continue for some years thereafter (Pyke 1983b, Goldingay 2000), but in *Lomatia silaifolia* abundant flowering only occurs in the first or second year after fire (Denham & Whelan 2000). Denham and Auld (1999) followed flowering, seed produced, post-dispersal predation of seed and seedlings recruited in *Telopea speciosissima* after the fires in Royal National Park in January 1994. They showed that seeds were first produced two years and also produced three years and, in diminished abundance, four years after the fire. They found that establishment of seedlings from seed occurred in one site in each of the years, but in a second site, where predation of seed was higher, seedling establishment was much lower and was zero four years after the fire. In *Lomatia silaifolia*, the only other species of the region's Proteaceae currently known to belong to this group, data are required on all aspects of its life cycle, if the model of Bradstock (1995) is to be applied in understanding effects of fire on its populations and in predicting outcomes of various fire regimes and weather in their survival or variation in abundances of plants in them.

Resprouters with soil seed banks

Almost nothing is currently known of the population dynamics of resprouting Proteaceae in the Sydney region with soil seed banks. They comprise some species of *Persoonia* and possibly some species of *Grevillea* (see account below by Benson and McDougall (2000) in *Ecology of Sydney plant species*, Part 7b). In two species, *Persoonia levis* and *Persoonia linearis*, most adults have a fire-resistant trunk with thick, flaky bark through which epicormic shoots emerge after fire. Of all of the five groups of Proteaceae in the region's fire-prone habitats outlined in Table 2, this group still requires the most basic data on how their seed banks are maintained, recruitment of seedlings from seeds, and survival of plants through fires, for populations of even just one species in this group.

Bradysporous resprouters

In contrast to the last group, there are both data and models on population dynamics of some species in bradysporous resprouters from the region's fire-prone habitats. It is generally taken as given that juveniles become fire-tolerant long before they reach reproductive maturity. Zammit and Westoby (1987a) established that juveniles of *Banksia oblongifolia* could survive fire and resprout from a lignotuber before they reproduced sexually. In *Isopogon anemonifolius* and *Banksia serrata*, the work of

Bradstock & Myerscough (1988) identified stages of the life cycle critically affected by fire and assessed survival of populations through various fire regimes. They showed that, if fires occur before newly-established plants are fire-tolerant, populations will be expected to decline. In *Banksia serrata*, the age at which juveniles become fire-tolerant is about six years, while in *Isopogon anemonifolius* it is about 13 years. Short intervals between fires prevent recruitment of juveniles into adults in each species, Thus, despite having adults that resprout (so that populations of these species are buffered from local extinction by a single short interval between fires), they are susceptible to decline under a long-term regime of frequent fires. In *Banksia serrata*, frequent fires may prevent fire-tolerant juveniles from progressing to the adult arborescent form. Under such a regime, each fire kills their aerial stems and maintains them as lignotuberous fire-tolerant juveniles for longer periods than under regimes where at least one interval between fires is long enough to allow them to develop fire-resistant arborescent stems of adults.

In *Isopogon anemonifolius*, the adult shrub is lignotuberous, so, once the juvenile has become fire-tolerant, its progress to maturity does not require a change of form that depends on a long enough interval between fires. Based on observations of accumulation of viable seed in the seed bank between fires, post-fire recruitment of juveniles and survival of various stages of the life cycle through fire, models of Bradstock and Myerscough (1988) indicate that, under a regime of fires at intervals of five years, greater declines would be expected in populations of *Banksia serrata* than in those of *Isopogon anemonifolius*, while, under a regime of fires at intervals of ten years, the converse would be expected, particularly if the intensities of the fires were high.

