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Post-fire response of shrubs in the tablelands of eastern Australia: do existing models explain habitat differences?

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Abstract. Fire is an important ecological factor that influences the distribution and abundance of plant populations of shrub species in fire-prone habitats. Comprehensive information about the fire-response syndromes and post-fire recruitment of seedlings in tableland habitats of eastern Australia is poorly known. In particular, data on shrubs occurring in grassy habitats are lacking for temperate regions of Australia. The post-fire response and recruitment patterns of shrub taxa were recorded from research burns and wildfires on the New England Tablelands over 4 years in the following four habitats: grassy woodlands and open forests, shrubby open forests, wet heaths and rocky outcrops. The ratio of obligate seeder to resprouter species differed among habitats, with the highest ratio occurring on rocky outcrops (90 : 10) and the lowest in grassy forests (19 : 81). Post-fire recruitment of seedlings was also highest on rocky outcrops whereas seedlings were rarely observed in the wet heaths and grassy forests. The following six models that explain these patterns were reviewed: fire and grazing frequency, soil nutrients and texture, habitat openness and environmental variability. No one model could uniformly explain differences in fire response across all habitats but a combination of disturbance-frequency and regeneration-niche models may provide a mechanism for the patterns observed. Field and laboratory experiments are needed to examine allocation to persistence (resprouting) and reproduction in species with different fire-response syndromes. These experiments also need to examine both disturbance-frequency and regeneration-niche factors in manipulative experiments.

Introduction

Fire is an important ecological factor that influences the distribution, abundance and performance of shrub populations in fire-prone habitats (Whelan 1995; Bond and van Wilgen 1996). Until recently, the response of plant species to fire has received little attention, but with the growing realisation that fire regimes can have profound effects on populations of plants, intensive efforts have been made to garner basic data on the response of plants to fire (e.g. Gill and Bradstock 1992; Benson and McDougall 1993). In particular, data on whether a species is killed by fire or resprouts after fire and where seeds are stored have been the focus of fire-response classificatory systems (e.g. Gill and Bradstock 1992). This approach has been criticised since genetic (ecotypic) factors, climate and fire intensity can produce variable fire-responses (e.g. Morrison and Renwick 2000). Nevertheless, with these limitations in mind information on the response of species to a crown scorch fire can be useful in preliminary modelling of the threats posed to populations by too many or too few fires in fire-prone habitats. By contrasting these traits across habitats, fire-response syndromes may also provide the basis for understanding how these traits have been selected. Also more general classification ‘strategies’ have been used that combine both the response of the standing population to fire and post-fire seedling recruitment (Naveh 1975; Benwell 1998; Pausas 1999), although this approach is prone to be affected by local environmental conditions, for example post-fire rainfall, unless spatial and temporal factors are controlled.

The fire-response of shrubs in temperate tablelands of south eastern Australia is poorly known and compilations of data for the New England Tablelands have often relied on sources of information outside the region. While much of the New England Tablelands has been extensively modified by clearing and grazing, a variegated landscape exists in which the structural elements of the vegetation are still present (McIntyre *et al.* 1995). The largest areas that remain intact are those occurring on the poorest soils mainly derived from leucogranites and porphry rocks, while at the other end of the spectrum only remnant communities occur on nutrient-rich soils derived from alluvium or basaltic rocks. As a broad generalisation, the nutrient-poor siliceous soils provide

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habitats for scleromorphic shrub-dominated woodlands and forests while the more clayey soils derived from metasediments and basalts support grassy woodlands and forests (Benson and Ashby 2000). Shrubs occur throughout the landscape but are less abundant and less-species rich in the grassy woodlands. Also wet heaths and sedgelands occur in areas of impeded drainage (Williams and Clarke 1997; Clarke *et al.* 1998; Benson and Ashby 2000) while rocky outcrops support species-rich scrub and dry heath (Hunter and Clarke 1998). Data on the fire-response of plants on rocky outcrops has been collected but it mainly focussed on rare taxa (Clarke and Fulloon 1997).

The aim of this study was to compare the post-fire response of shrub species in four contrasting habitats on the New England Tablelands in northern New South Wales. The four habitats were grassy woodlands and forests, shrubby forests, rocky outcrops and wet heaths. The wetter forests along the escarpment of the New England Tablelands were excluded from the study. Specifically, we examined whether the ratio of obligate seeders to resprouters was significantly different among habitats and whether there were differences in seedling recruitment patterns. We then review a series of hypotheses to explain these patterns.

Methods

Study area

The study area is located in the New England Tablelands of eastern Australia that falls within the Cfb (dry cool temperate) climate region. No comprehensive account of the vegetation types exists for the north-eastern Tablelands but surveys of the central portion by Benson and Ashby (2000) identified 24 plant communities that cluster into the following four major groups: shrubby forests, grassy forests, wet heaths and rocky outcrops. A detailed account of the plant composition and floristic variation on rocky outcrops across the New England Batholith has also been described in Hunter and Clarke (1998) and the floristic composition of the grasslands has been described (McIntryre *et al.* 1995).

Post-fire response data for shrubby forests, wet heaths and rocky outcrops were collected in several years, following fires at Torrington State Recreation Area (Clarke *et al.* 1998), Gibraltar Range National Park (Williams and Clarke 1997) and Cathedral Rocks National Park, to ensure consistency across the region. Post-fire response from grassy woodlands was collected in several years following fires at Torrington State Forest, Imbota Nature Reserve and Booroolong Nature Reserve. These data were collected as a part of research into mechanisms of recruitment of shrubs in grassy woodlands on the north-eastern Tablelands.

