

CHAPTER 6

6 Plant regenerative mechanisms



6.1 Introduction

An important regenerative trait for plants is how they persist or move into a site following disturbance (Noble and Slatyer, 1980). Response types vary between species and with the nature of the disturbance. In order to manage vegetation in relation to fire, knowledge of the responses of individual plant species or functionally similar groups is important (Bradstock et al., 1995). Functional groups are species that function in a similar manner within an ecosystem, and in this case, in response to fire. By classifying plant responses to fire in functional groups, the complexity of individual plant responses can be simplified.

Two main plant regenerative strategies following fire have been recognised. The first concerns plants that die as a result of canopy scorch, commonly called ‘seeder’ species due to the reliance on seed for regeneration. The alternative strategy concerns plants that survive crown scorch and resprout vegetatively from the parent plant. These species are commonly called ‘resprouters’ (Gill and Bradstock, 1992). These were discussed in further detail in Section 1.6.

Identifying the mode of regeneration has been the focus of a number of studies (see studies in the National Fire Response database of Gill and Bradstock (1992)). Studies in the early 1920s distinguished these strategies in American chaparral communities (Jepson, 1922; Horton and Kraebel, 1955). In Australia, the adaptive traits of plant species were summarised into the categories of seeder and resprouter (Gill, 1975) and formalised in a response table for application in ecological studies (Gill, 1981). Many studies have collected fire response information following either unplanned wildfires or controlled burns providing information on a suite of plant species (Purdie, 1977a; 1977b; Wark et al., 1987; Fox, 1988; Russell-Smith et al., 1998). Alternatively, studies have focused on individual species and the capacity to resprout. In fire-prone regions the resprouting response is often the main mechanism for regeneration following many types of disturbance including drought and fire. Studies isolating the regenerative capacity of the lignotuber have used clipping of the plant above the lignotuber to assess resprouting vigour and the mechanisms within the lignotuber to support regrowth (Riba, 1997; Canadell and Lopezsofia, 1998). The combination of clipping and burning has been used to investigate the regenerative ability of the lignotuber in the presence and absence of heating (Gill and Ingwersen, 1976; Bradstock and Myerscough, 1988).

To derive more information on the regenerative strategy of selected species in Guy Fawkes River National Park for fire management planning, an experiment was undertaken to test the regenerative mechanism of species not previously studied in the area.

The specific objectives were to:

- (1) Determine the regenerative capacity of the lignotuber in the presence (burning) and absence (clipping) of heat;
- (2) Determine the mode of regeneration following full crown scorch of the selected species;

- (3) Investigate the relationship between lignotuber size and the capacity to resprout; and
- (4) Measure the time taken for the plants to reproduce (this experiment was established but the results were lost due to an unplanned bushfire).

6.2 Method

6.2.1 Study Area

The specific location of the study region was based on the fire history derived and described in Chapter 3 and sites used for the vegetation survey (Chapter 4).

6.2.2 Plant burning

The species selected for study were from both the Tablelands and the Gorge study regions. The species selected satisfied fire-related and abundance criteria. The abundance criterion was that more than 40 individuals of each plant had to be available at a site. This was to protect the populations of each species, as the experiment had the potential to kill 20 plants per site. None of the species studied was classified as rare or threatened.

The fire-related criterion was to select those species for which little information was available on the mode of regeneration following fire. The Tablelands species selected were *Persoonia oleoides*, *Acacia irrorata* and *Banksia integrifolia*. *Persoonia oleoides* is common and abundant throughout the Tablelands as a small shrub. Previous experimental burns (described in Chapter 5) had indicated the species appeared to regenerate following fire. *Acacia irrorata* is a common midstorey shrub species on the New England Tablelands and its regenerative strategy was unclear. *Banksia integrifolia* is a serotinous small tree and its regenerative strategy varies in NSW (Ingwersen, 1977; Gill and Bradstock, 1992).

The Gorge species selected were *Rapanea variabilis* and *Goodia lotifolia*. *Goodia lotifolia* was selected due to evidence that this species regenerates from seed (Gill and Bradstock, 1992). *Goodia lotifolia* is abundant in some sites in GFRNP with a history of frequent fires. The question was whether this was a seeder species persisting in areas of moderate NOF and short SIFI. For *Rapanea variabilis*, literature suggested it resprouts (Benson and McDougall, 1997) but no evidence existed on the Northern Tablelands of NSW. It occurred in a number of frequently burnt sites suggesting resilience to frequent fires. Due to limited access to certain sites, *Rapanea variabilis* was only found in suitable numbers at one site. Two other species of interest, *Acacia diphylla*, a less abundant Gorge *Acacia*, and *Alyxia ruscifolia*, an uncommon rainforest margin species occurring in some open-forest sites in GFRNP, were tested for the mode of regeneration but on fewer individuals. *Rapanea variabilis* was tested with 10 controls, 10 burns and 10 clipped plants at one site. For *Acacia diphylla*

and *Alyxia ruscifolia* 5 plants of each species were burnt. Due to the low numbers, these species were not analysed statistically.

