Ecology of the Fabaceae in the Sydney region: fire, ants and the soil seedbank

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Abstract

Auld, Tony D. (NSW National Parks and Wildlife Service, PO Box 1967 NSW 2220 Australia) 1996. Ecology of the Fabaceae in the Sydney region: fire, ants and the soil seedbank. Cunninghamia *4(4): 531–551.* Some 230 native species (in 33 genera) occur in the Fabaceae in the Sydney region, south eastern Australia. This represents about 10% of the native vascular plant flora of the region. These plants reach their greatest diversity in heaths, woodlands and dry forests on sandstone soils. Twenty-five species in the region are rare or threatened at the state or national level, including 15 local endemic species. Several introduced species, including *Acacia* species native to other parts of Australia, pose serious threats as environmental weeds.

Fire is the most widespread disturbance affecting the Fabaceae in the Sydney region and a mixture of fire-sensitive and resprouting species occur, although details of how species vary in their response to different fires is lacking. Most species flower in winter to spring with seeds released in October to December. There is a high level of seed dormancy. Initial seed dispersal varies from passive to explosive, while secondary seed dispersal is primarily by ants, although distances seeds are dispersed are generally less than 10 metres. A few species are likely to be dispersed by other animals such as birds. Members of the Fabaceae are likely to have persistent soil seedbanks with germination linked to fire. Heating of the soil during the passage of a fire is the primary mechanism for breaking seed dormancy and allowing germination. Effective management of plant communities containing legumes needs to allow sufficient times between fires for seedlings to flower and replenish the soil seedbanks, as well as for juveniles of resprouting species to become fire-resistant. In addition, sufficient soil heating is needed during fires to break seed dormancy and allow germination after fires.

Introduction

In this paper I treat the Fabaceae in the broad sense (Polhill et al. 1981), including the subfamilies Mimosoideae, Caesalpinioideae and Papilionoideae (Faboideae) and define the Sydney region as the Central Coast and Central Tableland botanical divisions (cf. Benson & McDougall pages 553–746). Species within the Fabaceae are a significant element of the flora of the Sydney region both in terms of the number of species and the contribution of these species to structure and functioning of

vegetation communities within the region. There are some 230 currently recognised native species (in 33 genera) in the Fabaceae in the Sydney region, representing about 10% of the vascular plant flora. Prominent and widespread genera include *Acacia* (86 species), *Bossiaea* (13 species), *Daviesia* (10 species), *Dillwynia* (13 species), *Gompholobium* (9 species) and *Pultenaea* (32 species). While rarely being a major structural canopy dominant, members of the Fabaceae occur in all major vegetation types in the region, from rainforest to dry heathlands. The family is most abundant and dominant as a significant component of the understorey vegetation in heaths, woodlands and dry sclerophyll forests, with floristic diversity in the family being greatest on the Hawkesbury and Narrabeen sandstones. In contrast, few species occur in rainforests in the Sydney region, although a number are associated with rainforest margins.

In trying to assess the ecology of a diverse array of species such as the Fabaceae, it is important to understand the dynamics of the species involved in relation to any major disturbance regimes that may operate in the region. In this paper, I look at how members of the Fabaceae are able to persist within plant communities in the Sydney region under a regime of repeated fires, as fire is the major disturbance influencing these communities. While other disturbances may play a role in certain vegetation communities (e.g. flooding in littoral communities or swamps, or the formation of canopy gaps in rainforests), the impact of fire occurs in all plant communities, including rainforests.

The distribution of plant communities in the Sydney region is controlled by a range of factors (edaphic, climatic, biotic, disturbance regimes etc.) and the distribution of individual species within the Fabaceae is clearly influenced by these factors. As well, species of the Fabaceae play an important role in community dynamics, e.g. vegetation structure, nitrogen fixing, sources of nectar and pollen etc. Here I wish to focus on the patterns within the Fabaceae that influence their ability to persist at a particular site or within a particular plant community. This involves an understanding of the dynamic processes within the life cycle of species from flowering and seed production through seed dispersal, the seedbank, germination and establishment. It is from an understanding of the patterns across species in relation to the maintenance of life cycle processes that insights can be gained into how best to manage species and the plant communities they inhabit, under the prevailing disturbance regimes, e.g. fire. In this paper, I will look at what is known about the ecology of Fabaceae species in the Sydney region and how we can apply this information to management of these species, stressing further work that is needed so that management effectively promotes the conservation of all members of the Fabaceae. In addition, I consider species that are rare or threatened nationally or of local conservation significance and some of the weedy members of the Fabaceae (non native and non local species) and the potential problem they present to maintaining natural communities. Nomenclature follows Harden (1991).

Fire response

Using the system of Gill (1981) members of the Fabaceae can be divided into different functional groups in terms of how they cope with fire. There have been several reports of the fire responses of Fabaceae in the Sydney region and others from outside the region that include species whose distribution extends into the region. The former provide a record of local fire response while the latter may give some indication of the likely fire response within the region.

In the simplest terms, the fire response of Fabaceae species covers both fire sensitive species with a soil-stored seedbank, and species resprouting via root suckers or basal sprouts that also possess a soil-stored seedbank (Table 1). Both strategies exist side by side in a range of species within the one plant community. Roughly half the Fabaceae genera are predominately fire sensitive (e.g. *Dillwynia, Pultenaea*), with the remainder able to resprout (e.g. *Bossiaea, Daviesia*), although within most genera species with either strategy may be found. *Acacia, Gompholobium* and *Mirbelia* contain a mixture of fire-sensitive and resprouting species. Within legume genera such a pattern of variation in fire response also occurs in the fire-prone fynbos of South Africa (Schutte et al. 1995). Variation in fire response often occurs within the one species, e.g. *Acacia floribunda, A. oxycedrus, A. parramattensis, A. terminalis, A. ulicifolia, Bossiaea obcordata, B. scolopendria, Gompholobium* species (pers. observ.; Auld & O'Connell 1991; Benson & McDougall pages 553–746). These species may be killed by fires in some situations but not others. The response of any one species may be variable across its distribution in response to:

  a) **variation in components of the fire itself.** The resprouting ability in a species will be influenced by the amount of heating that the resprouting organ or its dormant buds receive (Gill 1981);

  b) **the interaction between plant size** (or at least the size of the potential resprouting organ), **depth of burial of the resprouting organ and the heat output of the particular fire.** Morrison (1995) has shown that the size of the stem may influence survival after a low intensity fire in the legumes *Acacia binervia* and *Jacksonia scoparia* and the non legumes *Casuarina littoralis* and *C. torulosa*. For non legumes resprouting from lignotubers, Bradstock (1990) found that the size of the lignotuber affects plant survival in a fire, while Auld (1990) found that both the size and depth of burial of the lignotuber were important for survival during a fire.

  c) **the genetic variation within a species.** Some forms of a species may have evolved different responses to others. For example, *Pultenaea elliptica* appears to have distinct ecological taxa which show different fire responses.

  d) **variation in particular site characteristics.** Deep sand at a site for example, may insulate the base of the stem from lethal fire heating, allowing it to survive and hence regrow after fire in a species that is otherwise fire-sensitive.

The interpretation of reported variation in fire response in any species must be made in the light of the above four factors.

