CHAPTER 5

5 SPECIES RESPONSES to FIRE - seed banks and post-fire regeneration

Since only the kiss of the flame is needed to rouse dormant seed from decades-long sleep, is it not strange that botanists do not turn arsonists on occasion that some floral phoenix might arise from the ashes?

-- John Thomas Howell, 1946 taken from Keeley et al. (1981)

5.1 Introduction

The work reported in Chapter 4 established that fire frequency influenced species richness and abundance in the Tablelands and Gorge vegetation of GFRNP. What was the below-ground potential of vegetation stored as seeds, and how had fire frequency affected the soil seed bank? Soil contains the seed of future plants. Plants can disappear from the above-ground vegetation, but retain viable seed in the soil, ready for suitable conditions in which to germinate. Disturbance such as fire can induce conditions suitable to initiate germination. These conditions may include the post-fire site conditions of reduced biomass, increasing light and nutrients, or the physical nature of the fire that brings heat and smoke to the soil.

Frequent fires can reduce the size of stored soil seed banks if burning occurs prior to the reproductive life-stage of a plant. Frequent fires will favour those species that reproduce rapidly or those that protect regenerative parts from flames. Frequent fires may lead to extinction of some species (Bradstock et al., 1995). Under a regime of less frequent fires, those species that require more time to reproduce will have a higher likelihood of survival.

The storage of viable dormant seed in the soil can be a major recruitment source for plant species in fire-prone environments. North American chaparral and South African fynbos (Keeley and Bond, 1997) are habitats where the soil is a source of dormant seed for future plant regeneration. In Australia, a number of soil seed bank studies have focused on woody plant species, especially serotinus plants with canopy-borne seed banks (e.g. Enright and Lamont, 1989; Bellairs and Bell, 1990; Lamont et al., 1991; Vaughton, 1998; Enright et al., 1998a; 1998b). The timing of fires and mechanisms for seed release, influences the quantity and availability of seed for post-fire generations.

The soil seed banks of herbaceous species, especially in grassy woodlands and temperate grasslands, have attracted recent interest (e.g. Lunt, 1990; Gilfedder and Kirkpatrick, 1993; Lunt, 1994; Marsden-Smedley et al., 1997). These ecosystems are threatened with extinction due to clearing, grazing and inappropriate fire regimes. The soil seed bank has a role in buffering populations against disturbance events or unfavourable germination conditions (Lunt, 1997).

Studies of soil seed banks in relation to fire regimes in open-forest ecosystems are relatively few. The role of fire in managing grasslands and their seed banks for the conservation of native species has been studied (Lunt, 1994; Morgan, 1998). Others studied have focused on specific plants and the influence of fire (Ashton, 1986; Bradstock et al., 1994) and on *Acacia* species due to their reliance on heat for seed germination (Auld, 1986b). Studies have also been undertaken on specific families (e.g. Restionaceae and Epacridaceae) (Meney et al., 1994) and their seed bank features, particularly their response to fire-related germination cues. In forest ecosystems, in areas of mined for bauxite, seed banks and fire have been investigated in relation to rehabilitation conditions following disturbance (Grant and Koch, 1997; Ward et al., 1997). In the United States, the

Californian chaparral has been the focus of a number of studies on plant population dynamics in relation to fire regimes (Keeley, 1977; Zammit and Zedler, 1988; Moreno and Oechel, 1991).

While the size of the soil seed bank can be influenced by fire frequency, the innate dormancy of some seeds can require specific conditions for germination success. The heat requirement of *Acacia* seeds (see Section 1.7.2) is an example of plants requiring high intensity fires to break hard seed coats and initiate germination. Similarly, smoke is a dormancy breaking agent for a number of species in fire prone environment (see Section 1.7.3). While the primary role of germination treatments in this study was to maximise germination rates to establish the contents of seed banks the study provided an opportunity to explore individual species' responses to germination treatments.

The impact of different fire intensities on the seed bank was investigated by experimental burning. GFRNP is thought to have had a long history of many low intensity fires (Reid et al., 1996) prior to the fire history of the last 25 years. Changing the fire intensity, both in-situ and through germination treatments, provided the potential to investigate seed bank processes under varying condition. This study provided the opportunity to investigate the influence of a fire of higher intensity, thereby exploring other components of the fire regime.

Post-fire succession has been studied through experimental burns and the assessment of the regeneration potential by seed and vegetative means of plants in forests of south-east Australia (e.g. Purdie, 1977a; 1977b). Vegetation succession theory has used a number of models to describe the sequence of species changes observed through time. Some of these concepts were discussed in Section 1.2.

In order to complement the above-ground vegetation survey information (Chapter 4) with data on the pattern and processes of below-ground vegetation and post-fire regeneration for fire management, this study aimed to determine the impact of fire frequency on the richness and abundance of the soil seed bank and above-ground vegetation composition and to explore regeneration of the major vegetation types following disturbance.

The main objectives of these experiments were to:

(1) Determine how the richness and abundance of the viable stored soil seed bank varies in relation to fire frequency;

(2) Determine how the richness and abundance of the viable soil stored seed in an area of high numbers of fires may vary before and after fire;

(3) Investigate the role of germination treatments on the establishment of plant species from the soil seed bank;

(4) Compare species richness in the soil seed bank with that of the above ground vegetation;

(5) Investigate temporal vegetation changes, specifically in woody plant species, following burning; and

(6) Determine the mode of regeneration of some woody shrub and tree species.