For each species, two sites were identified with over 30 individuals per site. The sites were those used in the vegetation survey (Chapter 4). Plants were randomly selected as controls or for clipping or burning. The height of the tallest stem and diameter of the stem at the base above any woody swelling was measured for all species. Any woody swelling, or lignotuber, was measured at the location of greatest width. Around those plants identified for the clipping or burning treatments, all leaf material in a 0.25 m² quadrat surrounding the plant was cut back to cleared earth.

Clipping and burning treatments were undertaken to assess the regenerative capacity of the lignotuber, and to investigate lignotuber size on regrowth. For the clipping treatment, the stems were clipped to the base, within 1-4 cm of the ground to remove all live foliage and simulate damage by burning in the absence of heat. Bradstock and Myerscough (1988) had developed a method for simulating a low intensity burn of 100% crown scorch that was reproduced in this experiment. The burn treatment was undertaken with a hand-held burner using liquid petroleum gas (LPG). A flame was applied evenly over the 0.25 m² quadrat for 120 seconds. Figure 6.1 shows the application of the burn treatment and Figure 6.2 shows the plant area immediately following the burn.

Following the burn, all sites were labelled with an aluminium tag and flagging tape. Each site was revisited after three months to assess the regenerative response of the plant, measure the size and growth of any new foliage, and measure the size of the lignotuber.

The final objective of this study was to measure the time to the first reproductive stage of each species to define either the primary (for seeder species) or secondary (for resprouter species) juvenile periods. Due to a wildfire in the sites nine months following the burns, this information was not collected.



Figure 6.1. Application of the burn treatment to *Banksia integrifolia* in the plot area.



Figure 6.2. The burn area immediately after the treatment. Note location tag.

6.2.3 Data analysis

Total number of plants resprouting or seeding three months following the burn was calculated by site and treatment. Each species was classified as either a seeder or resprouter based on the level of mortality. Where mortality was greater than 70% of the total population, the species was classified as a seeder. If mortality was less than 30%, the species was classified as a resprouter (Gill and Bradstock, 1992).

The relation between lignotuber size and the resprouting response (mortality or survival) was analysed using a generalised linear model with a binomial data structure for the response data and a log link function. The results were explored using graphs of the proportion of plants surviving the treatments by lignotuber size.

6.3 Results

6.3.1 Mode of regeneration and impact of treatments (burning versus clipping)

Of the 40 *Persoonia oleoides* plants either clipped or burnt, 88% (35) were alive and resprouting three months following the burn. Within the burn and clipped groups, three and two individuals respectively, did not resprout, so the average mortality was low (13%) (Table 6.1). However, all of the plants that did not resprout occurred in site 1 where mortality was 25%. The burn treatment resulted in a marginally higher mortality (15%) than the clip treatment (10%). There were no deaths in the controls. Figure 6.3 shows the growth of vegetative sprouts from the base of a *Persoonia oleoides* plant.

	Total plants tested	Total plants survived	Mortality (%)	Average mortality (%)
By site (control excluded)				
Site1	20	20	0	13
Site2	20	15	25	
By treatment				
Burn-site1	10	10	0	15
Burn-site2	10	7	30	
Clip-site1	10	10	0	10
Clip-site2	10	8	20	
Control-site1	10	10	0	0
Control-site2	10	10	0	

Acacia irrorata suffered high mortality in response to burning, with only one out of the 20 regenerating vegetatively. In contrast, 50% of those clipped resprouted. There was only a small difference between sites (Table 6.2), but the treatments varied, with 95% mortality in those burnt and

50% mortality in those clipped. There were no deaths in the controls. The only *Acacia irrorata* that survived the burn treatment is shown in Figure 6.4



Figure 6.3. A *Persoonia oleoides* plant resprouting three months after burning.

Table 6.2. Mortality in <i>Acacia irrorata</i> between sites and treatments.				
	Total plants tested	Total plants survived	Mortality (%)	Average mortality (%)
By site (control excluded)				
Site1	20	7	65	73
Site2	20	4	80	
By treatment				
Burn-site1	10	1	90	95
Burn-site2	10	0	100	
Clip-site1	10	6	40	50
Clip-site2	10	4	60	
Control-site1	20	20	0	0
Control-site2	20	20	0	

Banksia integrifolia was found to be a resprouter, regenerating from basal buds. Out of the 40 plants clipped or burnt, 95% had regenerated vegetatively after three months. There was no difference between sites or treatment, with each having a mortality level of 5% (Table 6.3). There were no deaths in the controls. Figure 6.5 shows a resprout after three months from one of the larger stemmed mature *Banksia integrifolia* plants.



Figure 6.4. *Acacia irrorata* resprouting from the woody base three months after burning. Arrow indicating bulbous swelling.



Figure 6.5. *Banksia integrifolia* resprouting three months after being clipped.

	Total plants tested	Total plants survived	Mortality (%)	Average mortality (%)
By site (control excluded)				
Site1	20	19	5	5
Site2	20	19	5	
By treatment				
Burn-site1	10	9	10	5
Burn-site2	10	10	0	
Clip-site1	10	10	0	
Clip-site2	10	9	10	5
Control-site1	10	10	0	0
Control-site2	10	10	0	

Of the 40 *Goodia lotifolia* plants, 65% had resprouted after three months. Of these, the burnt plants had a higher survival rate (80%) than the clipped plants (50%). There was only a small difference in mortality (10%) between the sites (Table 6.4). There was a greater (30%) difference in mortality between the burn and clip treatments. There were no deaths in the controls. Figure 6.6 shows the regrowth of *Goodia lotifolia* following the burn.