Table 1. Simplified fire response of Fabaceae genera in the Sydney region

Data based on personal observations, data from the National Fire Response Registrar (Gill & Bradstock 1992, Gill unpubl.), Auld & O'Connell (1991), Benson & McDougall (pages 553–746), and Morrison (1995).

Genus	Fire response[1]
Acacia	a mixture of FS and R (a few species show a variable response, e.g. *Acacia oxycedrus, A. parramattensis, A. terminalis, A. ulicifolia*)
Almaleea	**FS**
Aotus	**R** (occasionally FS outside Sydney)
Bossiaea	**R** (a few species show a variable FS/R response)
Daviesia	**R** (occasionally FS)
Desmodium	**R** (occasionally FS outside Sydney)
Dillwynia	**FS** (occasionally R in some species, e.g. *Dillwynia glaberrima, Dillwynia stipulifera*)
Glycine	**R** (occasionally FS outside Sydney)
Gompholobium	a mixture of R and FS and species showing both responses
Hardenbergia	**R** (occasionally FS or variable)
Hovea	**R** (occasionally FS)
Indigofera	**R** (occasionally FS)
Jacksonia	**R**
Kennedia	a mixture of R and FS
Mirbelia	a mixture of R and FS and species showing both responses
Oxylobium	**R** with some species variable FS/R
Phyllota	**R** with some species variable FS/R
Platylobium	**R** (occasionally FS)
Pultenaea	**FS** with a few species R (e.g. *Pultenaea divaricata*) or variable (e.g. *Pultenaea elliptica*)
Sphaerolobium	**FS**
Viminaria	**FS**

[1] **FS:** fire sensitive with a soil seedbank; **R:** resprouting via root suckers or basal sprouts and with a soil seedbank.

Questions for research:

1) Quantify the fire responses of all species.

2) For resprouters, quantify the proportion of individuals that resprout after a range of fires in relation to components of fire intensity and season as well as the size structure of the populations.

3) Examine the variability in fire response in species across different sites.

Flowering and seed production

Patterns of flowering in legumes in the Sydney region have been well documented. Most species flower in winter (wattles) to spring (peas) (Price 1963; Benson & McDougall pages 553–746), with the timing of flowering varying slightly from year to year depending on environmental conditions and location within the Sydney region. Fruiting usually follows flowering by several months with many species maturing fruits in October to December (Auld 1983). There is a trend for flowering and fruiting to be earlier in the north of the region and later in the far south and west. Most seed release occurs in October to December even for those species that flower early in the year, such as the wattles *Acacia linifolia* and *Acacia terminalis* (Auld 1983). This implies that seed and fruit development times will be different in different species, especially within the acacias which appear to show the most variation. Other species flower at different times of the year, e.g. *Acacia elata, Acacia longissima, Acacia parramattensis* and some *Senna* species flower in summer (Price 1963; Benson & McDougall pages 553–746). Some species may fruit outside the normal October to December period, e.g. *Pultenaea elliptica* flowers in summer and fruits in April to July (Auld 1983). However, though the timing of flowering and fruiting is reasonably well known, there has been little quantification of the magnitude of fruiting in legumes in relation to plant age or size. For *Acacia suaveolens,* the magnitude of fruiting is greatest in the first few years post-fire and then declines markedly (Auld & Myerscough 1986). We have little understanding of the patterns in other species and this limits our ability to understand how quickly species replenish their soil seedbanks after fire.

Numerous insects are associated with legumes during flowering and fruiting. Some like native and introduced bees, wasps, beetles and flies are potential pollinators (Armstrong 1979; Clifford & Drake 1981; Bernhardt 1987; Morrison 1987; Gross 1992) while others are phytophagous feeders, stem miners, gall formers or seed predators in developing fruits and include Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera. The impact of the introduced honey bee, *Apis mellifera*, on pollination and subsequent seed production is unknown. While native bees are known to pollinate legumes (Gross 1992) and to collect pollen from *Acacia* species (Bernhardt 1987), whether these native species are impacted on by honey bees remains unclear (Sugden & Pyke 1991). New (1984) has summarised the relationships between a range of insects and *Acacia* species. Many wattles have generalist pollinators, including birds in a few species (Knox et al. 1985) and *Acacia* species can vary from highly self-incompatible (Bernhardt et al. 1984; Kenrick & Knox 1989) to a mixture of out-crossing and self compatibility (Morrison & Myerscough 1989). There is also evidence of self-incompatibility in the peas *Dillwynia* and *Pultenaea* (Gross 1990). However, little of this work was done in the Sydney region and there is much scope for more work on breeding systems of Sydney legumes.

The relationship between predispersal seed predators and legumes has been explored in some detail (Auld 1983, 1986a, 1991). Certain beetle seed predators appear to be totally dependent on legumes for their persistence, e.g. *Melanterius* on *Acacia, Plaesiorhinus* on *Bossiaea* and *Bruchidius* on several genera *(Dillwynia, Mirbelia, Oxylobium, Pultenaea, Swainsona* and *Senna).* Recent work on seed predators of some non leguminous species (Auld unpubl.) supports the notion that these insect genera

are confined to legumes. For other insect seed predators, there are a wide range of potential legume and non legume hosts, e.g. the wasp *Eurytoma*, although host-specific relationships have yet to be studied. These seed predators play a role in reducing the annual seed-crops of legume species and after fire they may influence the rate at which the soil seedbank is replenished. Auld and O'Connell (1989) found that for *Acacia elongata*, most of the fruits produced in the first flowering season after a fire were destroyed by weevil seed predators. This implies that the replenishment of the soil seedbank is delayed and longer intervals between fires may be required than are inferred by simply noting time to first flowering after fire. In contrast, for *Sphaerolobium vimineum*, the first post-fire seed-crop escaped seed predation implying a rapid replenishment of the soil seedbank. Thus, the impact of seed predators may vary greatly between species and in relation to the fire regime. As well, these patterns may vary across different sites and different fires.

Questions for research:

1) What is the magnitude of fruiting in relation to times since fire, plant age and plant size for a range of species?

2) What are the breeding systems of Sydney Fabaceae?

3) What is the impact of feral bees on the magnitude of fecundity in legume species, choosing both small and large flowered species?

4) What role do predispersal seed predators play in limiting the replenishment of soil seedbanks after fire and hence, in influencing the minimum fire free intervals between fires recommended for management of natural communities?

5) How do the effects of predation vary between different sites and fires?

Seed dormancy

The Fabaceae generally have hard dormant seeds, with an impermeable testa preventing the uptake of water and hence ensuring seed dormancy. The seeds dry out during ripening, with the testa becoming impermeable to water below a certain moisture content (around 10–15%) (Quinlivan 1971; Tran & Cavanagh 1984; van Staaden et al. 1989).

For 35 species in 15 genera in the Fabaceae of the Sydney region, Auld and O'Connell (1991) and Morrison et al. (1992) examined the dormancy of seeds at release and after 3.5 years of storage. Three types of seed dormancy patterns were found:

a) most species had high 90–100% dormancy levels (Acacieae and Mirbelieae);

b) some species showed moderately high dormancy levels (generally between 64–90%) (Mirbelieae);

c) a few species had high dormancy levels at release but dormancy declined after 3.5 years (Bossiaeeae and Phaseoleae), suggesting a possible change in dormancy as seeds age.