5.2 Methods

5.2.1 Study area

The location of the soil seed bank study was a site of approximately 3 x 3 km (Figure 4.2) on the Tablelands. The area included patches within high and low NOF. The vegetation in the low NOF sites had a more complex structure than the high NOF sites that had a more simple structure.

Six areas of 100 x 100 m with a history of high NOF and short SIFI (HSS) and three areas of low NOF and long SIFI (LLL) were identified. Within each area, a 0.1 ha (approximately 32 x 32 m) sample site was randomly placed and the soil seed bank and the above-ground vegetation of the sites were sampled (method given below). The three LLL sites, to be referred to as 'LLL-unburnt', were compared to the three HSS sites to be referred to as the 'HSS-unburnt' sites (Figure 5.1A). The three HSS-unburnt sites were randomly placed in the high NOF area after the burns so the sites were unaffected by smoke. The LLL-unburnt and HSS-unburnt sites enabled a comparison of the stored soil seed bank in relation to fire frequency.

The other three HSS sites were sampled before and after three moderate intensity burns that were undertaken in October and November 1998. These sites will be referred to as the 'HSS-preburn' and 'HSS-postburn' sites (Figure 5.1B) and will enabled a temporal comparison of the HSS area before and after burning. Within each area, the three 0.1 ha sites will be referred to as sites. Within each site, there were 10 x 1 m^2 plots to assess forb and grass species abundance. All sites were spatially non-contiguous to optimise replication (Hurlbert, 1984). This terminology of area, sites and plots will be used throughout this chapter.

To minimise the effects of bedrock and landscape position the sites were selected with similar geology, slope, elevation and aspect. There were some differences in the density and species richness of the woody shrub layer between the sites. Those within the HSS area all contained open *Eucalyptus*-dominated forest with a sparse shrub cover including *Allocasuarina littoralis*, *Leucopogon lanceolatus* and *Persoonia oleoides*. The LLL sites were *Eucalyptus*-dominated forest with a moderate shrub cover. These included the shrub species found in the HSS area along with *Acacia irrorata, Banksia integrifolia, Hakea microcarpa* and moderate levels of *Eucalyptus* regrowth.