	Total plants tested	Total plants survived	Mortality (%)	Average mortality (%)
By site (control excluded)				
Site1	20	14	30	35
Site2	20	12	40	
By treatment				
Burn-site1	10	9	10	20
Burn-site2	10	7	30	
Clip-site1	10	5	50	50
Clip-site2	10	5	50	
Control-site1	10	10	0	0
Control-site2	10	10	0	



Figure 6.6. *Goodia lotifolia* three months following burn.

A comparison of mean mortality for each species over the two sites for the clipped and burned treatments ($n=20$) is shown in Figure 6.7. *Acacia irrorata* suffered highest mortality followed by *Goodia lotifolia*. *Persoonia oleoides* had the highest variability in mortality between sites. The differences between the clip and burn treatments for each species is summarised in Figure 6.8.

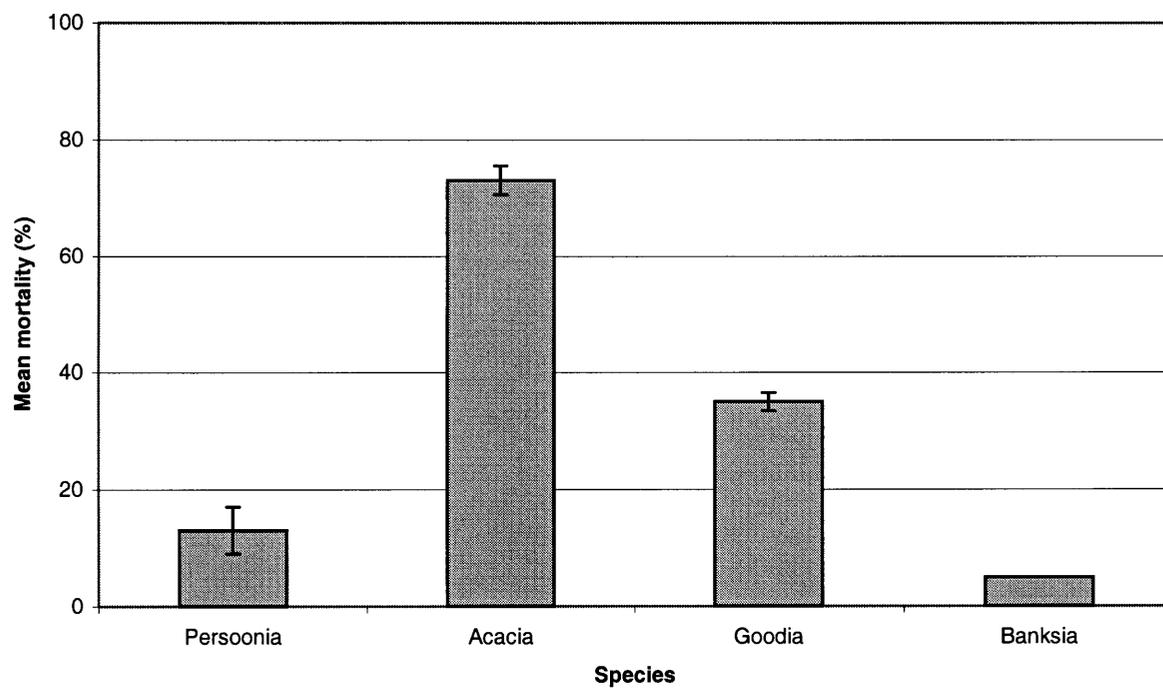


Figure 6.7. Average mortality (%) of four species tested. The average calculated over two sites and the two treatments (n=20) (\pm SE bars)