Field records

Individuals of commonly occurring shrub species in the four habitats were tagged before experimental fires and then monitored after fire to assess crown scorch and ability to resprout after fire. Infrequent and rare taxa tend to be under-represented in fire-response records, hence special effort was made to tag taxa known to be sparse in the landscape. Between 3 and 10 individuals of each species were tagged and, where possible, more than one population was tagged. Post-fire observations were spread over several years after autumn and spring fires from 1996 to 2000. By this method, the response of 105 species was followed and the presence of post-fire seedling recruits was also recorded and in some cases their fates are being followed. In addition to these observations, post-fire observations of other (non-tagged) shrub species were recorded following wildfire and research burns (74 species). For some species, the regeneration response has not been observed, although it was possible to infer a response by examining root structures and correlating this with observations of related species (21 species). No attempt was made to apply ‘phylogenetic control’ to the data set as the shrub taxa come from a wide variety of plant families and genera and no one group is numerically more frequent across all habitats.

Analyses of fire traits

Plant species were classified into one of the seven classes of fire-response syndromes as defined by Gill and Bradstock (1992). Note that for species classified as resprouters, the presence or absence of a seed bank in the soil for non-serotinous species was not measured. The seven fire-response syndromes were further aggregated into two groups (obligate seeders and resprouters). Post-fire observation of seedling recruitment was recorded for those species that were tagged and they were classified into (i) those that had more than one seedling per parent present post-fire and (ii) those with less than one seedling per parent. The relative frequency of traits was compared among habitat groups and recruitment classes, by a *G*-test for independence (Sokal and Rohlf 1981).

Results

Species

Data on the fire-response of 200 taxa were collected, of which 51 species occurred in more than one habitat (Appendix 1). Wet heath habitats had the lowest number of shrub taxa (38) while the shrubby forests had more than 100 shrub species with data records (Table 1). Grassy woodland, outcrop and wet heath habitats have data records for almost all shrub taxa recorded in these habitats (see McIntyre *et al.* 1995; Clarke *et al.* 1998; Hunter and Clarke 1998; Benson and Ashby 2000). However, data on the shrubby forest shrub taxa are less comprehensive as about 200 shrub species are known to occur in leucogranite habitats on the north-eastern Tablelands. Therefore, some bias in the data may occur where less-common shrubs in shrubby forests are not well represented. In all habitats, small-leaved scleromorphic shrubs in the families Fabaceae, Epacridaceae, Myrtaceae and Proteaceae are represented. Asteraceae shrub taxa are, however, more common in the grassy landscape and Myrtaceae shrubs appear more commonly in the wet heaths. Rutaceae and Lamiaceae taxa appear to be more common on the outcrops (Appendix 1).

Fire-response syndromes and recruitment patterns

The most common fire syndrome was resprouting from basal stem buds or root suckers, followed by species regenerating only from seed with soil-stored seed banks and then those regenerating only from seed with canopy-stored seed (Table 1). The *G*-test for association for frequency of fire syndromes among species between habitats was significant ($G^2 = 87.4$, $P < 0.001$), i.e. the spectrum of syndromes was

Table 1. Summary of contingency-table analyses for fire-response and post-fire recruitment response of shrub species occurring on the New England Tablelands

Attribute	Habitats				Totals	G^2-test
	Grassy open forests	Shrubby open forest	Rocky outcrops	Wet heath		
Fire response (I–VII[A])						
I. Killed, canopy-stored seed bank	1	1	2	1	5	$G^2 = 87.4$
II. Killed, soil-stored seed bank	9	29	50	7	76	$P < 0.001$
IV, V. Resprouts below ground	44	79	6	29	117	
VI, VII. Resprouts above ground	0	2	0	1	2	
Total	54	111	58	38	200	
Fire response						
Killed	10	30	52	8	81	$G^2 = 88.9$
Resprout	44	81	6	30	119	$P < 0.001$
Total	54	111	58	38	200	
Recruitment						
None or very low	30	41	6	10	65	$G^2 = 33.1$
>1 seedling	3	19	21	5	40	$P < 0.001$
Total	33	60	27	15	105	

[A]Roman numerals are classes used by Gill and Bradstock (1992).

different with the percentage of resprouters being higher in the grassy forests (81%), heaths (79%), shrubby forests (73%) than in rock outcrops (10%) (Table 1). Species that had canopy-stored seed banks and were killed by fire were not common in any landscape (Table 1).

Significant differences were found also among habitats in the proportion of species that had post-fire recruitment of seedlings (G^2 = 33.1, P < 0.001). For those species where seedling recruitment was measured (105 species), seedlings were most commonly observed in rocky outcrop taxa (78%), followed by shrubby and wet heath species (31%) and the least number of burnt species with seedling recruits was found in the grassy forests (9%) (Table 1). This result reflects the number of obligate seedling taxa giving rise to seedlings (70%) *v.* seedlings present in resprouting taxa (30%) (G^2 = 32.7, P < 0.001). Of the resprouting taxa that had post-fire seedlings, most had canopy-stored seed banks. Nevertheless, the status of the seed bank for other resprouting species is not known as this would require sampling the seed bank.

Discussion

Do habitats show different functional responses?