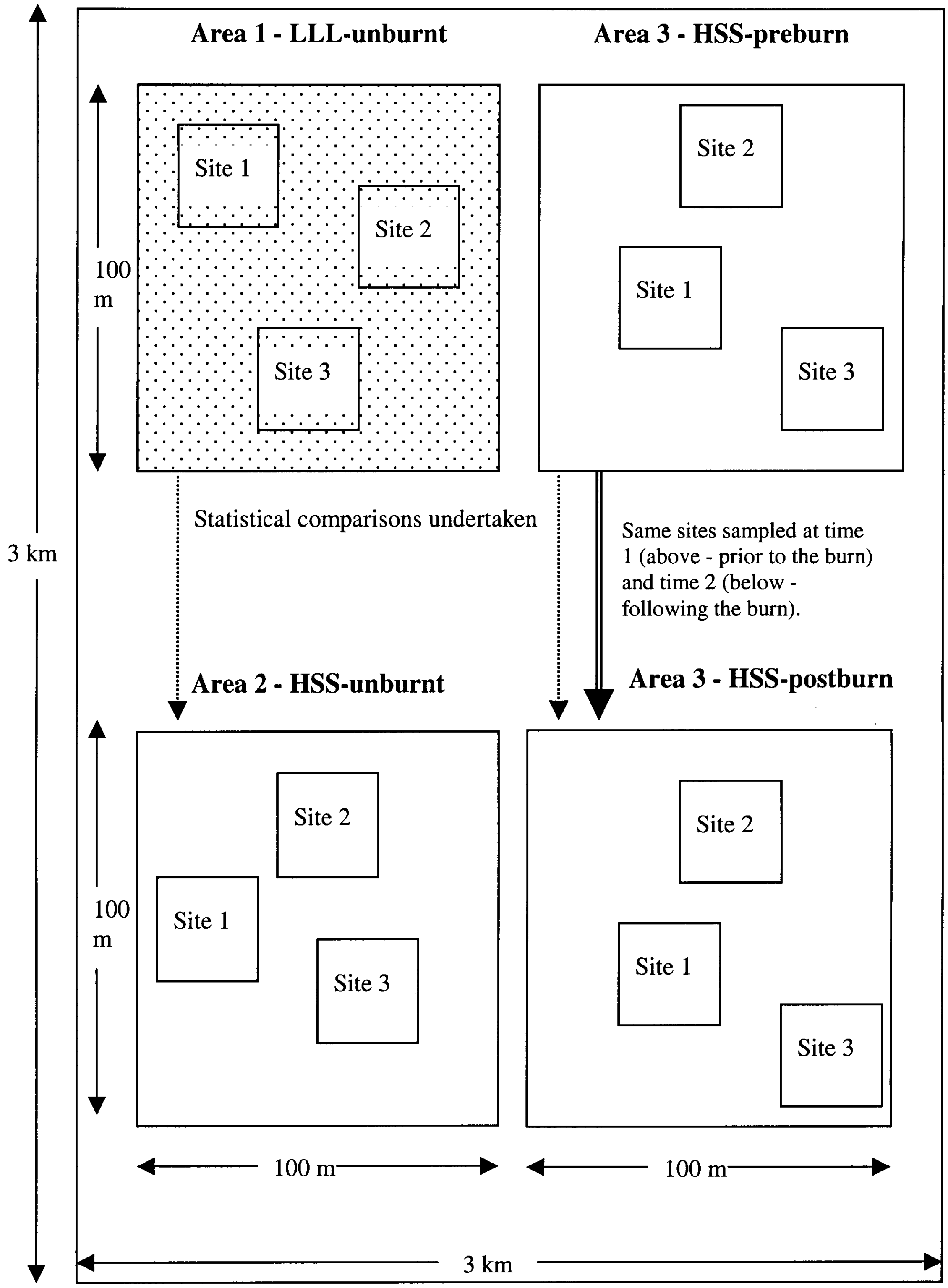


Figure 5.1. Experimental design of seed bank study. Area 1 is the unburnt area in the LLL fire category (dotted background). Area 2 is the unburnt area in the HSS fire category (clear background). Area 3 is the burnt (pre) and post-burn states being the same area in the HSS fire category sampled at two times. The sites were all 0.1 ha and contained 10 plots (1 m^2). All areas were spatially non-contiguous. The diagram is not to scale and does not represent the actual spatial layout in the field. The dotted arrows indicate the statistical comparisons made between areas.

5.2.2 Soil seed bank germination methods

Two main methods are used for quantifying soil seed banks; seed separation and seedling emergence methods (Ter Heerdt et al., 1996). Seed separation methods typically use flotation or sieving to separate seed from the soil. Commonly the residual material still contains seed and sorting under a microscope is needed to retrieve all seed. Seed separation is highly effective for large seeded species (Ter Heerdt et al., 1996) and has the advantage of not being affected by germination requirements. However, accuracy levels can be low if all seeds are not detected. In addition, the technique can be time consuming for large-scale studies.

The seedling emergence method relies on germination of the seed in the soil. Samples are spread in trays in a glasshouse and maintained under conditions optimum for germinating as many species as possible. The seedling emergence method is the simplest, least time consuming and most appropriate for large-scale studies. However, Thompson and Grime (1979) stated that this method is 'not designed to provide a complete assessment of the seed flora present'. It provides an estimate of the readily germinable fraction of the seed bank (Gross, 1990). The main problem with this method is determining the most suitable germination conditions for as many species as possible.

5.2.3 Field sampling - soil seed bank

For a soil seed bank study, the size of the soil cores and the number and dispersion of cores sampled over the study area relates to the amount of soil sampled and thus, the likelihood of sampling species. Increasing the sampling density increases the amount of soil collected, which in turn increases the likelihood of species detection. There is a trade-off between collecting enough soil to optimise the likelihood of sampling all species, and the time and resources available for the collection and processing of soil. Generally, a number of smaller samples rather than fewer larger samples is optimum for a greater spread of collection points, providing a higher likelihood of sampling seeds, particularly those with a clustered distribution (Brower and Zar, 1977).

In this study, the distribution and seed abundances were unknown. Published germination levels of species from soil seed banks (e.g. Shea et al., 1979; Lunt, 1997; Morgan, 1998) vary with habitat types, from 2 931 seeds/m^2 in *Acacia* forest, to 3-53 seeds/m^2 in subalpine forests (Baskin and Baskin, 1998). The woody understorey shrub, *Acacia pulchella*, which occurs in Western Australian Jarrah forest, has been found in average seed numbers of 20 seeds/m^2 ($\pm$7.5) (Shea et al., 1979). Lunt (1997) found *Acacia implexa* seeds at a density of 2 individuals/m^2 in south-east Australian grassy forest remnants, *Acacia suaveolens* has been found in densities of 5.6 - 23.3 seeds/m^2 averaged over three years, in the top 5 cm of soil in south-east Australia (Auld, 1986b).

Using these studies as a guide, a low seed density was chosen to estimate the amount of soil that had to be collected to maximise sampling of species with low seed abundance. In this study, a standard depth of 10 cm was sampled. The standard measure for volume is m^3, however for comparison with other seedbank studies, volume measures have been converted to m^2. The density of 12 seeds/m^2 was chosen as an average, low seed density. The formula for calculating the minimum detectable seed density was used to calculate a suitable level of sampling (Thompson et al., 1997).

$$Q > \ln(20) / (N \times A) \qquad \ldots(5.1)$$

where Q is the minimal detectable density of seeds per litre (m^2), N is the number of cores and A is the volume of each core (m^2).

A core of 5 cm diameter and 10 cm depth was selected (Figure 5.2), giving a volume of 196.35 cm^3 of soil, for the calculation of equation 5.1. Assuming Q could be as low as 12 seeds/m^2, the equation was solved for N. It was calculated that 127 samples were required from a 0.1-ha plot to have a 95% confidence interval for detecting species with an abundance of 12 seeds/m^2.

Figure 5.2. Soil corer (5 x 10 cm) used for sampling the soil for seed bank analysis.

A total of 130 samples were taken from each of the three 0.1-ha sites in each area. Four cores were taken on the corners of the 10 random 1 m^2 plots used to assess forb and grass species abundance. The remaining 90 cores were taken from ten transects running north-south within the site, with nine cores evenly placed along each transect. A total of 130 samples for the HSS-preburn and HSS-postburn sites were taken before and after moderate intensity burns in October and November 1998. The layout of the sites is shown in Figure 5.3.