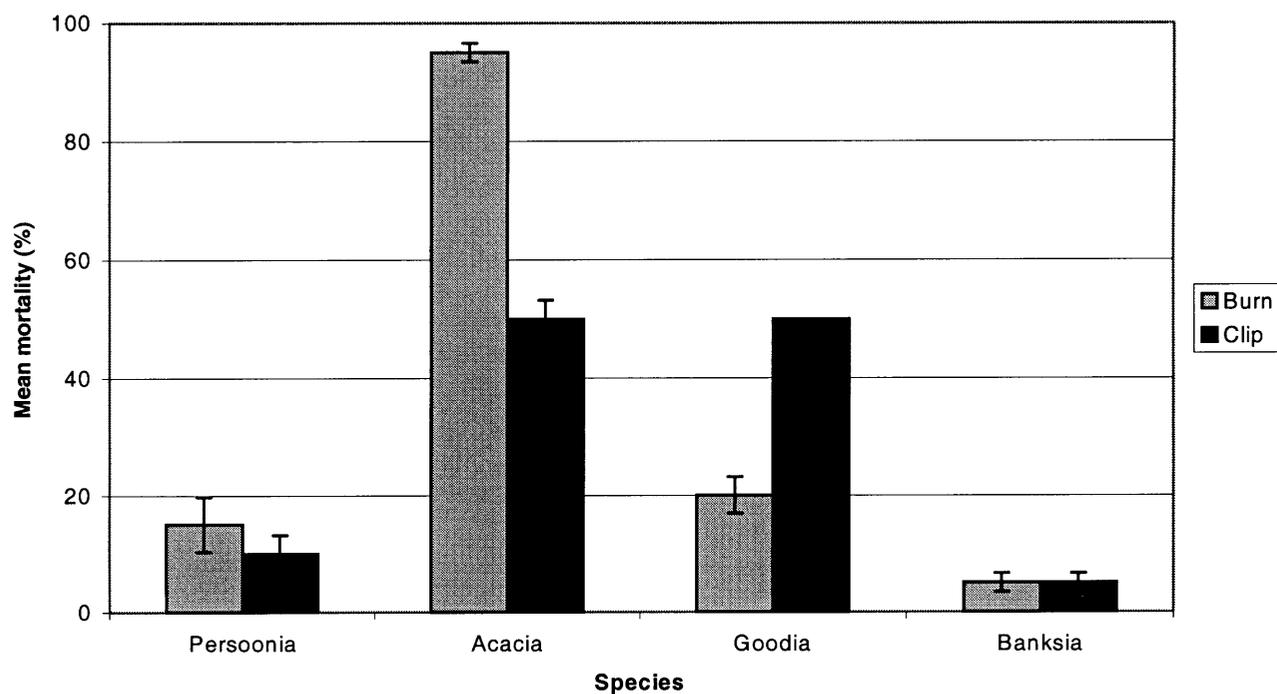


Figure 6.8. The variation in percentage mortality between the clip and burn treatments (n=10) for each species (\pm SE bars).

Rapanea variabilis was tested using 10 plants per treatment. The majority of plants (85%) regenerated vegetatively. There was only a small difference between the treatments, with 90% surviving the burn treatment and 80% surviving the clip treatment and 100% survival among controls.

Alyxia ruscifolia had a propensity to regenerate vegetatively, with only one of the five plants tested not resprouting from vegetative material. In contrast, none of the *Acacia diphylla* survived burning, there was no evidence of regeneration after three months. There were however, abundant individuals at the site that had been burnt approximately 3.5 years prior before. In both species there was 100% survival among controls.

The mortality of each species in response to the two treatments and their mode of regeneration are given in Table 6.5. The similar responses of *Persoonia oleoides* and *Banksia integrifolia* to the burn and clip treatments show that these species were resprouters. For *Goodia lotifolia* there was reduced vegetative sprouting from the clipped treatments, but overall the resprouting percentage was high. *Acacia irrorata* had high mortality, especially following the burn and was classified as a seeder. *Acacia diphylla* was also classified seeder. A summary of the species responses is given in Appendix 6.1

Table 6.5. Percentage mortality of each species following treatment. Greater than 70% mortality was defined as a seeder species (from Gill and Bradstock, 1992). There was no mortality in the controls.			
Species	Burnt	Clipped	Mode of regeneration
<i>Persoonia oleoides</i>	15	10	Resprouter
<i>Acacia irrorata</i>	95	50	Seeder
<i>Goodia lotifolia</i>	20	50	Resprouter
<i>Banksia integrifolia</i>	5	5	Resprouter
<i>Rapanea variabilis</i>	10	20	Resprouter
<i>Alyxia ruscifolia</i>	20	Not tested	Resprouter
<i>Acacia diphylla</i>	100	Not tested	Seeder

6.3.2 Regenerative capacity of the lignotuber

Three species showed strong resprouting capabilities. These were *Goodia lotifolia*, *Persoonia oleoides* and *Banksia integrifolia*, which had individuals across a range of lignotuber sizes that resprouted. The generalised linear model used to explore the response found the mortality or survival of any of the species was not significantly changed due to lignotuber size. These results were therefore explored in plots but were not significant.

In *Goodia lotifolia*, plants with a lignotuber diameter above 2 cm were more likely to survive (Figure 6.9).

The majority of *Persoonia oleoides* plants resprouted. Lignotuber size had no effect on this response (Figure 6.10).

In *Banksia integrifolia* only plants with a diameter less than 3 cm died (Figure 6.11). However, the high survival rate of plants with small lignotubers (< 1 cm) showed that even small plants had the capacity to resprout.

Acacia irrorata suffered high mortality after being burnt. There was no clear indication of a threshold of lignotuber size determining plant survival (Figure 6.12).