Shrub species on rocky outcrops are generally killed by fire (obligate seeders), while in the grassy forests, heaths and shrubby forests more than 70% of species sprout after fire (resprouters). Similarly, the most-dominant species in the grassy forests, shrubby forests and heaths were all resprouters while the dominant species on the rocky outcrops were mainly obligate seeders. This supports the results of a narrower study by Clarke (2001) who found that the abundance and ratio of all species killed by fire (obligate seeders) to resprouters was higher on rocky outcrops than in the adjacent shrubby forests in the higher-rainfall areas of the New England Tablelands. Data for the shrubby forests and heaths in our study probably overestimate the proportion of resprouters as rarer taxa tend to be obligate seeders and hence we believe that grassy forests contain the highest proportion of resprouter species. These findings agree, in part, with Keeley (1977), Myerscough *et al.* (1995) and Benwell (1998) who found a higher proportion of obligate seeders in more-open habitats in chaparral and in dry heaths.

Clear differences in post-fire recruitment patterns of seedlings were present among habitats. On rocky outcrops more than 75% of species had seedling recruits whereas the shrubby forests and wet heaths had around 31%, followed by the grassy forests with less than 10% of species showing post-fire seedling recruitment. This pattern, in turn, relates to the fire response of species and seedling recruitment behaviour, with 73% of species killed by fire producing seedling recruits. This result is similar to that found in coastal heaths (Benwell 1998) and chaparral (Keeley and Zedler 1978; Moreno and Oechel 1992) where obligate seeders have higher seedling density and survival in the post-fire environment than the resprouters. Congener contrasts among resprouters and seeders have also shown that resprouters typically produce fewer seedlings after fire (Enright and Lamont 1989; Groom *et al.* 2001). What stands out in our study is the absence of seedling recruits for common species occurring in grassy open forests and in wet heaths. This syndrome has been described as ‘obligate resprouting’ (Naveh 1975; Benwell 1998), suggesting that these species do not have the ability to set seed and accumulate seed banks. However, when seed of some of these species has been used in field experiments, post-fire recruitment of resprouters can occur when the seed bank is artificially enhanced (Williams and Clarke 1997; Clarke and Davison 2001; K. Knox, pers. comm.). Thus, the lack of post-fire seedlings may be related to low levels of fecundity and/or transient seed banks. Another explanation is that these species recruit in the intervals between fires and require shade for germination, being 'disturbance-free gap-avoiding recruiters' (Keeley 1978).

Links between life-history traits and the selective regime of fire have focussed on small-scale spatial patterns (e.g. Keeley 1977; Bond *et al.* 1988; Benwell 1998) and biogeographical patterns (e.g. Lamont and Markey 1995; Ojeda 1998) but rarely do they contrast habitat differences at a regional scale within a climate region. Several models may explain the pronounced patterns observed on the New England Tablelands (Table 2). They broadly fall into the following two categories: disturbance-frequency and regeneration-niche (Table 2); each is discussed below.

Disturbance-frequency (*fire and grazing*)

At local scales, frequent fires are thought to promote resprouting while intermediate fire intervals favour obligate seeders in sclerophyll vegetation (e.g. Bradstock and O'Connell 1988; Morrison *et al.* 1995) (Table 2). However, no studies have directly examined the effects of frequent fires on the floristic composition of vegetation on New England Tablelands. In rocky habitats, where fire is less frequent or intense, seeders should be more common than resprouters (Bond *et al.* 1988). Likewise, grassy ecosystems may be burnt more frequently, but less intensely than shrub-dominated communities (Bond and van Wilgen 1996). The effect of isolation from fires (low frequency of fires) in rocky habitats is likely to be as important as high fire frequency in forests as it can eliminate obligate seeding species by exhausting seed banks (Morrison *et al.* 1995; Keith 1996). Clarke (2001) found evidence for convergence in fire-response syndromes in 26 genera, which had congeners in contrasting habitats. Almost invariably shrub congeners on or near rocky outcrops were killed by fire whereas their related taxon in the forests were resprouters. This pattern does not explain why obligate seeders rarely occur in grassy open forests as in the past 50 years they have been infrequently burnt on the New England Tablelands. Rather than fire, perhaps grazing frequency may have removed obligate seeders from the grassy woodlands where both native and introduced herbivores occur in higher densities than in the shrub-dominated communities (Table 2). To test these ideas, defoliation experiments on obligate seeders are needed both in the field and under controlled conditions.

Regeneration-niche (*soil nutrients and texture*)

A number of studies have found seeders to be more dominant on poorer soils, while resprouters appear to be more dominant on more fertile soils (e.g. Lamont and Markey 1995; Wisheu *et al.* 2000). This pattern is partially consistent with our landscape patterns as the grassy forest and wet heaths have a higher nutrient status than the shrubby forests (Table 2). However, the nutrient status of soils and their texture are not independent as the low nutrient lithosol and

Table 2. Explanations for habitat differences in fire-response of shrub species occurring on the New England Tablelands