A more detailed demographic analysis by Bradstock (1990) looked at effects of interactions between fire intensity and intervals between fires on these populations. From the analysis, he predicted that in *Banksia serrata* populations, numbers of plants would decline when intervals between fires of high intensity were less than 9 years, while for fires of low intensity the critical interval was 11–12 years, while, in *I. anemonifolius*, the respective critical intervals were 14 and 16 years. The longer interval between fires of low intensity required for no decline in the populations is related to poorer post-fire release of seeds and recruitment of juveniles than after fires of high intensity. There are two problems related to generalising from these analyses. Firstly, there is the problem of variability in the estimates in data from populations in making predictions. Morrison and Cary (1994) further explored the sensitivity of Bradstock's (1990) model and showed that predictions of population trends in relation to fire regimes were also sensitive to variations in interfire mortality, not originally included in Bradstock's (1990) analysis. Their work reinforces the importance of basing predictions of population trends on robust data for key life history processes. Secondly, as Bradstock (1990) noted and data of Whelan et al. (1998) show, there is considerable variation in the degree of bradyspory and inter-fire recruitment of juveniles between populations of *Banksia serrata*, indicating that care is required in making predictions from observations of the population dynamics of one set of populations in one area to another set in another area. Nevertheless, demographic studies in this group of Proteaceae in the Sydney region have indicated that, in assessing the effects of fire regimes on their populations, not only has survival of resprouting adults through and between fires to be considered, but also their seed banks, post-fire and/or inter-fire recruitment of seedlings, the length of the fire-intolerant juvenile period and the transition from fire-tolerant juveniles to reproducing adults.

As Bradstock (1990) pointed out, it is not known if all species in this group of bradysporous resprouting Proteaceae in the region respond to fire similarly to the populations he studied. The group includes the localised bird-pollinated *Hakea bakeriana*, *Lambertia formosa* and the tallest-growing Proteaceae of infertile fire-prone habitats in the region, *Xylomelum pyriforme*. As a first step in understanding effects of fire across the species in group, length of the juvenile fire-tender stage could be determined. A second step could be to determine how long fire-tolerant juveniles take to become seed-producing adults, and whether, as in *Banksia serrata*, this period is also dependent on fire regime. In surveying these two stages of the life cycle, it would be possible to test the assumption which seems to be current that, in this group of plants, fire-tolerance in juveniles is always attained before sexual maturity. Testing this assumption would be particularly interesting in resprouting subspecies of those species, such as *Hakea teretifolia*, that have both obligate-seeding and resprouting subspecies.

Comparison of obligate-seeders & resprouters

Resprouters and obligate-seeders have been compared over a number of characteristics across their life cycles. Some generalisations have been tested in Proteaceae of the Sydney region, especially in bradysporous species. A number of differences between them were predicted by Carpenter and Recher (1979). Some of these have been refuted, especially those in systems of pollination and compatibility (see, for instance, Lamont et al. 1998). Predicted differences that appear still tenable are the relative longevity of plants (resprouters greater than obligate-seeders), age to first reproduction (resprouters greater than obligate-seeders) and growth rates of plants (resprouters less than obligate-seeders). Data of Bradstock and Myerscough (1988) indicate that age to first reproduction in the resprouter *Banksia serrata* is at least 20 years, while in the obligate-seeding *Banksia ericifolia* it is about 6 years (Bradstock & O'Connell 1988). Resprouting populations bear seed sooner after fire than obligate-seeding populations, due to the presence of resprouting adults, as Zammit and Westoby (1987a) showed in those of the respouter *Banksia oblongifolia* and the obligate-seeding *Banksia ericifolia*. Though they bore seed later after fire, populations of *Banksia ericifolia*, after ten years, had larger seedbanks than those of *Banksia oblongifolia*, due to faster rate of growth of individuals and greater reproductive output of individuals of comparable size. Furthermore, Zammit and Westoby (1987b) showed that *Banksia oblongifolia* is less bradysporous than *Banksia ericifolia*, releasing seed more readily without the passage of fire, releasing them more readlily after fires of low intensity and releasing them over a shorter period after fire than *Banksia ericifolia*. After fire, partly due to longer period over its seed is released and slower germination from released seed, seedling establishment is held to be less risky in *Banksia ericifolia* than in *Banksia oblongifolia* (Zammit and Westoby 1987b). Work of Bradstock and Bedward (1992), however, indicated that, under varying soil moisture conditions, the resprouter *Banksia serrata* has a greater spread of seed germination and seedling emergence than the obligate-seeding *Banksia ericifolia*, where emergence is more risky, being rapid under conditions of high moisture.