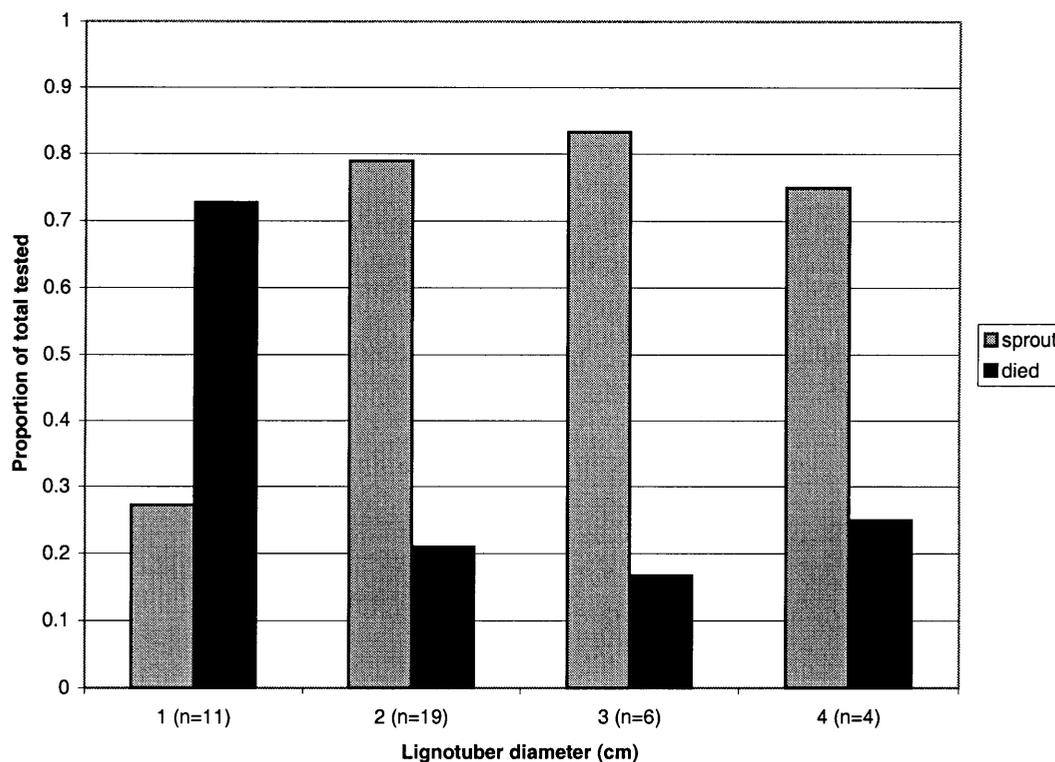


Figure 6.9. The proportion of the sample size of *Goodia lotifolia* plants surviving by lignotuber size (total n = 40).

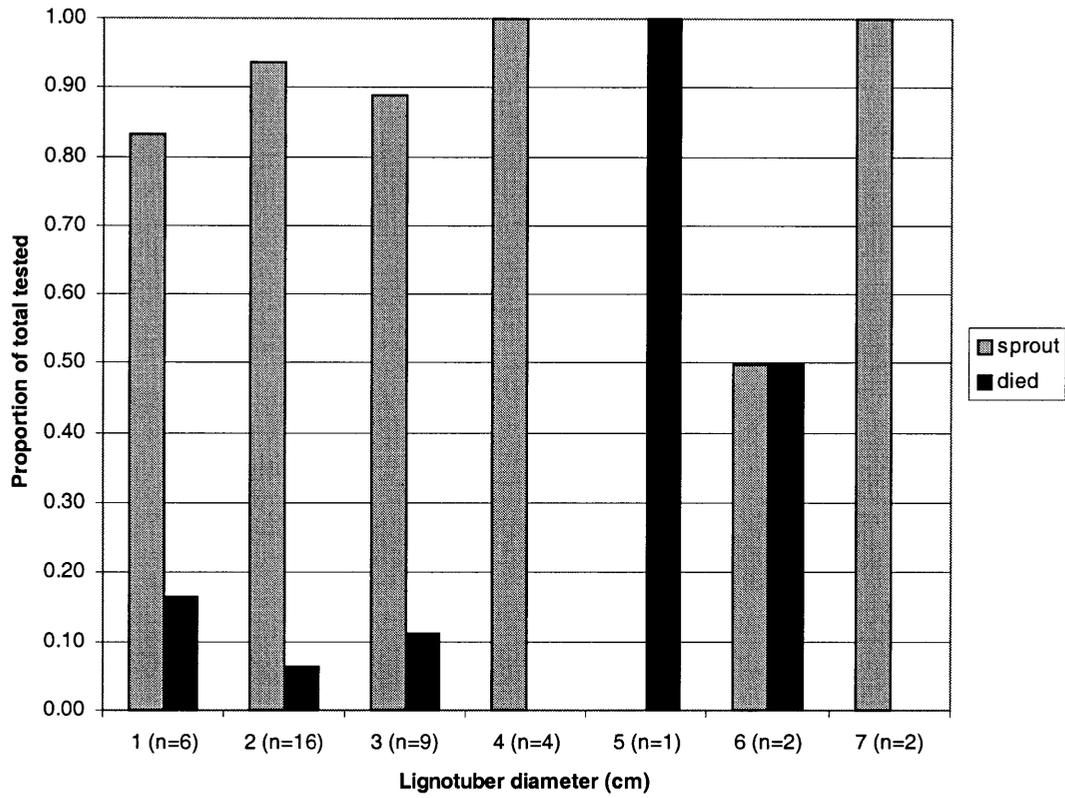


Figure 6.10. The proportion of the sample size of *Persoonia oleoides* plants surviving by lignotuber size (total n = 40).