Model	Mechanism for habitat differences in fire response traits	Predictions (hypotheses)	Do data support model?
Disturbance-frequency			
Fire	Frequent fires remove obligate seeders from fire-prone landscapes.	Obligate seeders restricted to areas infrequently burnt.	Support model for rocky habitats, but not for infrequently burnt grassy habitats.
Herbivory	Frequent grazing remove obligate seeders from palatable grassy landscapes.	Obligate seeders are restricted to low-nutrient unpalatable vegetation.	Support model for sclerophyllous habitats, although in low-nutrient habitats they also coexist with resprouters.
Regeneration-niche			
Soil nutrients	Obligate seeders are better able to use transient nutrients for growth.	Resprouter species are restricted to environments with higher soil nutrients.	Support model for grassy habitats although in low-nutrient habitats they also coexist with obligate seeders.
Soil texture and moisture	Obligate seeders allocate to root growth rather than storage organs.	Obligate seeders are restricted to well-drained sandy soils.	Support model, but resprouter also coexist on sandy, well-drained soils.
Openness	Shade restricts the recruitment of obligate seeders.	Obligate seeders are found in open habitats.	Support for model on rocky outcrops although they also coexist with resprouters in other habitats.
Rainfall variability	More variable environments restrict the recruitment of obligate seeders.	Obligate seeders are restricted to habitats that have more predictable moisture.	No evidence for differences in response among habitats. Regional evidence within the rocky outcrop habitat.

podsols (rock outcrops and shrubby forests) also have a sandy, well-drained texture. Conversely, the grassy and wet heath soils have a higher nutrient status but have finer-textured soils with more compact surfaces. Wisheu *et al.* (2000) suggest that seeders are able to utilise post-fire nutrients better than resprouters (Table 2). In the post-fire environment the pulse of nutrients released by fire lies mostly on top of the soil, which may be inaccessible for new growth in resprouters. However, Lamont and Markey (1995) proposed that nutrient status is not driving these patterns as such and that the physical properties of these soils are more important. In their study, the poorly structured soils (deep sands) store more accessible water than the more fertile soils (lateritic soils). Clarke (2001) has also suggested that obligate seeders shrubs allocate resources to root length rather than near surface storage organs (Table 2). Hence, sandy soils or lithosols with deep cracks will favour the growth of obligate seeders when moisture is limiting and where fire frequency does not eliminate populations. This idea contrasts with root allocation of obligate seeders in the Mediterranean Basin which are reported to have shallow root systems (Pausas 1999).

Regeneration-niche (*openness*)

More open habitats, such as rocky outcrops, may promote seeders through the availability of open spaces where competition from resprouters is less (Keeley 1977; Keeley and Zedler 1978; Myerscough *et al.* 1995) (Table 2). However, the role of competition and fire-mediated open space in selection for resprouting remains contentious (Bond and van Wilgen 1996). In habitats with bare ground, post-fire gap sizes may be expected to be large and hence recruitment of seeders is enhanced (Keeley and Zedler 1978; Carrington and Keeley 1999; Enright and Goldblum 1999). These habitat patterns can be explained by space-limiting recruitment. In more open habitats there are increased opportunities for faster-growing seeders to complete their life cycles as long as fire intervals are shorter than the primary juvenile period. This model may also explain why grassy forests and the wet heaths have few obligate seeders as both of these habitats have a ground stratum dominated by grasses or graminoids which tend to close gaps rapidly in the post-fire environment (Table 2).

Regeneration-niche (*rainfall variability*)

In environments with low, or more variable resources, persistence (sprouting) may be favoured over seedling recruitment as the risks of failure are higher (Higgins *et al.* 2000). One model that explains this is the 'environmental variance' model where less predicable environments favour plant allocation to persistence (resprouting organs) because of greater risks involved in seedling germination and recruitment (Benwell 1998; Higgins *et al.* 2000; Bond and Midgley 2001) (Table 2). Such effects should be strongest in fire-killed species with short-lived seed banks that lack a 'storage effect'. This is supported by the absence or low numbers of obligate seeding serotinous shrub species (e.g. *Banksia*, *Callistemon*, *Hakea*, *Grevillea*) compared with equivalent coastal habitats. This suggestion is consistent with studies of *Erica* and *Banksia* that have shown resprouters to be more widespread and seeders to be more common in predictable environments (Lamont and Markey 1995; Ojeda 1998). While this model appears to account for increasing frequencies of resprouters on the tablelands compared with coastal habitats it does not seem to explain fire-response patterns within our region (Table 2).

Conclusion

The ratio of obligate seeders to resprouter shrubs was found to differ among habitats. Habitats with a higher proportion of obligate seeders and seedling recruitment occur on rocky outcrops and to a lesser extent in shrubby forests on well-drained nutrient-poor soils. Grassy open forests and woodlands have a higher proportion of resprouter shrubs and little seedling recruitment. Individually, disturbance-frequency models (fire and grazing) and models associated with the regeneration-niche (soil nutrients, soil texture, openness and rainfall variability) do not adequately explain the patterns we have described (Table 2). All models partly explain the patterns we have observed but neither disturbance-frequency nor regeneration-niche models can be adequately tested without experimental tests. Most of the shrub species on the north-eastern Tablelands appear to live longer than 20 years in the absence of fire, hence we think that the combined effects of disturbance-frequency and regeneration-niche factors may provide a general model to explain habitat differences among regeneration syndromes. To advance the development of these models, experiments are required to test hypotheses about reproductive allocation where both disturbance and regeneration-niche factors are manipulated.

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References

Benson DH, McDougall L (1993) Ecology of Sydney plant species part 1: ferns, fern allies, cycads, conifers and dicotyledon families Ancanthaceae to Asclepiadaceae. *Cunninghamia* **3**, 257–422.

Benson JS, Ashby EM (2000) Vegetation of the Guyra 1: 100 000 map sheet New England Bioregion, New South Wales. *Cunninghamia* **6**, 747–872.