In a survey of 2–4 year old plants recruited from seed in burnt habitats in south-western Australia, Pate et al. (1990) found that rates and patterns of seedling growth differed between resprouters and obligate-seeders. Across a number of families, including the Proteaceae, they found that obligate-seeders had a greater plant dry mass and a more than fourfold greater shoot:root dry-mass ratio than resprouters, and that starch was more concentrated in the roots of resprouters. Similar differences would be expected between resprouters and obligate-seeders among the Proteaceae of the Sydney region. Among woody-fruited Proteaceae of south-western Australia, Lamont and Groom (1998) found that resprouting species tended to have a few large viable seeds per plant while obligate-seeders have many smaller seeds. To what extent this applies to woody-fruited Proteaceae of the Sydney region is unknown, though it seems unlikely that such a generalisation holds in the region. Some preliminary data on seed size are available in the Sydney region for some species of *Banksia* in Hammill et al. (1998) and of *Hakea* in Bradstock et al. (1994). Also, in Proteaceae of the Sydney region, do characteristics differ as much between resprouting and obligate-seeding populations within species that have both types as between resprouting and obligate-seeding species?

Proteaceae & fire-prone landscapes

Populations of Proteaceae have distinctive patterns of distribution across the region's fire-prone landscapes, particularly discernible in heaths (e.g. Siddiqi et al. 1972), other shrublands (e.g. Buchanan 1980) and swamps (e.g. Buchanan 1980, Keith & Myerscough 1993, Keith 1994). Some of these patterns are variations in distribution of populations between habitats, as in the examples just cited. Other patterns occur in time within habitats due to fire effects. For example, Siddiqi et al. (1972) described variation between habitats in heath on leached sand on Mourawaring Point, with heath on better drained areas dominated by *Banksia aemula* while on less well drained areas the canopy was dominated by tall-growing shrubs of *Banksia ericifolia* and *Hakea teretifolia* together with *Allocasuarina distyla*. These tall-growing shrubs are all killed by fire, and Siddiqi et al. (1976) noted that the structure of the vegetation is changed in the immediate post-fire period to a lower-growing canopy, an important component of which is then the resprouting *Banksia oblongifolia*, that, before the fire, was in the understorey beneath the canopy of the tall-growing obligate-seeding shrubs.

In heathland west of Jibbon Hill in Royal National Park, from a sequence of aerial photographs over a period of approximately 50 years, Keith (1995) mapped areas of thicket of these tall-growing obligate-seeding shrubs, and showed large temporal variation in extent of thicket, which was directly related to fires that occurred during the period. Siddiqi et al. (1976) showed that in areas where intervals between fires are less than the juvenile period of the obligate-seeding bradysporous shrubs, vegetation that may have contained them before the last fire now lacks even their seedlings and that the resprouting *Banksia oblongifolia* is left to occupy the canopy without being overtopped by them. Clemens and Franklin (1981) also reported extinction of populations of *Banksia ericifolia* at North Head after a short interval between fires. *Banksia oblongifolia* may thus occupy the canopy of certain heaths in the Sydney region in two ways. It may do so permanently in the absence of taller-growing obligate-seeding shrubs that include *Banksia ericifolia* and *Hakea teretifolia*, or, if they are present as seedlings after fire, transiently until these seedlings have grown to overtop its resprouting plants.