Morrison et al. (1992) attributed these differences between species to seed size (high seed dormancy occurs in large seeded species) and where differences were found

across time, this reflected a difference in seed testa construction. Variation in dormancy within species over space and fruiting seasons has been little examined, although one species, *Acacia suaveolens*, showed consistently high seed dormancy levels (92–99%) over several sites and years (Auld 1986b). Tozer (1996) has shown that the dormancy levels in *Acacia saligna* (a species from south western Western Australia and now naturalised in Sydney) is controlled by the lowest relative humidity experienced during ripening. At maturation, seeds of *Acacia saligna* in Sydney generally have lower dormancy levels than those in their native habitat near Perth and this has consequences for the invasive potential of this species.

Questions for research:

1) Examine variation in seed dormancy across space and time for species.

2) Examine the impact of variation in dormancy and change in dormancy with time on maintenance of soil seedbanks.

Dispersal

Within the Fabaceae, initial seed release from the parent may be passive, ballistic or explosive (Berg 1975). In some legume species, seeds may be ejected a small distance from the fruits. The species involved generally have pods that twist spirally upon dehiscence (Berg 1975, 1979; pers observ.). Species known to have such a release mechanism include species of *Acacia* (e.g. *Acacia myrtifolia*), *Daviesia, Kennedia* and *Hardenbergia*. Other species such as *Dillwynia* and *Pultenaea* have fruits which may eject seeds short distances upon dehiscence (Berg 1975). Other species have a passive release mechanism. Irrespective of the dehiscence mechanism, primary seed dispersal is short (generally 0–2 m).

In seeds of Sydney Fabaceae, the connection between the seed and the parent fruit tissue frequently expands during late seed ripening to produce an aril. This lipid body is attractive to ants and where ants move such seeds (myrmecochory) the aril is referred to as an elaiosome. Work by Berg (1975) and Rice and Westoby (1981) has shown that myrmecochory is widespread in the flora of south eastern Australia and in the Fabaceae *(Acacia, Aotus, Bossiaea, Daviesia, Dillwynia, Gompholobium, Goodia, Hardenbergia, Hovea, Kennedia, Mirbelia, Phyllota, Platylobium, Pultenaea)*. Other non legumes also have seeds dispersed by ants so that heathlands and related shrub dominated vegetation communities have a high percentage of myrmechochores (Berg 1975). Within the genera listed above, Rice and Westoby (1981) found some species that showed no evidence of myrmecochory or uncertain evidence. In some cases this may be in response to a virtual lack of development of the aril *(Acacia ulicifolia)* or simply because no seed movement by ants was detected in the sampling regime *(Aotus ericoides)*. It is possible that species with no development of the aril are not moved by ants, e.g. *Canavalia rosea, Glycine clandestina, Jacksonia scoparia* and *Sphaerolobium vimineum* (cf. Berg 1975; Rice & Westoby 1981), but this remains to be experimentally verified.

Whilst the movement of seeds by ants is not in doubt, the role ants play in the dynamics of the plant species involved remains in question. A number of roles for ant

dispersal of seeds have been postulated (Table 2). Some of these appear to be unimportant for Sydney legumes, e.g. seed escape from predators (although this may be important in other genera, e.g. *Grevillea*, Auld & Denham unpubl.) and avoidance of competition between seedlings and parents in fire-sensitive species. Others are likely to be important in Sydney, e.g. dispersal distance and burial in safe sites (Hughes & Westoby 1992). However, not all movement of seeds by ants is beneficial to plants. Some ant species consume much of the seed they move (Hughes & Westoby 1992) while other seeds may be buried in 'unsafe' sites (Auld 1986c) and are effectively lost from the soil seedbank. Clearly further testing of the ideas in Table 2 is warranted.

Seed dispersal by ants is not the only secondary dispersal mechanism for legumes in the Sydney region; it is simply the most widespread and best documented. Some legumes may be dispersed by mammals (*Desmodium* species, McIntyre et al. 1995) as the seeds may adhere to hair. Other species may be dispersed by both birds and ants, with the birds being attracted to arils while the seeds are in ripe open fruits in the parent canopy. These birds only consume the aril and either the seed is discarded or is regurgitated or passed through the gut intact (O'Dowd & Gill 1986). Bird dispersal of *Acacia* seeds occurs in arid Australia (Davidson & Morton 1984) and may also occur in local species such as *Acacia melanoxylon, Acacia longifolia, Acacia prominens* and *A. sophore* (Forde 1986; O'Dowd & Gill 1986; French 1991). This implies that long distance dispersal in Fabaceae in the Sydney region may be limited to a few *Acacia* species (and generally moist eucalypt forest and rainforest habitats) and perhaps *Desmodium*. Where the family is most diverse, in heaths, woodlands and dry forests dispersal is likely to be by ants and be limited to a distance of a few metres.

Can the distribution of the Fabaceae be explained by this pattern of dispersal, and if so, what are the consequences for fragmentation of the landscape when dispersal distances are so limited in most species? I suggest that occasional long distance dispersal events may have been important in accounting for the current distribution of Fabaceae in Sydney and beyond, and that a likely agent for such dispersal is the emu *(Dromaius novaehollandiae)*. Emus are known to eat a wide range of plant material, including seeds and fruits and to disperse a range of species in arid and semi-arid Australia (Davies 1978; Noble 1991; pers. observ.) and south western Australia (Keighery 1996). They were also found in the Sydney region but are now extinct in much of the area and it may be that with the loss of emus there has been the loss of the major long-distance dispersal agent for a number of plant species, including possibly the Fabaceae. The consequences of this are that once plant communities become fragmented by urban and rural development, the effective ability of most plant species to disperse between patches is gone and once a species is lost from a patch, no recovery is likely.

Questions for research:

1) Are all legumes, especially those with no aril development such as *Canavalia, Glycine, Jacksonia* and *Sphaerolobium,* myrmecochorous?

2) Test models on the role of ant dispersal of seeds on plant dynamics (see Table 2).

Table 2. Postulated roles for ant dispersal of seeds with elaiosomes.

Role	Evidence in Fabaceae in Sydney region
Seed escape from predators e.g. rodents	Unlikely, seed losses to predators after initial seed fall are low (3–4%, Auld 1986c, Hughes & Westoby 1990), but some ants may consume seeds (see below).
Distance dispersal	Ants only move seeds small distances (usually < 2 m, Hughes & Westoby 1992), but they can move seeds away from parent canopies.
Avoid competition between seedlings and parents	i) For fire-sensitive plants, parents are killed and there is no such competition.
	ii) for resprouting plants this needs to be examined.
Burial in safe or favourable sites, including:	
a) Protection of seeds from fire and high summer temperatures by burial	i) Lethal fire temperatures may occur near the soil surface (0–2 cm) and ants must move seeds deeper than this to be effective. This certainly occurs in Sydney legumes (Auld 1986c, Hughes & Westoby 1992) but will vary between ant species (Hughes & Westoby 1992).
	ii) Some seeds are buried too deeply by ants to either successfully reach the soil surface or to have their dormancy broken by soil heating in fires (Auld 1986c, Hughes & Westoby 1992).
	iii) some ants consume the elaiosome then discard the seeds on the surface so that burial may not occur (Hughes & Westoby 1992).
	iv) some ant species consume most of the seeds removed, although some seeds may remain intact in soil chambers (Hughes & Westoby 1992).
b) favourable microhabitat for germination and establishment	i) No evidence for this in Sydney (Rice & Westoby 1986) but this can occur in other habitats (Davidson & Morton 1981).
	ii) Increased seedling competition may result from ant dispersal where seedlings emerge in clumps (Culver & Beattie 1980, Davidson & Morton 1981), but this needs to be examined in a Sydney context.
Increased germination rates in nests or discard piles via aril removal by ants	No evidence in legumes with hard, dormant seeds.