Benwell AS (1998) Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany* **46**, 75–101.

Bond WJ, Midgley J J (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* **16**, 45–51.

Bond WJ, van Wilgen BW (1996). 'Fire and plants.' (Chapman and Hall: London)

Bond WJ, Midgley JJ, Vlok J (1988) When is an island not an island? Insular effects and their causes in fynbos shrublands. *Oecologia* **77**, 515–521.

Bradstock RA, O'Connell MA (1988) Demography of woody plants in relation to fire: *Banksia ericifolia* L.f. and *Petrophile pulchella* (Schard) R.Br. *Australian Journal of Ecology* **13**, 505–518.

Carrington ME, Keeley JE (1999) Comparison of post-fire establishment between communities in mediterranean and non-mediterranean climate ecosystems. *Journal of Ecology* **87**, 1025–1036.

Clarke PJ (2001) Habitat insularity and convergence of fire response traits: evidence from a sclerophyll archipelago in eastern Australia. In 'The ecology of insular biotas'. p. 16 (Victoria University of Wellington: Wellington)

Clarke PJ, Copeland LM, Hunter JT, Nano CE, Williams JB, Wills KE (1998) 'The Vegetation and plant species of Torrington State recreation area.' (Botany Department, University of New England: Armidale, NSW)

Clarke PJ, Davison EA (2001) Experiments on tree and shrub establishment in temperate grassy woodlands: seedling emergence. *Austral Ecology* **26**, 400–412.

Clarke PJ, Fulloon L (1997) 'Fire and rare plants: Torrington State recreation area.' (Botany Department, University of New England: Armidale, NSW)

Enright NJ, Lamont BB (1989) Seed banks, fire season, safe sites and seedling recruitment of five co-occurring *Banksia* seedlings. *Journal of Ecology* **77**, 1111–1122.

Enright NJ, Goldblum D (1999) Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age drought and disease. *Plant Ecology* **144**, 71–82.

Gill AM, Bradstock RA (1992) A national register for the fire response of plant species. *Cunninghamia* **2**, 653–660.

Groom PK, Lamont BB, Wright IW (2001) Lottery (stochastic) and non-lottery (biological) processes explain recruitment patterns among eight congeneric shrub species in southwestern Australia. *Journal of Mediterranean Ecology* **1**, 1–14.

Higgins SI, Pickett STA, Bond W J (2000) Predicting extinction risk for plants: environmental stochasticity can save declining populations. *Trends in Ecology and Evolution* **15**, 516–520.

Hunter JT, Clarke PJ (1998) The vegetation of granitic outcrop communities on the New England batholith of eastern Australia. *Cunninghamia* **5**, 547–618.

Keeley JE (1977) Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. *Ecology* **58**, 820–829.

Keeley JE, Zedler PH (1978) Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *American Midland Naturalist* **99**, 142–161.

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

Lamont BB, Markey A (1995) Biogeography of fire-killed and resprouting *Banksia* species in south-western Australia. *Australian Journal of Botany* **43**, 283–303.

McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes—their relationship to disturbance responses in herbaceous vegetation. *Journal of Ecology* **83**, 31–44.

Moreno JM, Oechel WC (1992) Factors controlling postfire seedling establishment in southern California chaparral. *Oecologia* **90**, 50–60.

Morrison DA, Renwick JA (2000) Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. *Australian Journal of Botany* **48**, 71–79.

Morrison DA, Cary GJ, Pengelly SM, Ross DG, Mullins BJ, Thomas CR, Anderson TS (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.

Myerscough PJ, Clarke PJ, Skelton N (1995) Plant coexistence in coastal heaths: floristic patterns and species attributes. *Australian Journal of Ecology* **20**, 482–493.

Naveh Z (1975) The evolutionary significance of fire in the Mediterranean region. *Vegetatio* **29**, 199–208.

Ojeda F (1998) Biogeography of seeder and resprouter *Erica* species in the Cape Floristic Region—where are the resprouters? *Biological Journal of the Linnean Society* **63**, 331–347.

Pausas JG (1999) Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecology* **140**, 27–39.

Sokal RR, Rohlf FJ (1981) 'Biometry.' (Freeman and Company: San Francisco)

Whelan RJ (1995) 'Ecology of fire.' (Cambridge University Press: Cambridge)

Williams PR, Clarke PJ (1997). Habitat segregation by serotinous shrubs in heaths: post-fire emergence and seedling survival. *Australian Journal of Botany* **45**, 31–39.

Wisheu IC, Rosenzweig ML, Olsvig-Whittaker L, Shmida A (2000) What makes nutrient-poor mediterranean heathlands so rich in plant diversity? *Evolutionary Ecology Research* **2**, 935–955.