Coastal heaths that contain *Banksia oblongifolia*, with or without *Banksia ericifolia* and *Hakea teretifolia* according to their fire history, occur both north (Siddiqi et al. 1972, 1976) and south of Sydney (Keith & Bradstock 1994, Keith 1995). Keith and Bradstock (1994) investigated populations of *Banksia oblongifolia* two years after fire in relation to the pre-fire absence or, if they were present, the variation in cover and height of taller-growing, obligate-seeding bradysporous shrubs of *Banksia ericifolia*, *Hakea teretifolia* and *Allocasuarina distyla*. Their study was in sites near Jibbon Beach in Royal National Park. The density of plants of *Banksia oblongifolia* was greatest in sites where a canopy of taller-growing shrubs had been absent and was least where there had been a tall canopy of them. Furthermore, they showed that the number of follicles produced per plant in *Banksia oblongifolia* was greatest where tall-growing shrubs had been absent. The relationship in these heaths between populations of *Banksia oblongifolia* and those of taller-growing bradysporous obligate-seeders is thus a dynamic one dependent on fire regime, particularly intervals between fires. Where intervals between fires are less than their juvenile periods, the bradysporous obligate-seeders are excluded, but, where fire regimes with intervals between fires of 15–20 years obtain for some time and the density of populations of *Banksia ericifolia* is maximised (Bradstock & O'Connell 1988), *Banksia oblongifolia* may be excluded from an area.

Keith and Bradstock (1994) noted an inverse relationship between the presence of a dense overstorey and floristic diversity in this heathland, consistent with earlier broad ranging correlations noted by Specht and Specht (1989). They hypothesised that a dense overstorey of bradysporous shrubs, as promoted by successive intervals between fire of moderate length, would competitively exclude not only understorey shrubs, as noted, but also herbaceous species. Further studies on the effects of overstorey canopies (Tozer & Bradstock in review) have confirmed strong evidence for competitive exclusion of understorey species. Tozer and Bradstock (in review) demonstrated that competitive exclusion of some understorey species (both total exclusion and reductions in density) can occur beneath shrub canopies within a single long-interval between fires (30 years). Their work however indicated that competitive effects are not unilateral, and that a multi-strata hierarchy of effects may lead to some species of low-stature being favoured by the presence of shrub crowns, while others are excluded, and that soil moisture may mediate the outcome of competition.

Should local extinction of either bradysporous obligate-seeding or resprouting woody-fruited Proteaceae occur, it is possible that dispersal of seed after fire from surrounding areas may allow re-establishment of their populations. Hammill et al. (1998) showed that, after fire, the winged seeds released from the woody fruits of *Banksia serrata*, *Banksia ericifolia*, *Banksia marginata*, *Hakea sericea* and *Hakea teretifolia* were dispersed through the air in windy conditions up to 12 m from the fruits, and thence may be blown further along the surface of the ground. The modal distance seeds of *Banksia ericifolia* moved, after being released from 3 m above ground in a 35 km/h wind in a recently burned heathland site, was 10–14 m, but nearly 10% of seeds moved more than 21 m (see Fig. 3.19 of Whelan 1995). Hammill et al. (1998) also showed that, although post-fire recruitment of seedlings of *Banksia ericifolia* was highest near the source of the seed and decreased log-linearly away from it, some seedlings occurred up to 40 m away.

Given the nature of the demography of shrubs of Proteaceae and emerging knowledge of their competitive interplay with other co-habiting species in shrub/heathlands in the region, it is likely fire regimes will strongly affect floristic composition of these communities. Management of fire regimes is therefore a pivotal conservation issue. While much knowledge described above is based on empirical studies at fine spatial scales, the nature of fire regimes and their ecological effects transcend such local effects. Comprehension of the ultimate outcome of local extinction, dispersal, and recolonisation requires resolution of these processes at the scale of landscapes.

Keith (1995) validated the demographic model for *Banksia ericifolia* of Bradstock and O'Connell (1988) by examining fluxes in overstorey cover in relation to fire regimes for a 50-year period in the Jibbon heath landscape of Royal National Park. His results, derived from analyses of historical aerial photograph sequences and local records of fires, indicate considerable local instability of overstorey cover at any point within the landscape, within the range of the fire regimes that occurred. Nonetheless, the canopy-dominant obligate-seeders such as *Banksia ericifolia, Hakea teretifolia* and *Allocasuarina distyla* persist to the present. A question that arises is whether such species can be eliminated both 'locally' (point-scale) and 'globally'. What range of fire regimes would be required to achieve such an effect? Bradstock et al. (1996) explored this question using a spatially-explicit simulation model, encapsulating the key life history processes of bradysporous, obligate-seeder shrubs summarised above. Importantly, their model was scaled to account for the relatively short-range dispersal typical of these species, as reported by Hammill et al. (1998). The results indicated that extinction probability (landscape scale) was related to both the size and frequency of fires; low risk of extinction occurred when fires were relatively large and of moderate frequency, relative to the life-span of the species. This somewhat counter-intuitive result, indicated that patchiness of fire cannot be relied upon per se in management to ensure persistence of species.