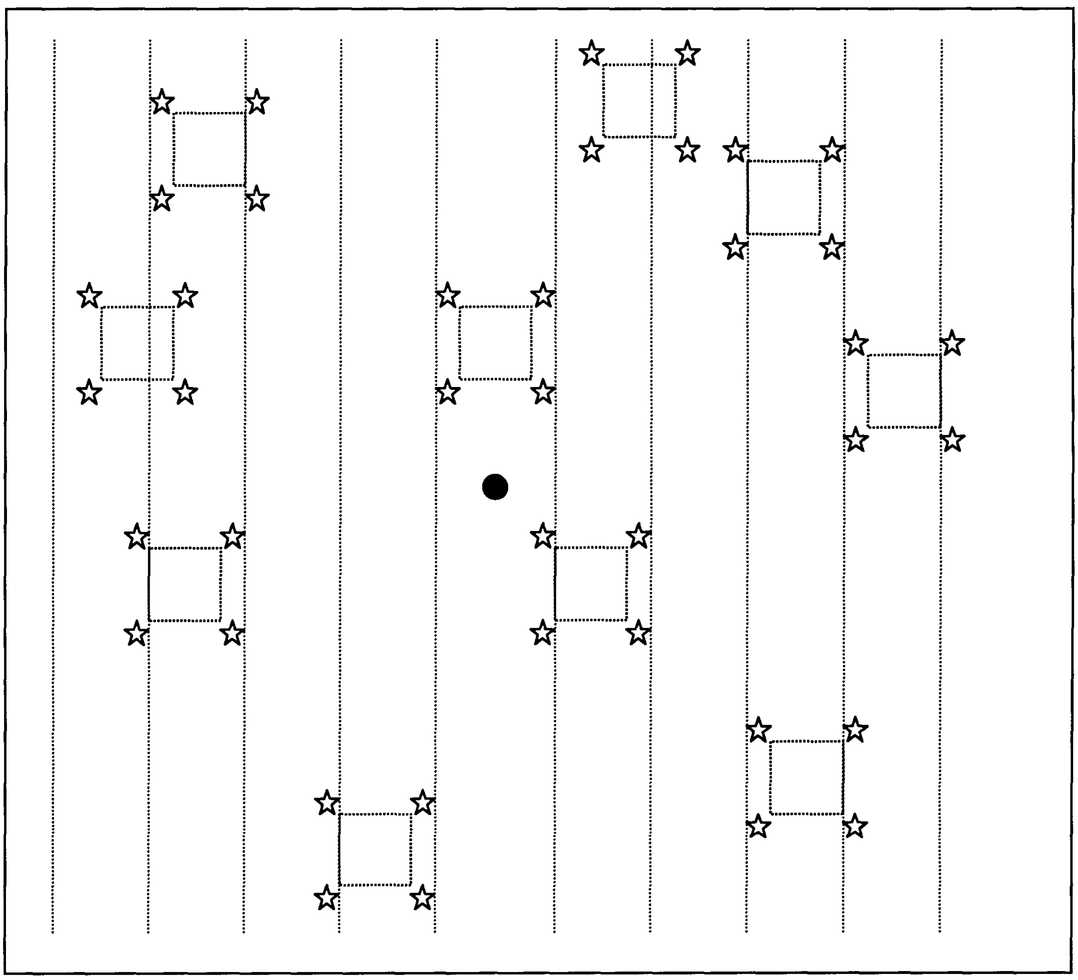


Figure 5.3. Layout for each of the 0.1 ha sites. Black dot is the site centre peg. The dashed lines are the 10 transects for general soil collection. The dashed boxes are the 10 x 1m^2 plots for ground cover vegetation sampling (randomly placed so the actual location differed between sites) and the stars on each corner are the location of the soil samples.

5.2.4 Germination treatments

Treatments were chosen to optimise seed germination. Three dormancy-breaking treatments were undertaken: heat, smoke and gibberellic acid. Many studies have shown temperature, especially heat, to be an important germination cue (Pitt et al., 1997); there is increasing evidence of positive germination responses to smoke from species in fire-prone environments (de Lange and Boucher, 1990; Keeley and Fotheringham, 1998). Gibberellic acid is known to increase germination rates in some species (Bell et al., 1995). These germination treatments were discussed in Section 1.5. There was also a control where no treatment was applied.

The soil was air-dried and stored prior to treatment. Due to the large amount of soil requiring processing in this study, the seedling emergence method was used. The four samples taken around the 10 randomly placed 1 m^2 plots were combined and divided into four sub-samples using a riffle. The soil was placed in 17 x 13 cm foil trays lined with sterile cloth (Figure 5.4). The other samples taken from transects were mixed and divided into three replicate samples for each of the four treatments. The soil was spread over sterile potting mix in a number of larger (34 x 29 cm) plastic seed trays (Figure 5.5). Trays were randomly assigned to a treatment.

The trays were placed in a dry oven at a temperature of approximately 80°C for 30 minutes before being placed in the glasshouse. This temperature was chosen as it had been established to be the optimum heat treatment for *Acacia* species (Auld, 1986b; 1986c) enabling heating of the soil to transfer heat to the seed.

'Seed Starter' smoked water was purchased from Kings Park Research Laboratories and made up to the 1:10 concentration recommended. The smoke treatment trays were kept moist with this solution for one week before being placed in an unheated glasshouse.

Gibberellic acid at a concentration of 50 parts per million (ppm) was prepared. Plummer and Bell (1995) had tested a number of concentrations of GA from 0-500 mg L^{-1} and found effective concentrations ranged from 1-100 mg L^{-1}. The samples were watered with GA every second day for 6 days, and then placed in an unheated glasshouse. The glasshouse temperatures ranged from 2-38°C over the six months of the experiment.