Seedbank dynamics

Wattles and peas are generally thought to have long-lived persistent seedbanks. In the Sydney region, high levels of seed dormancy at seed release (Auld & O'Connell 1991) imply that long-lived persistent seedbanks should be common. The difficult nature of sampling soil seedbanks, especially in species with high levels of seed dormancy and small-seeded species, has led to few comprehensive studies of soil seedbanks in the Sydney region. For the Fabaceae, most work has been on the common shrub *Acacia suaveolens*, for which a model of the dynamics of the soil seedbank has been developed (Auld 1986c, 1987). Essentially, in this fire-sensitive shrub, post-fire inputs of seeds to the soil seedbank are high after two years as the

plants are relatively quick to mature. The seedbank reaches a maximum some 10 years after a fire, after which it declines in response to seed decay in the soil, adult mortality and a decline in adult fecundity. A seedbank of sufficient size to replace the population would remain in the soil well beyond the loss of all plants above ground and beyond the likely maximum fire frequency interval in the habitats in which it occurs. *Acacia suaveolens* is characterised by high seed dormancy, high levels of plant fecundity in 2–5 year old plants, low levels of seed decay in the soil and short adult life spans (half life of 3.65 years, Auld 1987). Other legume species are likely to have different seedbank accumulation curves in response to different life history parameters. The important points to determine are the size of the soil seedbank in relation to the time between fires and the amount of seed that is stimulated to germinate in each fire.

Question for research:

1) Develop models of the seedbank for species other than *Acacia suaveolens*.

Germination and establishment

In fire-prone habitats fire is the major stimulus to breaking seed dormancy and allowing subsequent seed germination. In Sydney, recruitment is generally limited to the immediate post-fire period (Auld 1986d; Auld & Tozer 1995) as occurs elsewhere (Weiss 1984; Tyler 1995). Auld (1986d) and Auld and O'Connell (1991) have demonstrated that dry heat is capable of breaking seed dormancy in legumes in the Sydney region, a pattern common to legumes in fire-prone communities throughout the world (Martin et al. 1975; Floyd 1976; Jeffery et al. 1988; Keeley 1991). Auld and O'Connell (1991) found that species fell into classes according to whether dormancy was broken by a temperature of 40, 60 or 80°C, although they did not look at finer temperature intervals. Auld (1986d) working on *Acacia suaveolens* over a range of heating intervals of 5 or 10°C, found there was some gradual increment in the levels of dormancy broken when seeds were exposed to temperatures between 40 and 60°C. In these and other comparable studies (e.g. Floyd 1966,1976), duration of heating had little impact on the level of seed dormancy broken, except where temperatures became lethal to seeds. Generally, temperatures of 120°C are lethal to legume seeds except for very short (1 minute) durations.

Soil temperatures under fires in the Hawkesbury Sandstone soils around Sydney have been examined by Auld (1986d) and Bradstock and Auld (1995). They found that lethal soil temperatures for seeds are likely to be confined to near the surface (0–1 cm or 0–2 cm). Below this zone there is a zone of soil heating that should break seed dormancy in legumes and below this, soil heating should be insufficient to break seed dormancy. The actual amount of heating in the soil is controlled by the amount of fine fuel consumed by the fire (Bradstock & Auld 1995). Thus, legume seeds should be stimulated to germinate by the passage of the fire (as demonstrated by Auld & Tozer 1995) and germination after a fire should be from seeds within a narrow band of soil depths. This pattern is clearly shown in distributions of emerging seedlings post-fire in *Acacia suaveolens* (Auld 1986d; Bradstock & Auld 1995). Tyler (1995) has suggested that post-fire recruitment will also be influenced by the season of burn, rainfall prior to the burn and the distribution of fuel prior to the burn.

While the role of soil heating during the passage of a fire in breaking seed dormancy is now well documented, the impact of other fire-related cues is less well known. During a fire, there may be a number of dormancy breaking cues apart from heat, including:

> **a) leachates from charred wood**. This has been shown to occur in the chaparral of California (Keeley 1991) and south western WA (Bell et al. 1987).

> **b) smoke**, as shown in the South African fynbos (Brown 1993) and south western WA (Dixon et al. 1995).

> **c) nitrates**, (Thanos & Rundel 1995, working in Californian chaparral);

> **d) another unknown fire cue**. Many species in fire-prone communities have abundant seedling recruitment only after a fire but the fire related cue to germination remains to be determined (cf. Keeley 1991).

> **e) an interaction of any of the above factors.** The obvious extension of the above, as all factors will operate together during the passage of a fire. This is currently unexplored.

As well there is likely to be an interaction of season and temperature (Bellairs & Bell 1990; Bell & Bellairs 1992), with different responses expected after fires in different seasons. Whilst these mechanisms are thought to operate on species other than legumes, the possible interaction between heat and these and other potential germination cues during the passage of a fire remains to be investigated.

Questions for research:

1) Do fire-related cues apart from heat break seed dormancy in legumes?

2) Is there an interaction between heat and other dormancy breaking cues?

Conservation status

The Sydney region contains a number of local endemic Fabaceae (25 species or varieties). A high proportion of these (64%) are nationally threatened or rare as are several other species not confined to the area (Table 3). Such species are threatened primarily by habitat loss as a result of urban and rural development. This habitat loss continues today, but even where intact bushland remains there are a number of threats to the survival of threatened plants and the communities they inhabit. These threats include weed invasion, nutrient enrichment, disturbance via rubbish dumping, vehicle use, and a failure to implement the appropriate fire regime required by species, in particular the impact of a regime of high fire frequency (see below). Not only rare or threatened species are affected by these threats but several species more common outside Sydney are now either extinct or severely reduced in distribution in the Sydney area (Table 3). Other species are of conservation significance as they are at the limit of their geographical range or they represent disjunct populations of a wider distribution (Table 3). There are also restricted habitats in Sydney, such as windswept coastal headlands. These headlands contain prostrate forms of many taxa including the legumes *Acacia myrtifolia, Acacia suaveolens* (Auld & Morrison 1992), *Dillwynia retorta* and *Viminaria juncea*. Protecting and managing populations of such species will assist in the conservation of genetic diversity at the species level and below.

Question for research:

1) Determine the management requirements for the long-term conservation of rare
   and threatened species of Fabaceae.