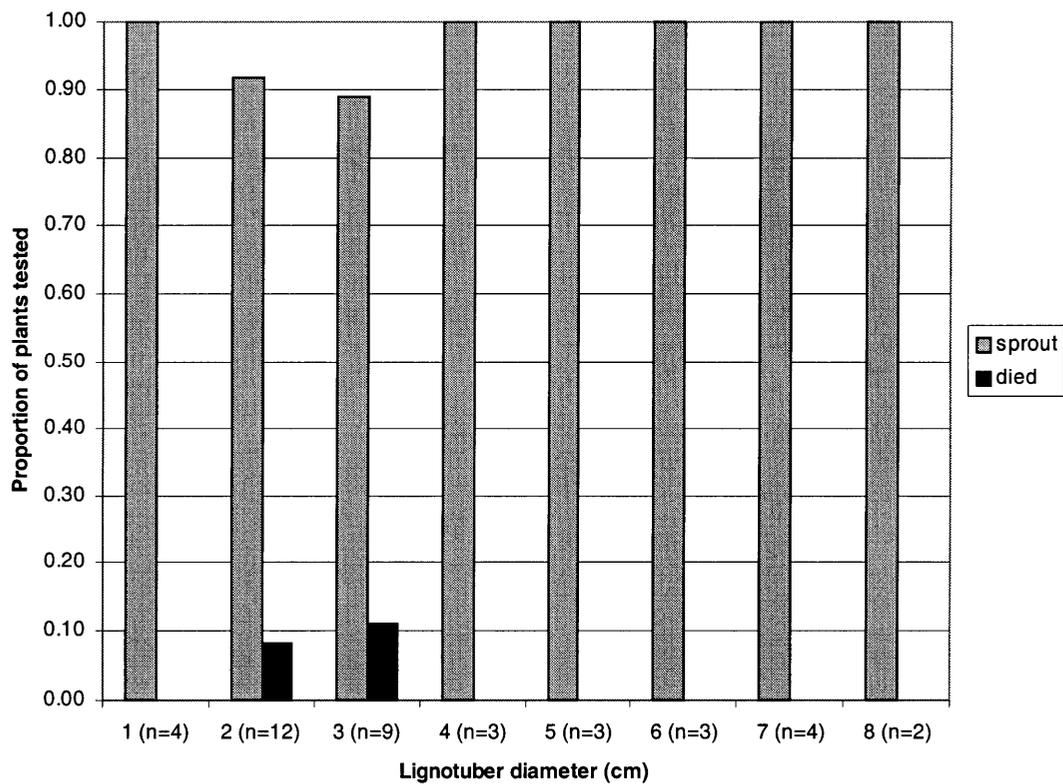


Figure 6.11. The proportion of *Banksia integrifolia* plants surviving by lignotuber size (total n = 40).

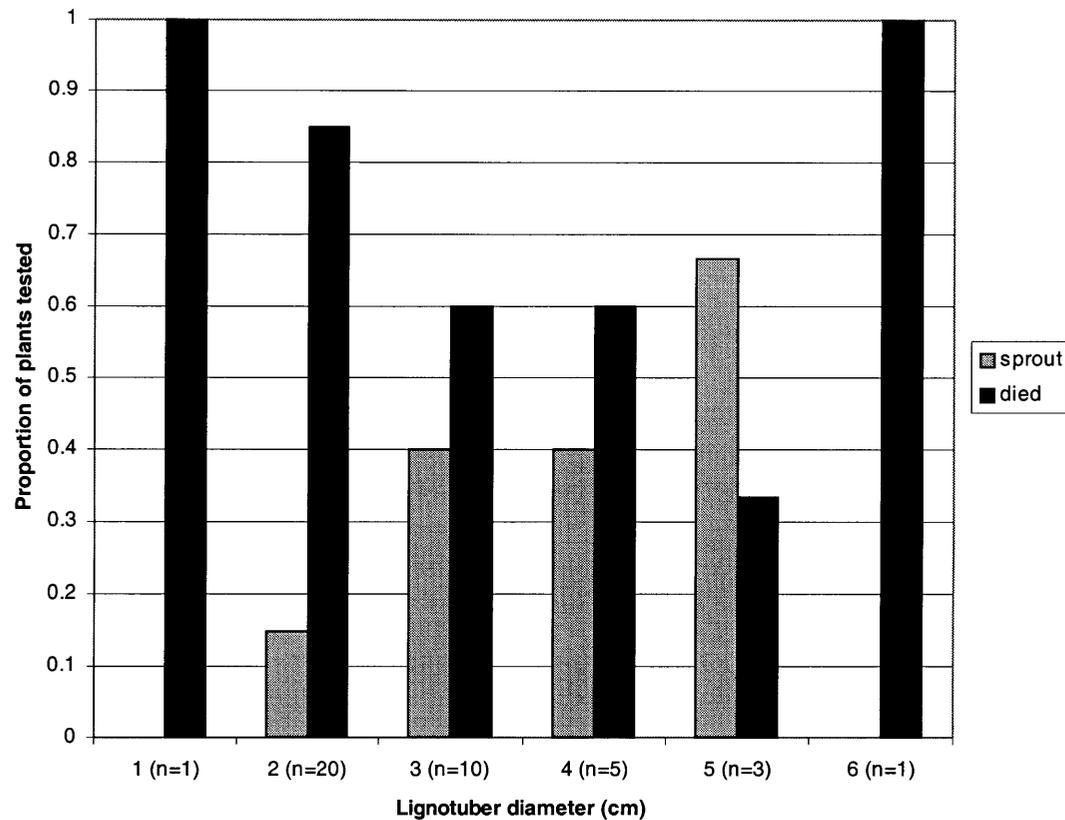


Figure 6.12. The proportion of *Acacia irrorata* plants surviving by lignotuber size (total n = 40).