The 250 trays were randomly placed in the glasshouse. They were spray-watered twice a day and moved approximately every month to maintain randomness of conditions. The trays were monitored for seedling germination at 1, 2, 3, 4, 6 and 7 months. A germinant was defined as any emerged seedling. All emergent seedlings were identified, counted and removed. Unidentified seedlings were potted to flowering for identification. Some of these potted species died due to faults in the glasshouse watering system. Some species could not be identified and were grouped as either 'forb-unknown' (unknown herbs); Poaceae spp. (unknown grasses) or Cyperaceae spp. (unknown sedge and rush species). All woody plants were identified to species level.

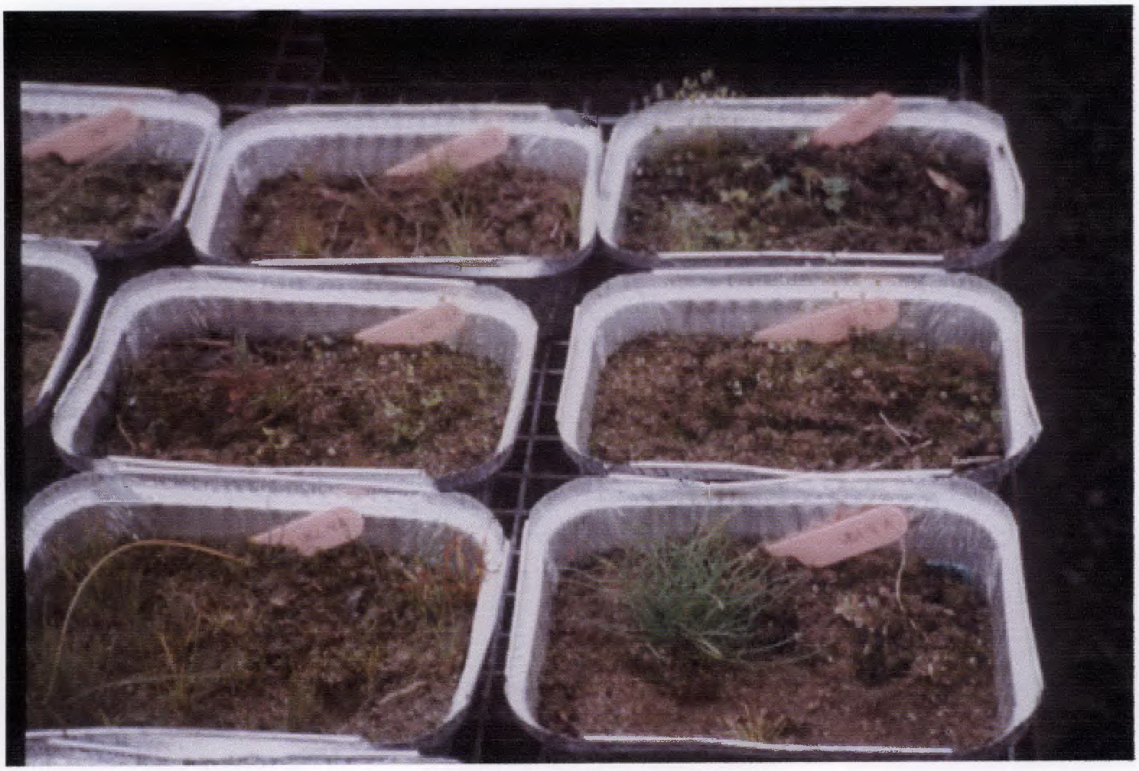


Figure 5.4. Smaller foil trays with soil samples and germinants after 3 months of growth. The smaller trays contained the soil from the 1m^2 plots within the sites.

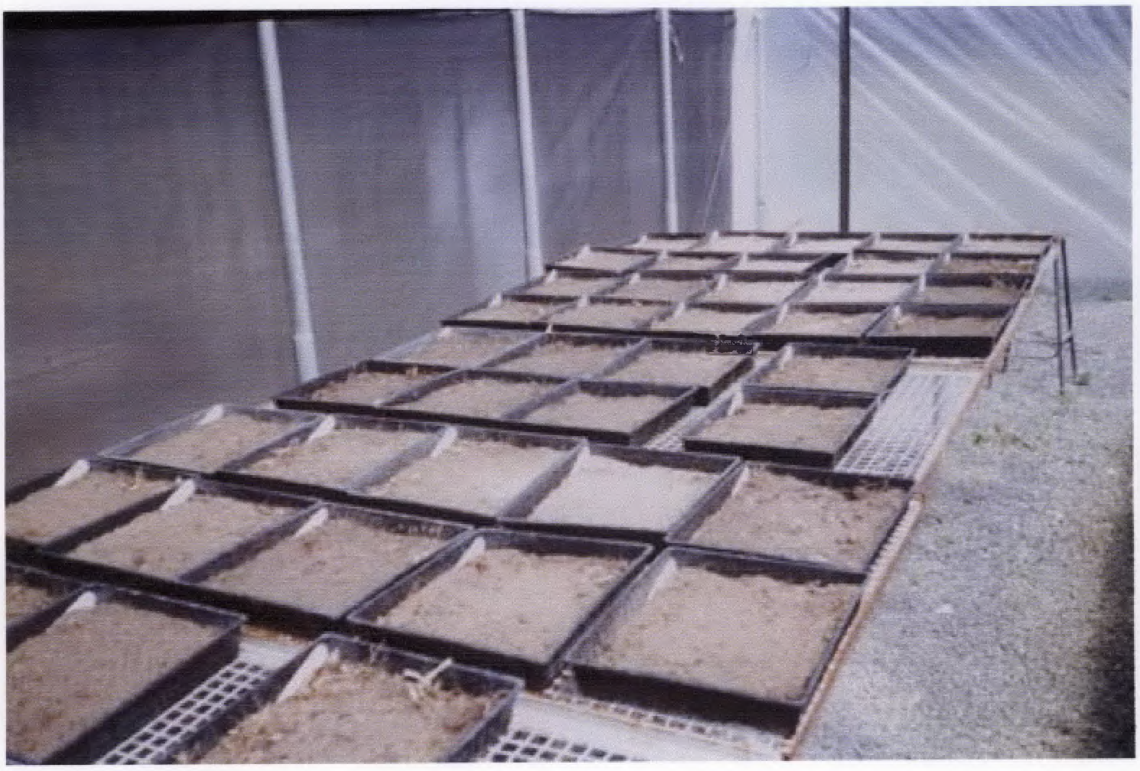


Figure 5.5. Trays of treated soil from the site transects.