**Table 3. Fabaceae of conservation significance in Sydney region. Local endemic
species are marked with an [E].**

State or nationally threatened (TSC Act [1], ROTAP [2])

ENDANGERED:

Pultenaea parrisiae subsp. *elusa*
Pultenaea parviflora [E]
Senna acclinis

VULNERABLE:

Acacia baueri subsp. *aspera* [E]	*Dillwynia tenuifolia*
Acacia bynoeana [E]	*Kennedia retrorsa*
Acacia clunies-rossiae [E]	*Phyllota humifusa* [E]
Acacia flocktoniae [E]	*Pultenaea aristata* [E]
Acacia pubescens	*Pultenaea glabra* [E]
Bossiaea oligosperma [E]	

Nationally rare (ROTAP [2])

Acacia asparagoides [E]	*Acacia meiantha* [E]
Acacia bulgaensis	*Acacia subtilinervis*
Acacia chalkeri [E]	*Almaleea incurvata* [E]
Acacia fulva	*Dillwynia stipulifera* [E]
Acacia jonesii	*Pultenaea villifera*
Acacia matthewii [E]	

Poorly known (ROTAP [2])

Acacia gordonii [E]

Possibly extinct in Sydney region (extant elsewhere) [3]

Aotus subglauca var. *filiformis*
Gompholobium virgatum var. *virgatum*
Neptunia gracilis
Pultenaea pedunculata
Senna clavigera
Swainsona sericea

Rare or declining in Sydney region [3]

Acacia amblygona	*Lepedeza juncea* var. *sericea*
Acacia caesilla	*Mirbelia baueri*
Acacia cheelii	*Mirbelia oxyloboides*
Acacia mollifolia	*Mirbelia platyloboides*
Acacia quadrilateris	*Mirbelia pungens*
Acacia tindaleae	*Oxylobium cordifolium*
Bossiaea bracteosa	*Oxylobium aciculiferum*
Canavalia rosea	*Pultenaea altissima*
Chorizema parviflorum	*Pultenaea dentata*
Daviesia umbellata	*Pultenaea lapidosa*
Dillwynia juniperina	*Senna barclayana*
Dillwynia parvifolia	*Swainsona monticola*
Gompholobium virgatum var. *aspalathoides*	*Swainsona reticulata*
Hovea beckeri	*Zornia dyctiocarpa* var. *dyctiocarpa*

Table 3. (continued)

Local endemics (not rare or threatened)

Acacia dorathea [E]	*Phyllota grandiflora* [E]
Acacia ptychoclada [E]	*Pultenaea canescens* [E]
Acacia trinervata [E]	*Pultenaea echinula* [E]
Bossiaea lenticularis [E]	*Pultenaea ferruginea* var. *deanei* [E]
Dillwynia floribunda var. *teretifolia* [E]	

Disjunct distributions

Acacia fulva
Pultenaea pedunculata

Southern limit in Sydney region

Acacia baueri subsp. *baueri*	*Bossiaea stephensonii*
Acacia diphylla	*Chorizema parviflorum*
Acacia echinula	*Daviesia umbellata*
Acacia elata	*Gompholobium virgatum* var. *virgatum*
Acacia fulva	*Gompholobium uncinatum*
Acacia quadrilateris	*Hovea acutifolia*
Acacia prominens	*Neptunia gracilis*
Acacia pubescens	*Mirbelia speciosa* subsp. *speciosa*
Acacia saliciformis	*Oxylobium pulteneae*
Acacia schinoides	*Pultenaea euchila*
Aotus subglauca var. *filiformis*	*Pultenaea subternata*
Bossiaea neo-anglica	

Northern limit in Sydney region

Acacia hamiltoniana	*Dillwynia stipulifera*
Acacia jonesii	*Gompholobium grandiflorum*
Acacia kybeanensis	*Mirbelia baueri*
Acacia leprosa	*Mirbelia platyloboides*
Acacia mearnsii	*Phyllota squarrosa*
Acacia obtusata	*Pultenaea capitellata*
Acacia oxycedrus	*Pultenaea ferruginea* var. *ferruginea*
Bossiaea bracteosa	*Pultenaea hispidula*
Bossiaea foliosa	*Pultenaea laxiflora*
Bossiaea kiamensis	*Pultenaea pedunculata*
Bossiaea scolopendria	*Pultenaea rosmariniifolia*
Dillwynia brunioides	*Pultenaea villifera*
Dillwynia cinerasens	*Pultenaea viscosa*
Dillwynia parvifolia	

Species with known prostrate forms on exposed coastal headlands

Acacia myrtifolia
Acacia suaveolens
Dillwynia retorta
Viminaria juncea

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[1] NSW Threatened Species Conservation Act;
[2] Briggs & Leigh (1996);
[3] excludes species considered to be state or nationally rare or threatened (from Benson & McDougall pages 531–746).

Management of species in fire-prone habitats

In managing fire-prone habitats and the plant and animal species they contain it is important to remember that fires occur repeatedly at a particular place and we must understand how species interact with the fire regimes: fire frequency; fire intensity; fire season; and fire spatial extent.

Fire frequency

Fire frequency is the most important component of the fire regime in terms of the survival of plants and animals. All fires burn areas of vegetation that have been burnt some time before. Not only have there been different numbers of fires over time for different parts of the landscape but, in some places these fires have been many years apart, while in others there have been instances of two or three fires in close succession. How does this patchiness of fires through time affect the survival of legume plants and the communities they inhabit?

Those plants that are killed by fire, fire-sensitive plants, rely on seed germination after fires to survive at a particular location. For these plants there must be sufficient time between successive fires for seedlings to mature and produce more seeds and hence, add seeds to the seedbank. This time will vary between species, with some species like *Acacia suaveolens* flowering in the first two years after fire. Other species, such as *Dillwynia*, may take 3–5 years to reach maturity (Benson 1985; Keith 1991). If another fire should occur before these plants have matured, dramatic changes in the vegetation may occur. The patterns in legumes are typical of other co-habiting species, with values for time to first flowering in non-leguminous fire-sensitive species in Sydney ranging from 0.5–2 to 6–9 years (Benson 1985; Keith 1991). Fire-sensitive plants with woody capsules usually release all their seeds after a fire and no residual seeds remain in cones. These plants are the most susceptible group to two fires in short succession and can be eliminated locally by two fires occurring close enough together to kill any seedlings that emerged after the first fire before they were mature. Plants that have seeds stored in the soil (including legumes) usually are expected to have some residual seedbank remaining in the soil following post-fire germination. For these species, a second fire before seedlings mature will severely reduce the size of the population, but it may not eliminate species locally. The risk of local extinction will depend on how much of the soil seedbank emerges after any one fire. For *Acacia suaveolens* (Auld & Denham unpubl.), some 30–70% of the seedbank not killed by soil heating can emerge after a fire. Consequently, some residual seedbank is likely to remain, however, this residual may not be available to germinate in the next fire (e.g. it may be buried too deeply to be heated sufficiently to break seed dormancy). Thus, even for species with soil seedbanks two fires close enough together to eliminate seedlings before they mature should be avoided. Clearly more work in this area is needed.