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Appendix 1. Habitat occurrence, fire-response and presence of post-fire seedlings (>1 seedling per adult), for shrub (including subshrubs) species occurring on the New England Tablelands in northern New South Wales

*Inferred response from morphology and comparison with sister taxa; nomenclature follows Harden (1993), except where more recent revisions have occurred and have been accepted by the Royal Botanic Gardens, Sydney

Taxon	Habitat	Fire response	Seedlings
Araliaceae			
Astrotricha longifolia s.l.	Shrubby open forest	Resprouts*	
Polyscias sambucifolia	Shrubby open forest	Resprouts	N
Asteraceae			
Cassinia laevis	Grassy open forest	Obligate seeder	N
Cassinia leptocephala	Grassy open forest	Obligate seeder	N
Cassinia quinquefaria	Shrubby open forest/grassy open forest	Obligate seeder	N
Olearia myrsinoides	Shrubby open forest/grassy open forest	Resprouts	N
Olearia rosmarinifolia	Grassy open forest	Resprouts*	
Olearia sp. aff. *elliptica*	Shrubby open forest/grassy open forest	Resprouts	N
Olearia viscidula	Grassy open forest	Resprouts	N
Ozothamnus adnatus	Grassy open forest	Resprouts	
Ozothamnus diosmifolius	Shrubby open forest/grassy open forest	Resprouts	N
Ozothamnus obcordatus	Rocky outcrop	Obligate seeder	Y
Ozothamnus obcordatus (grassy ecotype)	Grassy open forest	Resprouts	N
Casuarinaceae			
Allocasuarina brachystachya	Rocky outcrop	Obligate seeder*	
Allocasuarina rigida ssp. *rigida*	Rocky outcrop	Obligate seeder*	
Celastraceae			
Maytenus silvestris	Shrubby open forest	Resprouts	
Chloanthaceae			
Chloanthes parviflora	Rocky outcrop	Obligate seeder	Y
Cupressaceae			
Callitris oblonga ssp. *parva*	Shrubby open forest	Obligate seeder	Y
Dilleneaceae			
Hibbertia acicularis	Wet heath/rocky outcrops	Resprouts	N
Hibbertia cistoidea	Shrubby open forest	Resprouts	N
Hibbertia linearis	Grassy open forest	Resprouts	N
Hibbertia obtusifolia	Shrubby open forest/grassy open forest	Resprouts	N
Hibbertia riparia	Wet heath/shrubby open forest	Resprouts	N
Hibbertia riparia (stellate hairs ecotype)	Grassy open forest	Resprouts	N
Hibbertia serpyllifolia	Shrubby open forest	Resprouts	N
Hibbertia sp. B (outcrop ecotype)	Rocky outcrop	Obligate seeder*	Y
Hibbertia vestita	Wet heath	Resprouts	N
Epacridaceae			
Acrotriche aggregata	Shrubby open forest	Resprouts	N
Brachyloma daphnoides ssp. *glabrum*	Shrubby open forest	Resprouts	N
Brachyloma saxicola	Rocky outcrop	Obligate seeder	Y
Epacris breviflora	Wet heath	Resprouts	
Epacris microphylla	Shrubby open forest/wet heath	Resprouts	N
Epacris obtusifolia	Wet heath	Obligate seeder	Y
Leucopogon attenuatus	Shrubby open forest	Resprouts	N
Leucopogon biflorus	Shrubby open forest/rocky outcrop	Obligate seeder	N
Leucopogon hookeri	Grassy open forest	Resprouts	N
Leucopogon lanceolatus var. *lanceolatus*	Shrubby open forest/grassy open forest	Resprouts	N
Leucopogon melaleucoides	Shrubby open forest	Resprouts	N
Leucopogon microphyllus var. *pilibundus*	Shrubby open forest/rocky outcrops	Variable	N
Leucopogon muticus	Shrubby open forest/rocky outcrops	Obligate seeder	
Leucopogon neo-anglicus	Rocky outcrop/shrubby open forest	Obligate seeder	Y
Leucopogon virgatus	Shrubby open forest	Resprouts	
Lissanthe strigosa	Shrubby open forest/grassy open forest	Resprouts	N
Melichrus erubescens	Shrubby open forest	Obligate seeder	
Melichrus procumbens	Shrubby open forest	Resprouts	N

Appendix 1. (*continued*)