5.2.5 Field sampling - above-ground vegetation

Data on the floristic composition of the vegetation was collected for comparison with the contents of the soil seed bank. Floristic data were also collected at the experimental sites to monitor pre and post-burn. The vegetation survey methods matched those adopted in the vegetation study described in Chapter 4.

Floristic data for each site were obtained using a nested design of ten concentric square sub-sites. The 'frequency score' method (Outhred, 1984) was used to record species' occurrence. This method has been used in a number of vegetation studies (Cary and Morrison, 1995; Morrison et al., 1995a; Clarke et al., 1997) and has been found to be a better measure of density than the traditional frequency method (Morrison et al., 1995b).

All woody trees and shrubs rooted in each site were recorded, together with height and diameter at breast height (DBH) if above 2 m tall, or diameter at base if below 2 m. The growth form and regenerative response to the fire was recorded for all species. Floristic information on the herbaceous vegetation of each of the sites was recorded for the 10 randomly placed 1 m^2 plots. Cover was recorded for all species rooted in the plot.

Vegetation change following burning was assessed using ground cover data for the ten 1 m^2 plots for the ground cover vegetation and density data for the woody trees and shrubs. Plots were monitored at 1, 6 and 12 months following the burn. All woody shrubs were tagged before the burn to monitor the regenerative mechanism and rate of regrowth. Approximately 60% of the juvenile plants of the main tree species were tagged and observed before and after the fire for mode of regenerative response.

5.2.6 Fire behaviour

A week prior to the experimental burning, fine fuels were sampled in each site (the three 'burnt' sites). Fine fuels are those combustible materials less than 6 mm in diameter (Luke and McArthur, 1978). All fine fuel, predominantly native grasses and small twigs, in a 0.25 m^2 plot was harvested at each of the site corners and along each side, a total of eight samples. The fine fuels were separated into grasses and twigs, weighed and oven dried and the fuel-load calculated for each site. After the burn, fuel samples were taken again, from plots 1 m away from the original samples. These were dried and weighed and the fuel consumed by the fire was calculated. The final weight was used to calculate the fuel-load and fuel-moisture.

Fuel moisture measures were taken on the day of the burn using an automatic fuel moisture meter (TH Fine Fuel Moisture Meter - Model ME2000). The temperature (wet and dry bulb), relative humidity, wind speed and direction were also measured. The sites were secured by spraying liquid foam around the edge. Due to the weather conditions and dry fuel moisture, only the 0.1 ha site within the 1 ha areas were burned.

To calculate the intensity of the fire, a number of measurements were taken during the burn. These were the variables required to calculate fire intensity using the Byram fire intensity (Byram, 1959) equation 1.1 (section 1.3.2). The rate-of-spread was measured using steel stakes placed at 5 m intervals in each site.

To generate a moderate intensity experimental burn, in an area with a history of low intensity fires, fine fuel (as seedless straw) was added to the sites identified for burning. The fine fuel load was increased to 1.6 kg/m^2. Research had established that 0.6-2.0 kg/m^2 of fine fuel can stimulate the germination of buried legume seeds whose dormancy was broken at approximately $\geq 60^{o}C$ (Bradstock and Auld, 1995). Therefore, 15 bales of straw, each weighing 14-15 kg were added to each site. This was spread evenly throughout the site and distributed down within the grass to replicate the existing fuel structure (Figure 5.6). The straw was added to all calculations of fuel load.

To measure the underground temperature, a data logger with 12 leads and temperature thermistors on the end, was buried in the centre of the site. The temperature thermistors measured from 0-100 ^{o}C in 0.1 ^{o}C intervals. Three leads approximately 10 m long were laid along the four axes of the compass. The thermistors were buried at depths of 5 cm, 2.5 cm and at the surface. One set of thermistors failed to work in the first burn, so for the third burn heat sensitive crayons were placed on boards buried to 10 cm below ground at the 4 points of the site.

The first two sites were burned on 29 October 1998 and the third on 5 November 1998. Following the burns, the sites were fenced to exclude cattle. The HSS-unburnt sites were established in areas unaffected by smoke a week following the final burn.

Figure 5.6. Burn site 1, prior to burning with addition of straw, 29 October 1998.

5.2.7 *Data analysis*

The mean number of germinants was calculated for each species by area and treatment. Individual species responses to site and treatment were assessed from the mean germinants to emerge from the soil seed bank for each of the three replicate sites, and for each germination treatment.