Ideally, land managers with concerns for the conservation of biodiversity should allow the interval between fires to be long enough not only for new seedlings to mature, but at a minimum, several fruiting seasons beyond this so that a sufficiently large seedbank can be established before the next fire occurs. Morrison et al. (1995, 1996) and Cary and Morrison (1995) attempted to infer the impact of fire frequency

on changes in species presence and abundance at sites with different fire histories. They found that the abundance of *Bossiaea scolopendria* was positively correlated with the length of the inter-fire interval. *Acacia suaveolens*, a fire sensitive species with high fecundity levels soon after fire, was able to persist even at sites which had very short fire intervals. Other non-leguminous, slower growing and maturing species declined in such situations. Given the times to first flowering identified by Benson (1985) and Keith (1991) it is likely that most leguminous species would decline under a fire regime of high fire frequency, although more work is needed to investigate this scenario. Morrison et al. (1995) also found that for some species, including the legumes *Dillwynia retorta* and *Pultenaea elliptica,* above ground abundance declined with time since fire, indicating that the soil seedbank is an important reserve for legume species.

For resprouter plant species, those that are capable of surviving and regrowing after a fire, the level of plant mortality will vary between fires, but the more heat produced by a fire, a component of fire intensity, the greater mortality there will be amongst resprouting species and the more new plants that need to be recruited to maintain the population. The key for resprouting plants is that there must be sufficient time between some fires at any one place for seedlings to grow big enough to become fire-resistant. In legumes, becoming fire-resistant usually involves the underground development of a lignotuber or rootstock. How long does it take for the juveniles of resprouting plants to be large enough to survive the next fire? Based on non leguminous resprouting species, it would appear that it may take seedlings some 6–15 years to become big enough to survive a fire (Keith 1996). This would mean that even for resprouting plants we need to allow periods of about a decade without fire in order to allow all species to persist at a site. This may not be necessary after all fires, but it is essential after at least some fires. As well, these resprouting plants will need to replenish their soil seedbanks after fire. Keith (1991) found that *Aotus ericoides* could flower in three years after resprouting following a fire, while seedlings took greater than five years to mature. However, other comparable data are lacking and the rate of seed accumulation in the seedbank in such resprouting legume species remains unknown.

Fire intensity

How hot a fire is will depend on how much combustible fuel is available, how dry this fuel is, the topography of the area and the weather conditions, such as humidity and windspeed. In many areas around Sydney, the heat output of a fire usually varies markedly even on a very small scale (i.e. over tens of meters). Even though an area is burnt, the impact of the fire on plants may be very different in different parts of the burnt area depending on how hot the fire was.

Under intense fires there are likely to be more resprouting plants killed, and longer periods needed before the next fire for recovery, compared with mild fires. As well, the amount of soil heating controls the degree of post-fire germination in wattles, peas and other non legumes. In general the more fine ground fuel that is consumed in a fire, the more soil heating there is (Bradstock & Auld 1995). Seeds can be killed if they lie near the soil surface (0–2 cm deep) but prolific germination can occur from seeds buried deeper in the soil. To maintain legume species fire managers need to ensure that fires produce sufficient soil heating.

Fire season

Given the prevalence of arson and widespread hazard reduction burning for the protection of life and property, fires can now be expected to occur at just about any time of the year in the Sydney region. The question is, for the survival of plants does it matter when the vegetation is burnt? Bradstock and Bedward (1992) have shown that late summer/autumn fires should be most favourable for seedling survival, given that seedlings from these fires should encounter favourable moisture conditions for growth. However, as they noted, seasonal rainfall is very variable in Sydney, and this pattern is weak. Auld and Bradstock (1996) showed that soil heating in the weeks following a summer fire was sufficient to promote germination in some legumes (independent of the soil temperatures reached during the actual fire). But soil heating was not sufficient after a winter fire or at an unburnt site in summer to promote such an effect. Consequently, fire season may influence post-fire germination levels in legumes. However, we still have a lot to learn about how fire controls germination in many plant species and it may be that fire season is more important than we currently recognise.

Fire spatial extent

Fires come in all shapes and sizes. Some burn very extensive areas, while others may only burn a hectare or so. Within the boundaries of a burnt area, fires may be widespread and burn most of the vegetation or leave large parts of the vegetation unburnt or simply lightly scorched. Fires will be different, depending on the terrain, rate of fire spread, amount of fuel available and its moisture content, weather conditions and the presence of natural or man-made fire breaks. As well, fires burning at night will have different patterns to those burning during the day as conditions at night are frequently milder. This results in patchiness of fires in area and intensity.

For plants, the spatial extent of fires may be important where burns occur on a very small scale (a few hectares). In such cases, native animals from surrounding unburnt vegetation may graze heavily on the new green shoots that appear after fire, causing a decline in particular plant species (Whelan 1995). Native animals may also consume many of the seeds that are produced in the first few years after fire for those fire-sensitive plants that are trying to replenish their soil seedbanks (Auld & Denham unpubl.). This will slow the rate of recovery of such plants and lengthen the time needed between fires to maintain populations. The spatial extent of fires may also influence the survival of insect seed predators and subsequently the magnitude of post-fire seed-crops. While these general principles apply, the impact of the spatial extent of fires on legumes is currently unknown.

The spatial extent of fires is also important when we think about frequent fire. Areas burnt in the recent past often may act as a barrier to the passage of a fire since fuel is reduced in such areas. However, in extreme weather conditions even areas burnt 2–6 months previously may carry a fire and if this occurs it will lead to local declines or extinctions of fire-sensitive plant species. Sites in small burnt areas surrounded by large tracts of unburnt vegetation, are likely to have increased fire frequency because when future fires burn the unburnt large tracts they are likely to also burn over the small, previously burnt areas. Such an increase in fire frequency will have detrimental effects on plants and associated animals.

Questions for research:

1) More data are needed on the primary and secondary juvenile periods, and the time to fire resistance across a range of species, sites and seasons. This will allow an assessment of the resilience of species to frequent fire.

2) What is the level of residual seedbank in soil for legumes and other species after fire and its distribution in the soil profile?

3) What is the impact of intensity (or its components) on germination cues other than heat?

4) How does season of burn affect germination and seedling survival after fire?

5) What is the interaction between season of burn and the various fire-related germination cues?

6) What is the impact of patchiness within fires on germination levels?

7) How does fire size/patchiness interact with fire season and intensity in relation to seed germination and post-fire seed predation?

Weeds

Some 75 species of Fabaceae have been introduced into the Sydney region (Benson & McDougall pages 553–746). Many of these are garden escapees and currently do not appear to pose a threat to native vegetation communities. However, a number of species are either already serious environmental weeds or have the potential to become such. Noble (1989) has suggested that a species may become invasive if is capable of significantly increasing fecundity in the new habitat where it is introduced compared to its native habitat. This has certainly occurred in several species such as *Cytisus scoparius* (broom) and *Senna pendula* where seed predators and insects that attack developing flowers and buds are absent. The introduction of agents for biological control can attempt to redress this problem. The same potential exists for several native Australian species now introduced outside their natural range. In Sydney, this includes several *Acacia* species (e.g., *Acacia baileyana*, *Acacia podalyriifolia* and *Acacia saligna*) and *Paraserianthes lophantha*. All these species have the potential to become invasive in local communities, especially given their ability to form a large soil seedbank that will allow the species to persist through fires. The potential impact of such invasive species on natural communities may be catastrophic, leading to a significant loss in species diversity as the introduced species are tall shrubs or small trees which can competitively exclude much of the understorey. Tozer (1996), working on *Acacia saligna*, offers some hope in suggesting that while well equipped to dominate road verges, this species may be a poor invader of undisturbed communities. At any rate, control of the spread of weed species and factors leading to weed invasion, such as urban runoff resulting in nutrient enrichment, is urgently needed.