6.4 Discussion

6.4.1 *Persoonia oleoides*

Persoonia oleoides was clearly a resprouter. All individuals had a lignotuber that varied from a large bulbous swelling under the soil to a small thickening at the base of the stem on smaller plants. *Persoonia oleoides* is a multi-stemmed shrub of less than 2 m, flowers in summer-autumn and fruits until April. It occurs primarily in dry and wet sclerophyll forest on various metamorphic and igneous substrates. Its common occurrence throughout the Tablelands suggests its capacity to resprout has enabled it to maintain populations in a range of conditions including areas of high NOF.

6.4.2 *Banksia integrifolia*

Banksia integrifolia resprouted in response to burning and clipping treatments. The mode of regeneration of *Banksia integrifolia* has been found to vary in NSW. It regenerates vegetatively at Jervis Bay (Ingwersen, 1977) but populations at Myall Lakes are killed by fire with seed stored on the plant (Fox, 1988). At GFRNP, generally *Banksia integrifolia* was a single stemmed shrub or small

tree without a lignotuber but with a thickening of the stem above the soil tapering into the stem. This thickening was marked with spots and horizontal fissures. New growth was observed sprouting from the parent plant from the stem thickening at the base. In the genus *Banksia*, 50% of species have been estimated to resprout, with about 34% having lignotubers (Zammit, 1988). The capacity of *B. integrifolia* to resprout has enabled its persistence in the areas of GFRNP with the highest NOF and shortest SIFI. In these populations, some of the smaller plants, burnt in the November 1994 fire, are now developing inflorescences. This indicates a secondary juvenile period of approximately 6-7 years. With the capacity to also regenerate from seed, the dual strategy of seed and vegetative regeneration contributes to its persistence in these areas.

6.4.3 *Acacia irrorata*

Acacia irrorata was classified as a seeder due to high mortality after both the burn and clip treatments. It has some capacity to resprout but only 50% of plants resprouted after clipping. Burning substantially increased mortality, indicating a low capacity to resprout following fire. *Acacia irrorata* is a single stemmed shrub with a basal thickening of the stem that in the most extreme case was a bulbous swelling above the ground (Figure 6.4). There was no obvious underground lignotuber in any of the plants. The seeds have thick coats and regenerate from the seed bank with a heat treatment (Chapter 6). The only record of its response in the National Fire Response database is as a seeder species. Its capacity to resprout under some circumstances is possibly linked to fire intensity or vegetative development of a lignotuber in some plants (Figure 6.4). The burn treatment was possibly too intense for vegetative response to occur; increased vegetative response may be found if the intensity was lower. The large number of juvenile *Acacia irrorata* plants observed in the field would suggest the majority of regeneration is due to seed-fall.

6.4.4 *Goodia lotifolia*

Goodia lotifolia had a mixed response. Most plants resprouted following burning but the 50% mortality after clipping demonstrated a response more like a seeder. *Goodia lotifolia* is a single stemmed shrub that grows as a pioneer species in disturbed sites, often in sheltered valleys and on rainforest margins (Harden, 1991). It was common and abundant in sites in the west of the Gorge of GFRNP. It had no obvious lignotuber, but a thickening at the base that, in some individuals, extended above the ground. There were signs that the tops of new juvenile growth were consumed by grazing animals, indicating other disturbance pressures. The National Fire Response database records this as primarily a seeder species. Four studies have found that it dies following crown scorch (Gill and Bradstock, 1992). One study in Victoria recorded in-soil seed storage (Chesterfield et al., 1990). The lower survival rate of those that were clipped compared to those that were burnt suggests that heat

may have played some role in assisting resprouting. This is in contrast to the response of *Acacia irrorata* where heat was detrimental for resprouting. Overall, *Goodia lotifolia* was classified as a resprouter due to the resprouting response (80%) following the burn.

6.4.5 *Rapanea variabilis*

Rapanea variabilis was a resprouter. This species is found in NSW in rainforest and open forests on the coast and adjacent ranges north from Milton, and often in exposed positions on the coast (Harden, 1990). The plants tested in this study primarily occurred on scree slopes, with all of the plants having thickened stems winding under rocks that may have afforded some fire protection. Other studies have found *Rapanea variabilis* to be a resprouter. In Lane Cove and Narrabeen in NSW, it is found to resprout from the base following high intensity fire, and flowered less than 2.5 years following the burn (Benson and McDougall, 1997). In GFRNP it was found to have vigorous basal sprouts three months following the burn, some reaching 10 cm in height or almost one-third of the average height of the mature plant.

6.4.6 *Alyxia ruscifolia*

The regenerative response of *Alyxia ruscifolia* was shown to be a resprouter. This species, generally growing in moist rainforest from sea level to 1200 m (Harden, 1992), was found here in sclerophyll forest. It was a multi-stemmed plant with an obvious thickening at the base that wound under the rocks of the scree slope. This may have afforded some protection from the heat of the burn. Its capacity to resprout contrasts with its response in Northern Australian monsoonal forests, where it dies following crown scorch (Russell-Smith et al., 1998).