To test the differences in species abundance of viable soil stored seed in relation to fire frequency (measured in the fire categories of HSS and LLL) and germination treatments, the soil seed bank of the HSS-unburnt and LLL-unburnt areas were compared using a split-plot ANOVA on the total germination for the 13 samples for each germination treatment for each site. The samples were analysed for variation between area, site, plot and germination treatment. The split-plot ANOVA used a nested design to test for significant differences between plots within sites, within each of the areas. The split-plot approach is a multistratum model where there is more than one source of random variation in an experiment and is most commonly used in agricultural trials (Venables and Ripley, 1999). It was used due to the stratified partitioning of the design. Woody species differences between the areas were tested with a two-factor ANOVA of area and treatment.

To determine the abundance of the viable soil stored seed between the HSS-preburn and HSS-postburn areas, the soil seed bank were analysed using repeated measures ANOVA, due to the spatial correlation between the sites. The repeated measures analysis added an error term for the correlation with time (Jongman et al., 1995). This analysis included an interaction between areas and treatment. Fire behaviour data collected from the burn were analysed for fire intensity using equation 1.1 (section 1.3.2).

The data were log-transformed prior to the analyses to correct for a left-skewed distribution. For both analyses, the residuals were investigated for non-normality and distribution. Visual inspection of the post-analysis plots indicated the log transformation was appropriate for the data structure.

To compare the differences between the soil seed bank and above-ground vegetation, between the HSS-unburnt and LLL-unburnt areas, species richness (total number of species per site) was compared across all sites. A comparison was made of the 10 most abundant species between the two areas.

The regeneration of woody species through time in the HSS-postburn and HSS-unburnt areas for a year following burning was analysed using the mean density of woody trees and shrubs before and 12 months after the burn. For the forb, grass and sedge and rush growth form groups, the proportion of plant cover in relation to the initial cover was calculated. The regeneration of other ground cover species, particularly forbs were compared using mean and standard error comparisons.

The individual responses of the woody plants were assessed using ANOVA between area and germination treatments. The combined species responses of the other growth forms were assessed in groups. All grasses were included in a 'grass group'; the Juncaceae, Cyperaceae and Lomandraceae species, plus one lily (*Arthropodium milleflorum*) were combined and broadly called the 'sedge and rush group'. The forbs were combined in a 'forb group'.

5.3 Results

5.3.1 Soil seed bank

The soil seed bank experiment recorded over 11 500 germinants, comprising 94 species (including 13 identified to genus level, 5 to family and one unknown herb). Each site had 2.55 m^2 of soil collected, totalling 7.66 m^2 per area. The majority of species had seed densities of less than $1/m^2$, but 11 species had densities over 5 seeds/m^2. The mean and SE of germinates for each species by site is given in Appendix 5.1.

Overall, more germinants were recorded in the LLL-unburnt area (Figure 5.7). This was largely due to the high mean of germinants in the second unburnt site, where the highest emergence rate was recorded. The third LLL-unburnt site had very similar mean germinant numbers to the burnt sites. Similarly, the HSS-preburn and HSS-unburnt sites had similar mean germinant numbers. There was an increase in germinants following the burns as seen by increasing germinant numbers in two of the post-burn sites. The mean species richness over the sites was highest in the HSS-preburn area (37 species), closely followed by the LLL-unburnt (34), HSS-burn (31) and the HSS-postburn area (27).

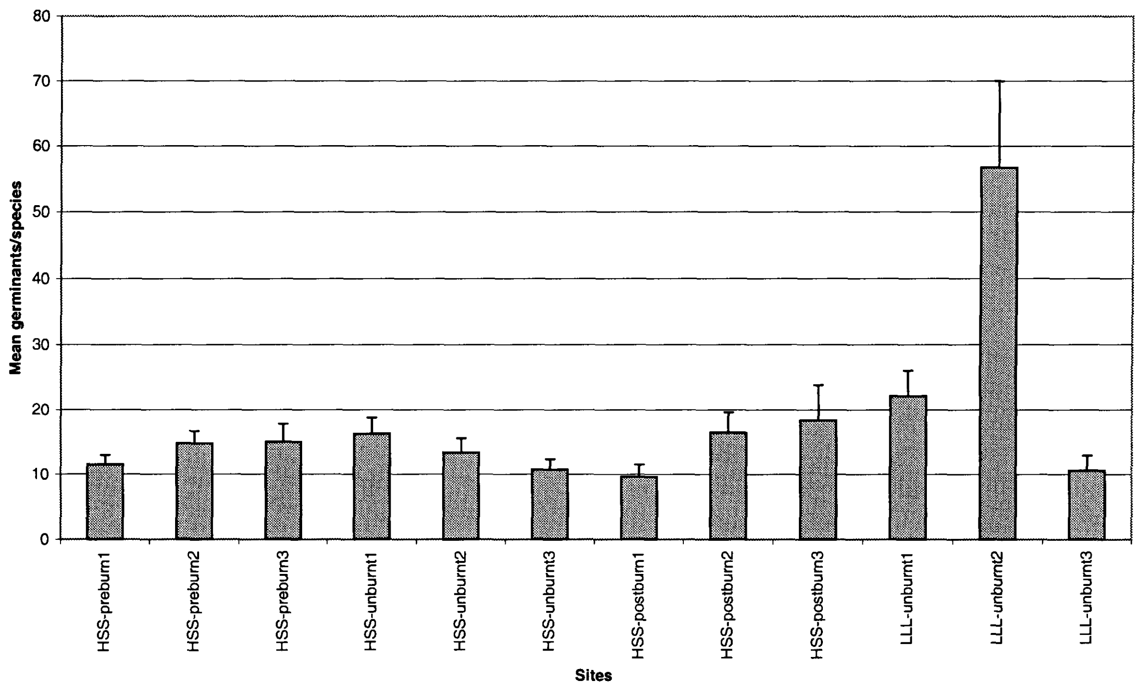


Figure 5.7. Mean number of germinants for each species for each site. Standard error bars shown.