Such models indicate that the additive effect of patterns and sizes of individual fires must be understood in order to determine the statistical distribution of fire regime components (e.g. fire frequency and intensity) and the resultant probability of persistence of species. Contemporary theory linking analytical life-history and fire-recurrence models (Clark 1991, Bond & van Wilgen 1996) offers a promising avenue for understanding the way that statistical properties of fire regimes may relate to the persistence of both obligate seeders and resprouters in landscapes. The Proteaceae of the Sydney region offer great potential for testing such theory. For example, mixtures of bradysporous, obligate seeder species tend to be uncommon at a fine-scale. Typically patches dominated largely by a single species (e.g. *Banksia ericifolia*, *Petrophile pulchella* or *Hakea teretifolia)* occur in shrub/heathlands and the understorey of woodlands. Do such patterns of local dominance reflect stochastic sorting of species in the post-fire 'regeneration niche' (e.g. Lamont & Groom 1998), or micro edaphic effects on establishment (Bradstock 1991) or wider but subtle demographic differences? A possible wild-card could be hitherto unconsidered interspecific effects, such as evidence that fires in dense shrub crowns (e.g. *Banksia ericifolia* thickets) may be lethal for the seedbanks of potential co-habitants such as the small-fruited *Hakea teretifolia* (Bradstock et al. 1994).

A key question that arises from consideration of landscape-level dynamics in species of Proteaceae, is the degree to which differing fire management actions (e.g. suppression of wildfires, prescribed burning) may affect the distribution of fire regimes in a landscape and hence probability of species persistence. Bradstock et al. (1998) extended their earlier modelling approach to consider this problem for several functional groups of woody plants (bradysporous obligate seeders and respouters, plus obligate seeders with soil storages of seeds). Their analyses indicated that trends in population size and extinction probability ('global') were affected by rates of both prescribed and unplanned ignitions. Population decline and high risk of extinction were both positively related to ignition rate from either source (and their interaction) though the nature of such responses was non-linear. High levels of prescribed burning (i.e. area treated per annum), sufficient to limit the spread of unplanned fires under severe weather condition through the creation of a mosaic of low fuel patches in the landscape, were predicted to lead to high risk of extinction of both obligate seeder functional groups (over 200 years) and decline in resprouters. These results cast doubt on the popular notion that broad-scale 'mosaic' burning is an effective and ecologically sustainable tool for the management of wildfires.

Further modelling (Williams & Bradstock 2000, Bradstock & Gill in press) has demonstrated that a strategic, rather than a broad-scale approach to use of prescribed fire (e.g. intensive treatment of urban interface and other key buffer areas), offers the best solution in urbanised landscapes containing vegetation with obligate seeders, as typified in the Sydney region, where fire management must achieve concurrent human protection and conservation objectives.

The modelling approaches discussed above have so far considered single species, rather than the response of the plant community as a whole. Extension of such approaches to the community level will require consideration of interactions between functional groups and strata within vegetation. Overstorey and understorey interactions (Keith & Bradstock 1994, Tozer & Bradstock in review) in proteaceous shrub/heathlands and their effect on overall floristics will be strongly influenced by fire regimes, given the demographic lability of the overstorey. Keith and Bradstock (1994), Tozer and Bradstock (in review) have hypothesised that the suppressing effects of overstorey are such that an unstable fire regime must prevail for maintenance of full floristic diversity. Bradstock et al. (1995) proposed a conceptual model that positively related variance in fire regimes (fire-intervals in particular) to floristic composition. It is noteworthy that this conceptual model, built on a foundation of demographic studies on individual overstorey species (e.g. Bradstock & O'Connell 1988) and specific overstorey/understorey interactions (Keith & Bradstock 1994, Tozer & Bradstock in review), is corroborated by studies of community floristic composition in relation to fire regimes (Morrison et al. 1995, Cary & Morrison 1995). Bradstock et al. (1995) quantified guidelines for management that would lead to a domain of variable fire regimes, sufficient to maintain floristic diversity. Their guidelines are intended for use as a simple decision support system to guide managers about choice of appropriate fire regimes within an adaptive framework (Bradstock 1999, Gill et al. in press, Keith et al. in press b).