Questions for research:

1) What species are likely to become invasive in native communities? How do we identify such species?

2) What are the best methods of integrated control for weedy legume species?

Conclusions

Legumes are an important component of the flora of the Sydney region. We are some way to understanding how legumes survive in a fire-prone environment and management of legume species should be concerned with avoiding a regime of repeated high frequency fires or one where little soil heating occurs. At the same time, many aspects of the biology of legumes are poorly understood and this limits our effective management of these species. In particular we need to collect data on the fire response of species (across a range of locations), the nature and dynamics of soil seedbanks in relation to the fire regime and further examine if cues apart from heat play a role in influencing post-fire germination levels. Some attempt should be made to include a focus on rare or threatened taxa in habitats away from the Narrabeen and Hawkesbury Sandstones, where much previous research has been carried out.

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References

Armstrong, J.A. (1979) Biotic pollination mechanisms in the Australian flora — a review. *New Zealand Journal of Botany* 17: 467–508.

Auld, T.D. (1983) Seed predation in native legumes of south-eastern Australia. *Australian Journal of Ecology* 8: 367–376.

Auld, T.D. (1986a) Variation in predispersal seed predation in several Australian *Acacia* spp. *Oikos* 47: 319–326.

Auld, T.D. (1986b) Dormancy and viability in *Acacia suaveolens* (Sm.) Willd. *Australian Journal of Botany* 34: 463–472.

Auld, T.D. (1986c) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: dispersal and the dynamics of the soil seed bank. *Australian Journal of Ecology* 11: 235–254.

Auld, T.D. (1986d) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: fire and the transition to seedlings. *Australian Journal of Ecology* 11: 373–385.

Auld, T.D. (1987) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: survivorship throughout the life cycle, a synthesis. *Australian Journal of Ecology* 12: 139–151.

Auld, T.D. (1990) The survival of juvenile plants of the resprouting shrub *Angophora hispida* (Myrtaceae) after a simulated low-intensity fire. *Australian Journal of Botany* 38: 255–260.

Auld, T.D. (1991) Patterns of predispersal seed predators in the Fabaceae of the Sydney region, south-eastern Australia. *Australian Journal of Zoology* 39: 519–528.

Auld, T.D. & Bradstock, R.A. (1996) Soil temperatures after the passage of a fire: Do they influence the germination of buried seeds? *Australian Journal of Ecology* 21: 106–109.

Auld, T.D. & Morrison, D.A. (1992) Genetic determination of erect and prostrate growth habit in five shrubs from windswept headlands in the Sydney region. *Australian Journal of Botany* 40: 1–11.

Auld, T.D. & Myerscough, P.J. (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: seed production and predispersal seed predation. *Australian Journal of Ecology* 11: 219–234.

Auld, T.D. & O'Connell, M.A. (1989) Changes in predispersal seed predation levels after fire for two Australian legumes, *Acacia elongata* and *Sphaerolobium vimineum*. *Oikos* 54: 55–59.

Auld, T.D. & O'Connell, M.A. (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* 16: 53–70.

Auld, T.D. & Tozer, M. (1995) Patterns in emergence of *Acacia* and *Grevillea* seedlings after fire. *Proceedings of the Linnean Society of NSW* 115: 5–15.

Bell, D.T. & Bellairs, S.M. (1992) Effects of temperature on the germination of selected Australian native species used in the rehabilitation of bauxite mining disturbance in Western Australia. *Seed Science and Technology* 20: 47–55.

Bell, D.T., Vlahos, J. & Watson, L.E. (1987) Stimulation of seed germination of understorey species of the northern jarrah forest of Western Australia. *Australian Journal of Botany* 35: 593–599.

Bellairs, S.M. & Bell, D.T. (1990) Seed stores for restoration of species-rich shrubland vegetation following mining in Western Australia. *Restoration Ecology* December: 231–240.

Benson, D.H. (1985) Maturation periods for fire sensitive shrub species in Hawkesbury Sandstone vegetation. *Cunninghamia* 1: 339–349.

Benson, D.H. & McDougall, L. (1996) Ecology of Sydney plants: Part 4: Fabaceae. *Cunninghamia* 4(4) 553–746.

Berg, R.Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* 23: 475–508.

Berg, R.Y. (1979) Legume, seed, and myrmecochorous dispersal in *Kennedia* and *Hardenbergia* (Fabaceae), with a remark on the Durian theory. *Norwegian Journal of Botany* 26: 229–254.

Bernhardt, P. (1987) A comparison of the diversity, density, and foraging behaviour of bees and wasps on Australian *Acacia*. *Annals of the Missouri Botanic Gardens* 74: 42–50.

Bernhardt, P., Kenrick, J. & Knox, R.B. (1984) Pollination biology and the breeding system of *Acacia retinoides* (Leguminosae: Mimosoideae). *Annals of the Missouri Botanic Gardens* 71: 17–29.

Bradstock, R.A. (1990) Demography of woody plants in relation to fire: *Banksia serrata* Lf. and *Isopogon anemonifolius* (Salisb.) Knight. *Australian Journal of Ecology* 15: 117–132.

Bradstock, R.A. & Auld, T.D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity: Consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32: 76–84.

Bradstock, R.A. & Bedward, M. (1992) Simulation of the effect of season of fire on post-fire seedling emergence of two *Banksia* species based on long-term rainfall records. *Australian Journal of Botany* 40: 75–88.

Briggs, J.D. & Leigh, J.H. (1996) *Rare or threatened Australian plants.* 1995 revised edition. (CSIRO Publishing: Collingwood).

Brown, N.A.C. (1993) Promotion of germination of Fynbos seeds by plant-derived smoke. *New Phytologist* 123: 575–583.

Cary, G.J. & Morrison, D.A. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: combinations of inter-fire intervals. *Australian Journal of Ecology* 20: 418–426.

Clifford, H.T. & Drake, W.E. (1981) Pollination and dispersal in eastern Australian heathlands, in *Ecosystems of the World. Heathlands and related shrublands.* Analytical Studies (R.L. Specht Ed.) pp. 39–49 (Elsevier Scientific Publishing Co.: Amsterdam).

Culver, D.C. & Beattie, A.J. (1980) The fate of *Viola* seeds dispersed by ants. *American Journal of Botany* 67: 710–714.

Davidson, D.W. & Morton, S.R. (1981) Myrmecochory in some plants (F. Chenopodiaceae) of the Australian arid zone. *Oecologia* 50: 357–366.

Davidson, D.W. & Morton, S.R. (1984) Dispersal adaptations of some *Acacia* species in the Australian arid zone. Ecology 65: 1038–1051.

Davies, S.J.J.F. (1978) The food of emus. *Australian Journal of Ecology* 3: 411–422.

Dixon, K.W., Roche, S. & Pate, J.S. (1995) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101: 185–192.