Taxon	Habitat	Fire response	Seedlings
Melichrus urceolatus	Shrubby open forest/grassy open forest	Resprouts	N
Monotoca scoparia	Shrubby open forest/grassy open forest	Resprouts	N
Sprengelia incarnata	Wet heath	Obligate seeder	Y
Styphelia triflora	Shrubby open forest	Obligate seeder	N
Euphorbiaceae			
Amperea xiphoclada var. *xiphoclada*	Shrubby open forest	Resprouts	N
Fabaceae			
Acacia betchei	Shrubby open forest	Obligate seeder	S
Acacia burbidgeae	Shrubby open forest	Obligate seeder	S
Acacia buxifolia ssp. *pubiflora*	Shrubby open forest	Resprouts	N
Acacia dealbata	Grassy open forest	Obligate seeder	N
Acacia falciformis	Shrubby open forest	Resprouts	Y
Acacia filicifolia	Grassy open forest	Resprouts/variable	N
Acacia fimbriata	Grassy open forest/shrubby open forest	Obligate seeder	Y
Acacia granitica	Rocky outcrop	Obligate seeder	Y
Acacia gunnii	Shrubby open forest/grassy open forest	Resprouts*	
Acacia hispidula	Rocky outcrops	Obligate seeder*	
Acacia implexa	Shrubby open forest/grassy open forest	Resprouts	
Acacia juncifolia	Shrubby open forest	Resprouts*	
Acacia latisepala	Rocky outcrops	Obligate seeder	Y
Acacia longifolia	Shrubby open forest	Obligate seeder	Y
Acacia macnuttiana	Shrubby open forest	Obligate seeder (75%)	Y
Acacia obtusifolia	Shrubby open forest	Obligate seeder	
Acacia penninervis	Shrubby open forest	Resprouts*	
Acacia pruinosa	Shrubby open forest	Resprouts	N
Acacia torringtonensis	Shrubby open forest/rocky outcrop	Obligate seeder	Y
Acacia triptera	Shrubby open forest/rocky outcrop	Obligate seeder*	
Acacia ulicifolia	Shrubby open forest/grassy open forest	Obligate seeder*	
Acacia venulosa	Rocky outcrop/shrubby open forest	Obligate seeder	Y
Acacia viscidula	Rocky outcrop	Obligate seeder	Y
Acacia williamsiana	Rocky outcrop	Obligate seeder*	
Almaleea cambagei	Wet heath	Resprouts	N
Aotus subglauca var. *subglauca*	Shrubby open forest	Resprouts	N
Bossiaea neo-anglica	Shrubby open forest	Resprouts	Y
Bossiaea obcordata	Shrubby open forest	Resprouts	N
Bossiaea rhombifolia	Shrubby open forest/rocky outcrops	Obligate seeder*	
Bossiaea scortechinii	Shrubby open forest	Resprouts	Y
Daviesia acicularis	Rocky outcrop	Obligate seeder	
Daviesia genistifolia	Grassy open forest	Resprouts*	
Daviesia latifolia	Shrubby open forest/grassy open forest	Obligate seeder/ variable	N
Daviesia mimosoides ssp. *mimosoides*	Shrubby open forest	Resprouts	
Daviesia ulicifolia	Shrubby open forest	Obligate seeder	
Daviesia umbellulata	Shrubby open forest	Obligate seeder	Y
Dillwynia phylicoides var. *phylicoides*	Shrubby open forest	Resprouts	Y
Dillwynia sieberi (grassland ecotype)	Grassy open forest	Resprouts*	
Dillwynia sericea	Shrubby open forest	Obligate seeder	
Dillwynia sieberi	Shrubby open forest	Obligate seeder	
Gompholobium huegelii	Shrubby open forest	Obligate seeder	
Hardenbergia violacea	Shrubby open forest/grassy open forest	Resprouts	Y
Hovea apiculata	Rocky outcrop	Obligate seeder	
Hovea graniticola	Rocky outcrop	Obligate seeder	Y
Hovea linearis (*heterophylla*)	Shrubby open forest/grassy open forest	Resprouts	
Indigofera adesmiifolia	Shrubby open forest/grassy open forest	Resprouts	N
Indigofera australis	Rocky outcrop/shrubby open forest	Resprouts	N
Jacksonia scoparia	Shrubby open forest/grassy open forest	Resprouts	N
Mirbelia pungens	Rocky outcrop	Obligate seeder	

Appendix 1. *(continued)*

Taxon	Habitat	Fire response	Seedlings
Mirbelia rubiifolia	Shrubby open forest	Resprouts	
Mirbelia speciosa ssp. *speciosa*	Rocky outcrop	Obligate seeder	Y
Phyllota phylicoides	Wet heath	Resprouts	
Podolobium arborescens	Shrubby open forest/rocky outcrops	Obligate seeder (75%)	Y
Podolobium ilicifolium	Grassy open forest	Resprouts	N
Pultenaea campbellii	Grassy open forest	Resprouts	N
Pultenaea microphylla	Grassy open forest	Resprouts	N
Pultenaea pycnocephala	Shrubby open forest	Obligate seeder	
Pultenaea stuartiana	Shrubby open forest	Resprouts	Y
Lamiaceae			
Prostanthera nivea var. *nivea*	Rocky outcrop	Obligate seeder*	
Prostanthera saxicola	Rocky outcrop	Obligate seeder	Y
Prostanthera scutellarioides	Rocky outcrop/shrubby open forest	Obligate seeder	Y
Prostanthera staurophylla	Rocky outcrop	Obligate seeder	Y
Myrtaceae			
Babingtonia densifolia	Rocky outcrop	Resprouts	N
Babingtonia odontocalyx	Rocky outcrop	Obligate seeder	Y
Baeckea omissa	Wet heath	Resprouts	N
Callistemon flavovirens	Shrubby open forest	Resprouts	
Callistemon linearis	Shrubby open forest	Resprouts	
Callistemon pallidus	Wet heath	Resprouts	
Callistemon pityoides	Wet heath	Resprouts	N
Callistemon pungens	Shrubby open forest	Resprouts	Y
Callistemon sieberi	Wet heath	Resprouts	
Callistemon sp. nov.	Rocky outcrop	Obligate seeder*	
Callistemon sp. aff. *flavovirens*	Shrubby open forest	Resprouts	Y
Calytrix tetragona	Rocky outcrop	Obligate seeder	N
Homoranthus lunatus	Rocky outcrop	Obligate seeder	Y
Homoranthus binghiensis	Rocky outcrop	Obligate seeder	Y
Kunzea bracteolata	Rocky outcrop	Obligate seeder	Y
Kunzea obovata	Rocky outcrop	Structure	
Leptospermum arachnoides	Wet heath	Resprouts	
Leptospermum brevipes	Rocky outcrop/shrubby open forest	Resprouts	
Leptospermum gregarium	Wet heath	Resprouts	
Leptospermum minutifolium	Wet heath/shrubby open forest	Resprouts	
Leptospermum novae-angliae	Rocky outcrop/shrubby open forest	Resprouts	S
Leptospermum polygalifolium ssp. *transmontanum*	Wet heath	Resprouts	
Leptospermum trinervium	Shrubby open forest	Resprouts	
Micromyrtus sessilis	Rocky outcrops	Resprouts / variable	
Olacaceae			
Olax stricta	Shrubby open forest/rocky outcrops	Resprouts	
Oleaceae			
Notelaea linearis	Forest	Resprouts	
Notelaea microcarpa var. *microcarpa*	Forest	Resprouts	
Pittosporaceae			
Bursaria spinosa ssp. *spinosa*	Grassy open forest	Resprouts	N
Rhytidosporum procumbens	Grassy open forest	Resprouts	
Rhytidosporum procumbens (heath ecotype)	Wet heath	Obligate seeder	
Proteaceae			
Banksia spinulosa ssp. *neoangica*	Shrubby open forest/wet heath	Resprouts	Y
Banksia integrifolia ssp. *monticola*	Shrubby open forest/grassy open forest	Resprouts	
Banksia marginata	Wet heath	Obligate seeder	Y
Conospermum taxifolium	Shrubby open forest	Resprouts	N
Grevillea acerata	Wet heath/shrubby open forest	Resprouts	
Grevillea beadleana	Rocky outcrop/shrubby open forest	Obligate seeder	Y
Grevillea juniperina ssp. *allojohnsonii*	Shrubby open forest	Resprouts	