Such an overview indicates that vegetation in the infertile habitats of the Sydney region dominated by Proteaceae, is inherently dynamic. Co-existence of species, at least at the point scale, may require instability of dominants in particular, perhaps with the necessity for dramatic fluctuations in density over relatively short periods of time. The fire regimes necessary to generate a shifting mosaic of 'unstable' patches in this manner but at the same time allowing for adequate dispersal and recolonisation of key species are currently unknown. The spatial modelling approaches described above offer an obvious means of exploring the problem.

Another possibility is that 'local instability' of key species may not always be driven by the influence of exogenous disturbances such as fire. Bond et al. (1995) used a population model to demonstrate that simple density-dependent effects on fecundity in South African proteaceous shrubs could generate chaotic population dynamics. The nature of such density-dependent effects on fecundity remain unexplored for analagous species in the Sydney region, though Bradstock (1985) and Bradstock and O'Connell (1988) showed that variations in soil depth may influence fecundity in bradysporous shrubs. Given the complex gradients in strata, soil depth and resultant soil moisture that are found at a variety of scales in sandstone-based habitats in the region, there is considerable potential for exploration of interactions of habitat-driven and endogenous effects on demography.

We hypothesise that the ultimate contribution of heterogeneity of the fire regime to maintenance of floristic diversity, will be constrained by habitat diversity and such endogenous demographic effects. A challenge for the future will be to carry out observations, experiments and modelling, at landscape scales, sufficient to provide critical insight into these processes.

General comments on fire interactions

While work on effects of fire on interactions between populations of bradysporous resprouting and those of obligate-seeding woody-fruited Proteaceae has allowed greater understanding, and thus a firmer basis for managing, certain heaths in the Sydney region, there is still much to be understood about effects of fire on Proteaceae. There is greater understanding of the effects of fire on Proteaceae in the region's infertile habitats, where Proteaceae are both diverse and abundant, than in more fertile habitats, where they are neither diverse nor abundant. Even in Proteaceae from infertile habitats, there is still much to be learned about effects of fire on their populations, particularly in those with soil seed banks and especially among resprouters among this group. In Proteaceae with soil seed banks, less is known in those species in which the unit of dispersal is either a fleshy fruit in species of *Persoonia* or a small achene as in *Conospermum* than in species of *Grevillea* where units dispersed are seeds. The Sydney region will continue to provide particularly fruitful opportunities for understanding effects of fire on Proteaceae and, more generally, the ecology of plants in fire-prone habitats. Such studies are badly needed if we are to meet the challenges of conserving their populations and the dynamics of their interactions across the region's fire-prone landscapes.

Questions for research:

1. What responses to fire have populations of *Helicia glabriflora*, *Stenocarpus salignus* and *Lomatia myricoides*?
2. Do populations of obligate-seeding bradysporous Proteaceae have slower dynamics (slower growth, rates of maturation and longer juvenile periods) at higher altitudes in the Blue Mountains than on the coast?
3. Among obligate-seeding populations, are responses to fire in species of *Conospermum* and *Persoonia* similar to those in species of *Grevillea*?
4. Can changes of abundance across intervals between fires be modelled in obligate-seeding Proteaceae with soil banks in a similar way to the modelling of Bradstock and O'Connell (1988) in obligate-seeding populations of two bradysporous species of Proteaceae?
5. Data are required on population processes to understand and predict fire effects better in populations of species such as *Telopea speciosissima* and *Lomatia silaifolia*, in which fire stimulates flowering and seed release follows in the first two years or so after fire.
6. What is the juvenile fire-tender period in each resprouting bradysporous species of Proteaceae?
7. How and when does seedling recruitment occur in populations of resprouting Proteaceae with soil seedbanks in fire-prone habitats?
8. Is it an invariable rule that juveniles of resprouting species of Proteaceae become fire-tolerant long before they reach reproductive maturity?
9. Are there consistent differences between seedlings of resprouters and those of obligate-seeders in rates and patterns of growth among Proteaceae of the Sydney region?
10. Among woody-fruited Proteaceae of the Sydney region, do resprouters typically have fewer but larger viable seeds per plant than obligate-seeders?
11. In Proteaceae of the Sydney region, are the differences between characteristics of resprouting and those of obligate-seeding populations within those species that have both types as great as differences between species that just have one or the other sort of population?
12. How large an area is required to conserve indefinitely heaths where populations of bradysporous resprouting and obligate-seeding woody-fruited Proteaceae are dynamically co-occurring?

Concluding remarks

The foregoing review reveals an enormous range of interesting features of the Proteaceae of the Sydney region. It also identifies a large number of questions about ecological and evolutionary processes that are at the cutting edge of our current knowledge. The diversity of taxa of Proteaceae, the range of habitat, soil and climatic zones they occupy, the variety (even among populations within species) of life-histories, fire responses, floral morphologies, pollinator types and breeding systems combine to make this family in the region a rich 'test bed' for many of these questions.

Proteaceae of the Sydney region increase in diversity and abundance inversely with fertility of habitats, as seems to be the case in south-western Australia (Lamont 1981). Much of the work done on the ecology of Proteaceae from infertile habitats in south-western Australia and in the Sydney region appears to produce comparable findings. It remains to be shown whether there are differences in them that can be related to differences in climate between the two regions. Work done on Proteaceae in the Sydney region has contributed particularly strongly to understanding of fire effects on populations of Proteaceae from infertile habitats and understanding breeding systems in them.

In the wider context of Australia, there is a need to achieve a more balanced understanding of the ecology of the Proteaceae. Little is known of the ecology of the Proteaceae that are endemic to the rainforests of north-eastern Queensland, and indeed of rainforest Proteaceae in general, including in the Sydney region. Similarly, little appears to be known of the ecology of the Tasmanian endemic genera *Agastachys*, *Cenarrhenes* and alpine *Bellendena*, or of alpine Proteaceae in general. Also, in the wide-ranging and diverse genera of *Hakea* and especially *Grevillea*, there is a scope for understanding whether particular characteristics change across the species with types of habitat they inhabit. In such a search for relationships between variation in habitat and plant characteristics in these genera, and indeed more widely in the family as a whole, the scheme of Westoby (1998) may be useful. In its use of leaf specific area, height of plant and seed mass, it might yield very different patterns of variation with variation in habitat in the Proteaceae than in the Myrtaceae. The Proteaceae tend to have sclerophyllous leaves in rainforest (Johnson & Briggs 1975) and, in the Proteaceae, seed mass appears not to reach such low levels as in some Myrtaceae and, within a given habitat, to have strong phylogenetic restraints (cf. small achenes of *Conospermum* with large seeds of some species of *Banksia* or *Grevillea*). It is clear that, in the ecology of Proteaceae, much remains to be understood both at the detailed level of demography or, more broadly, in terms of comparative investigation of plant characteristics and habitats across the whole of Australia.

Questions for research:

1. Have the Proteaceae of the rainforests of the Queensland moist tropics features not shared by other Australian Proteaceae?
2. Similarly, have Tasmanian Proteaceae endemics unique ecological characteristics?
3. In the wide-ranging genera *Grevillea* and *Hakea*, are there characteristics that change consistently across the species along gradients of fertility or moisture?
4. What patterns are apparent in the Proteaceae when the scheme of Westoby (1998) is applied to characteristics across habitats and species in the family?

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