6.4.7 *Acacia diphylla*

Acacia diphylla did not resprout and was classified as a seeder. The species is a single-stemmed shrub, highly abundant at the site, and generally found on steep slopes in dry sclerophyll and dry rainforests (Harden, 1991). The species had no obvious swelling at the base. It is possible that the three months between treatments and subsequent observations were too short for this species' regeneration which may occur in spring. Given the small sample size, these results are indicative only. Further research is warranted.

6.4.8 *Seeding versus resprouting*

Four out of the seven species studied were classified as resprouters based on the classification of Gill and Bradstock (1992). The resprouter trait in woody plants is assumed to be the ancestral condition

and the failure to sprout the derived condition (Bond and van Wilgen, 1996). These traits have differing resource allocation consequences. A study of the response of seeder and resprouter species indicated that seeder species are generally taller, with a fourfold greater shoot to root ratio (Pate et al., 1990). Some of the attributes resprouting species have, when compared to seeders, include greater longevity of individual plants, later age to first reproduction, slow growth rates in the first years after fire, lower rates of seed production, allogamy in the pollination system and smaller numbers of flowers per plant (Carpenter and Recher, 1979). The resprouting species allocate post-disturbance resources to replenish starch reserves in the lignotuber as opposed to plant stem and leaf growth in the seeders. These assumptions have been tested using *Banksia ericifolia* (as the seeder) and *Banksia spinulosa* (as the resprouter) and the predictions generally borne out and in agreement with a similar comparison between *Banksia marginata* (the resprouter) and *Banksia ornata* (the seeder) (Specht et al., 1957).

This study has shown that *Goodia lotifolia* and *Banksia integrifolia*, which in other locations in NSW have regenerated from seed, opt for the strategy of resprouting at GFRNP. This, plus evidence of the high numbers of resprouting species in the study region (Section 7.3.2), suggests conditions in GFRNP may have resulted in species opting for resource allocation to lignotuber or other vegetative regrowth. In an environment of frequent disturbance, this may be a more successful strategy for ensuring plant persistence. Alternatively, the past fire history in GFRNP may have resulted in the majority of seeder species declining from the general population and the number of resprouting species a reflection of past selection processes. These questions need further research.

6.4.9 Survival and lignotuber size

The majority of species tested lacked any correlation between the lignotuber size and the capacity for the plant to resprout. This was also found in a study of *Banksia serrata*, where stem diameter and fire intensity were more important determinants of plant survival (Bradstock and Myerscough, 1988). This would suggest that the development of the lignotuber is the primary requirement for resprouting, after which the size of the lignotuber is of lesser consequence.

Canadell and Lopezsofia (1998) undertook an extensive study of the reserves stored in the lignotubers of two Mediterranean shrubs. Very low starch levels in lignotubers were found to cause mortality in plants that were subject to multiple clipping treatments. Starch and nutrient resources in the lignotuber were heavily depleted after multiple disturbances. It was suggested that the low production of photosynthate after clipping was not enough to support new tissue growth and keep up with the respiratory demands of an extensive root system.

The lignotuber has two primary roles: (a) to store concealed buds that will resprout after disturbance, and (b) to store non-structural carbohydrates and nutrients that will support regrowth after disturbance

(Canadell and Lopezsofia, 1998). Thus lignotuber resources may best sustain regrowth in environments where multiple disturbance events occur before resource limitations cause plant mortality. The combination of disturbance frequency and environmental conditions in GFRNP may well select for vegetative regeneration rather than regeneration from seed.

The resprouting capacities of lignotubers have been linked to the capacity to store carbohydrates (Bamber and Mullette, 1978) rather than size. Size is related to protection of tissues, with sufficient thickness being required for insulation of the internal tissues (Bradstock and Myerscough, 1988). Failure of a plant to resprout after disturbance is related to a number of issues, including meristematic tissue damage, bud-bank size, tolerance to drought in post-disturbance conditions and availability of below-ground reserves (Noble, 1984; López-Soria and Castell, 1992; Canadell and Lopezsofia, 1998). Moisture stress can also limit the capacity of the plant to tolerate dry conditions, slowing post-fire regeneration.

6.5 Conclusions

This study has determined the mode of regeneration for a number of plants in this region. It has demonstrated that most species studied have the capacity to resprout, with some variation found between the responses to burning and clipping. For some species (e.g. *Acacia irrorata*), the added stress of burning resulted in higher plant mortality. In contrast, for other species (e.g. *Goodia lotifolia*), the added stress of burning resulted in higher survival rates.

The capacity of species to resprout in areas of high NOF increases the likelihood of their persistence in a regime of frequent fires. The variation in patchiness of burnt areas and in the intensity of the fire will afford some protection to species. In areas of high numbers of fires, lower intensity fires or patchy fires will result in the survival of some fire sensitive species. However, the death of some species suggests that longer fire intervals may increase the replenishment of lignotuber reserves and generate a higher likelihood of species continued presence at these sites.

The results on the primary or secondary juvenile period could not be completed due to an unplanned wildfire. This information would have supplemented the information on the mode of regeneration with a time to first reproduction for these plants. These two pieces of information can be used to determine the fire interval that enables species to persist in the community following a fire. Fire management planning can thus be targeted to achieve appropriate fire intervals for optimum species survival. This study has demonstrated a relatively straightforward approach to collecting more information on species' responses to fire. By obtaining more information on individual species' responses to fire, fire management outcomes can target the persistence of all species.