Appendix 1. (*continued*)

Taxon	Habitat	Fire response	Seedlings
Grevillea scortechinii ssp. *sarmentosa*	Shrubby open forest	Obligate seeder*	
Grevillea triternata	Shrubby open forest	Resprouts	
Grevillea viridiflava	Shrubby open forest	Resprouts	N
Hakea eriantha	Grassy open forest	Obligate seeder*	
Hakea laevipes ssp. *graniticola*	Shrubby open forest	Resprouts	N
Hakea macrorrhyncha	Rocky outcrop/shrubby open forest	Obligate seeder	Y
Hakea microcarpa	Wet heath	Resprouts	Y
Isopogon petiolaris	Shrubby open forest	Resprouts	
Lomatia fraseri	Shrubby open forest	Resprouts	N
Lomatia silaifolia	Shrubby open forest	Resprouts	N
Persoonia cornifolia	Shrubby open forest	Resprouts	N
Persoonia fastigiata	Shrubby open forest	Resprouts	
Persoonia rufa	Wet heath/shrubby open forest	Obligate seeder	
Persoonia tenuifolia	Shrubby open forest	Resprouts	
Persoonia terminalis ssp. *terminalis*	Rocky outcrop	Obligate seeder	N
Petrophile canescens	Shrubby open forest	Resprouts	N
Rhamnaceae			
Cryptandra amara (grassland ecotype)	Grassy open forest	Resprouts	N
Cryptandra amara var. *longflora*	Grassy open forest	Resprouts	
Cryptandra lanosiflora	Rocky outcrop	Obligate seeder	
Cryptandra scortechinii	Shrubby open forest	Resprouts	
Discaria pubescens	Shrubby open forest/grassy open forest	Obligate seeder*	
Pomaderris eriocephala	Grassy open forest	Resprouts*	
Rosaceae			
Rubus parvifolius	Grassy open forest	Resprouts	
Rutaceae			
Boronia algida	Shrubby open forest	Resprouts	
Boronia anethifolia (local ecotype)	Rocky outcrop	Obligate seeder*	
Boronia bipinnata	Rocky outcrop	Obligate seeder*	
Boronia granitica	Rocky outcrop	Obligate seeder	S
Boronia whitei	Shrubby open forest	Resprouts	N
Boronia microphylla	Shrubby open forest/wet heath	Resprouts	N
Boronia polygalifolia	Shrubby open forest/wet heath	Resprouts	
Correa reflexa (green perianth)	Grassy open forest	Resprouts	
Correa reflexa (red perianth)	Shrubby open forest	Obligate seeder	S
Leionema ambiens	Rocky outcrop	Obligate seeder	
Leionema rotundifolium	Rocky outcrop	Obligate seeder	S
Phebalium glandulosum ssp. *eglandulosum*	Rocky outcrop	Obligate seeder	S
Philotheca myoporoides ssp. *epilosus*	Rocky outcrop	Obligate seeder	S
Zieria aspalathoides	Rocky outcrop	Obligate seeder	
Zieria cytisoides	Grassy open forest	Resprouts*	
Zieria laevigata	Rocky outcrop	Obligate seeder	S
Sapindaceae			
Dodonaea boroniifolia	Shrubby open forest	Resprouts*	
Dodonaea hirsuta	Rocky outcrop	Obligate seeder	S
Dodonaea sp. aff. *triquetra*	Rocky outcrop/shrubby open forest	Resprouts	
Dodonaea triquetra	Shrubby open forest/grassy open forest	Resprouts	N
Dodonaea viscosa ssp. *viscosa*	Shrubby open forest/grassy open forest	Resprouts	
Thymelaeaceae			
Pimelea curviflora var. *divergens*	Grassy open forest	Resprouts	N
Pimelea linifolia ssp. *collina*	Wet heath	Obligate seeder	
Pimelea linifolia ssp. *linifolia*	Shrubby open forest/grassy open forest	Resprout	
Xanthorrhoeaceae			
Xanthorrhoea glauca ssp. *glauca*	Shrubby open forest/wet heath	Resprouts	
Xanthorrhoea johnsonii	Shrubby open forest	Resprouts	
Zamiaceae			
Macrozamia plurinervia	Shrubby open forest	Resprouts	