Floyd, A.G. (1966) Effect of fire upon weed seeds in the wet sclerophyll forests of northern NSW. *Australian Journal of Botany* 14: 243–256.

Floyd, A.G. (1976) Effect of burning on regeneration from seeds in wet sclerophyll forest. *Australian Forestry* 39: 210–220.

Forde, N. (1986) Relationships between birds and fruits in temperate Australia, *in The dynamic partnership: birds and plants in southern Australia* (H.A. Ford & D.C. Paton Eds). pp. 42–58 (Government Printer: South Australia).

French, K. (1991) Characteristics and abundance of vertebrate-dispersed fruits in temperate wet sclerophyll forest in southeastern Australia. *Australian Journal of Ecology* 16: 1–13.

Gill, A.M. (1981) Adaptive responses of Australia vascular plant species to fires, in *Fire and the Australian biota* (A.M. Gill, R.H. Groves, & I.R. Noble Eds): pp. 243–72 (Australian Academy of Science: Canberra).

Gill, A.M. & Bradstock, R.A. (1992) A national register for the fire responses of plant species. *Cunninghamia* 2: 653–660.

Gross, C.L. (1990) The breeding systems of three co-occurring legumes: *Dillwynia hispida, D. uncinata* and *Pultenaea densifolia* (Leguminosae: Papilionoideae). *Australian Journal of Botany* 38: 207–215.

Gross, C.L. (1992) Floral traits and pollinator constancy: foraging by native bees among three sympatric legumes. *Australian Journal of Ecology* 17: 67–74.

Harden, G.J. (1991) *Flora of New South Wales Volume 2* (NSW University Press: Kensington).

Hughes, L. & Westoby, M. (1990) Removal rates of seeds adapted for dispersal by ants. *Ecology* 71: 138–148.

Hughes, L. & Westoby, M. (1992) Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* 73: 1285–1299.

Jeffery, D.J., Holmes, P.M. & Rebelo, A.G. (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *South African Journal of Botany* 54: 28–34.

Keeley, J.E. (1991) Seed germination and life history syndromes in the California chaparral. *The Botanical Review* 57: 81–116.

Keighery, G.J. (1996) Phytogeography, biology and conservation of Western Australian Epacridaceae. *Annals of Botany* 77: 347–355.

Keith, D.A. (1991) Coexistence and species diversity in upland swamp vegetation: the roles of an environmental gradient and recurring fires. Ph.D. Thesis, University of Sydney.

Keith, D. (1996) Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of N.S.W.* 116: 37–78.

Kenrick, J. & Knox, R.B. (1989) Quantitative analysis of self-incompatibility in trees of seven species of *Acacia*. *Journal of Heredity* 80: 240–245.

Knox, R.B., Kenrick, J., Bernhardt, P., Marginson, R., Geresford, G., Baker, I. & Baker, H.G. (1985) Extrafloral nectaries as adaptations for bird pollination in *Acacia terminalis*. *American Journal of Botany* 72: 1185–1196.

Martin, R.E., Miller, R.L. & Cushwa, C.T. (1975) Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56: 1441–1445.

McIntyre, S., Lavorel, S. & Tremont, R.M. (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* 83: 31–44.

Morrison, D.A. (1987) A review of the biology of *Acacia suaveolens* (Smith) Willd. (Mimosaceae). *Proceedings of the Linnean Society* of N.S.W. 109: 271–292.

Morrison, D.A. (1995) Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of N.S.W.* 115: 109–119.

Morrison, D.A., Auld, T.D., Rish, S., Porter, C. & McClay, K. (1992) Patterns of testa-imposed seed dormancy in native Australian legumes. *Annals of Botany* 70: 157–163.

Morrison, D.A., Buckney, R.T., Bewick, B.J. & Cary, G.J. (1996) Conservation conflicts over burning bush in south-eastern Australia. *Biological Conservation* 76: 167–175.

Morrison, D.A., Cary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R. & Anderson, T.S. (1995) Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. *Australian Journal of Ecology* 20: 239–247.

Morrison, D.A. & Myerscough P.J. (1989) Temporal regulation of maternal investment in populations of the perennial legume *Acacia suaveolens*. *Ecology* 70: 1629–1638.

New, T.R. (1984) *A biology of* Acacias (Oxford University Press: Melbourne).

Noble, I.R. (1989) Attributes of invaders and the invading process: terrestrial and vascular plants, in *Biological invasions: a global perspective* (J.A. Drake et al. Eds) pp. 301–313 (John Wiley & Sons Ltd: New York).

Noble, J.C. (1991) On ratites and their interactions with plants. *Revista Chilena de Historia Natural* 64: 85–118.

O'Dowd, D.J. & Gill, A.M. (1986) Seed dispersal syndromes in Australian Acacia, in *Seed dispersal* (D.R. Murray Ed.) pp. 87–121 (Academic Press: Australia).

Polhill, R.M., Raven, P.H. & Stirton, C.H. (1981) Evolution and systematics of the Leguminosae, in *Advances in legume systematics*: *Part 1*. (R.M. Polhill & P.H. Raven Eds.) pp. 1–26 (Royal Botanic Gardens: Kew).

Price, D. (1963) Calendar of flowering times of some plants of the Sydney District, possibly associated with pollinosis. *Contributions from the NSW National Herbarium* 3: 171–191.

Quinlivan, B.J. (1971) Seed coat impermeability in legumes. *Journal of Australian Institute of Agricultural Science* 37: 283–295.

Rice, B. & Westoby, M. (1981) Myrmecochory in sclerophyll vegetation of the West Head, New South Wales. *Australian Journal of Ecology* 6: 291–298.

Rice, B. & Westoby, M. (1986) Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology* 67: 1270–1274.

Schutte, A.L., Vlok, J.H.J. & Van Wyk, B.E. (1995) Fire-survival strategy — a character of taxonomic, ecological and evolutionary importance in fynbos legumes. *Plant Systematics and Evolution* 195: 243–259.

Sugden, E.A. & Pyke, G.H. (1991) Effects of honey bees on colonies of *Exoneura asimillima,* an Australian native bee. *Australian Journal of Ecology* 16: 171–181.

Thanos, C.A. & Rundel, P.W. (1995) Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* 83: 207–216.

Tozer, M. (1996) The invasive potential of *Acacia saligna* (Labill.) H.L. Wendl in vegetation communities occurring on soils derived from Hawkesbury Sandstone. MSc. Thesis, University of Sydney.

Tran, V.N. & Cavanagh, A.K. (1984) Structural aspects of dormancy, *in Seed Physiology Vol. 2. Germination and Reserve Mobilisation* (D.R. Murray Ed.). pp. 1–44 (Academic Press: Sydney).

Tyler, C.M. (1995) Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83: 1009–1020.

van Staaden, J., Manning, J.C. & Kelly, K.M. (1989) Legume seeds — the structure: function equation, in *Advances in legume biology* (C.H. Stirton & J.L. Zarucchi Eds.). pp. 417–450 (Missouri Botanical Garden: St. Louis).

Weiss, P.W. (1984) Seed characteristics and regeneration of some species in invaded coastal communities. *Australian Journal of Ecology* 9: 99–106.

Whelan, R.J. (1995) *The ecology of fire* (Cambridge University Press: Cambridge, Great Britain).