The mean density of seeds per square metre was 345, ranging from 232 seeds/m^2 in the HSS-unburnt to 575 seeds/m^2 in the LLL-unburnt areas. When divided into the growth form groups, seeds from grasses and forbs dominated the species composition. The grass group contributed 28% of the total seeds/m^2, the sedge group 28%, the herb group 43% and woody species just over 0.5%.

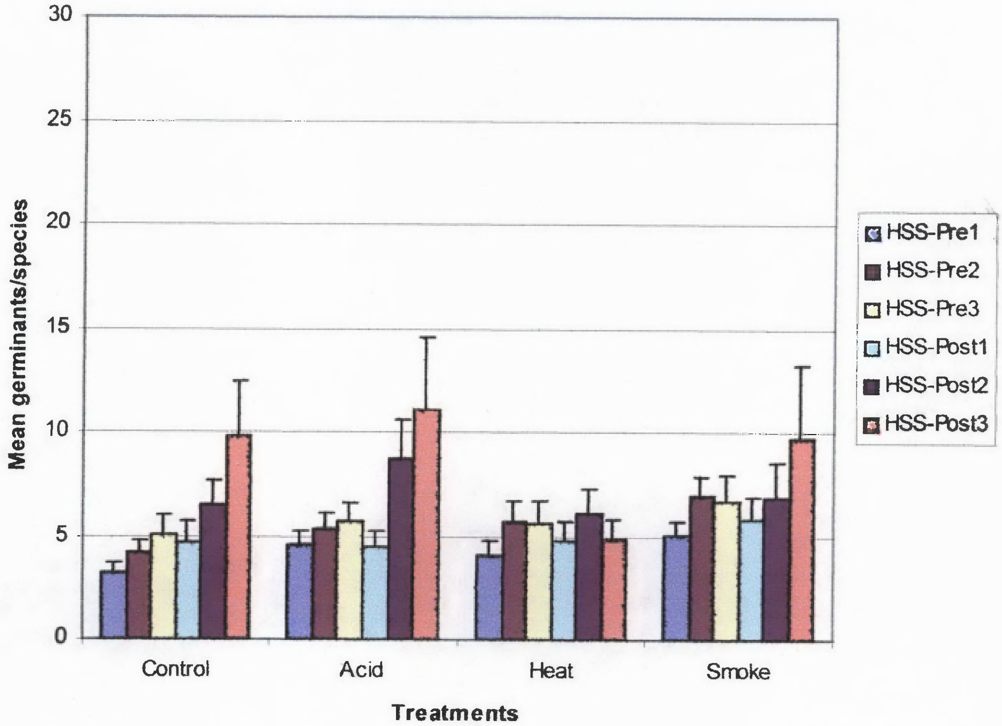
With regard to the germination treatments, high numbers of germinants (> 10/m^2) were found from the acid treatment for Poaceae sp. (in the UB area) *Poa sieberiana* (UB), *Sporobolus creber* (BP), *Bulbostylis densa* (UB), Cyperaceae sp. (UB) and *Cyperus sanguinolentus* (UB); from the heat treatment for Poaceae sp. (in the UB area), *Poa sieberiana* (UB), Cyperaceae sp. (UB); from the smoke treatment for *Bulbostylis densa* (UB), Cyperaceae sp. (UB), *Juncus subsecundus* (UB) and in the control treatment for Poaceae sp. (UB), *Bulbostylis densa* (UB), *Eleocharis gracilis* (UB) and *Centaurium erythraea* (BP). A full list of the mean germinants for each species in each of the areas by germination treatment is given in Appendix 5.2.

The total species richness of germinants in the control treatment was highest (34 species), followed by the acid and heat treatments (32 species) and the smoke treatment (29 species). Overall the highest number of germinants was recorded in the acid treatment, then heat and smoke. There were high germinant numbers in all treatments within the LLL-unburnt area (Figure 5.8).

5.3.2 Comparison of soil seed bank in high and low fire frequency sites

For the HSS-unburnt and the LLL-unburnt area comparison (see Appendix 5.1), grasses such as *Poa sieberiana* had higher counts in the HSS-unburnt area (3.2 seeds/m^2 compared to 10.0 seeds/m^2). A similar result was found for the unknown grass class of Poaceae sp. All grass species had similar germination numbers in the HSS-unburnt area. With regard to germination treatments, *Imperata cylindrica, Themeda australis* and *Microlaena stipoides* had lower germinants for all treatments when compared to the control. In contrast, *Digitaria* sp. and *Entolasia stricta* germinants were more abundant for all treatments when compared to the control and *Sporobolus creber* germinants were more abundant due to GA.

Germinants in the sedge and rush group were numerous in the LLL-unburnt area. The mean germinants per square metre were 0.89 in the HSS-unburnt compared to a mean of 4.4 germinants/m^2 in the LLL-unburnt area. Species-specific responses of higher germinants in the LLL-unburnt area were observed for *Bulbostylis densa, Carex breviculmis,* Cyperaceae sp., *Cyperus sanguinolentus*, *Eleocharis gracilis* and *Juncus subsecundus.* With regard to the treatments, Cyperaceae sp. had more germination for all treatments compared to the control. Decreased germination was found in *Cyperus sanguinolentus* and *Eleocharis gracilis* due to smoke, in *Bulbostylis densa* due to heat and in *Juncus subsecundus* due to acid. *Juncus* sp. showed increased germination due to the acid treatment.



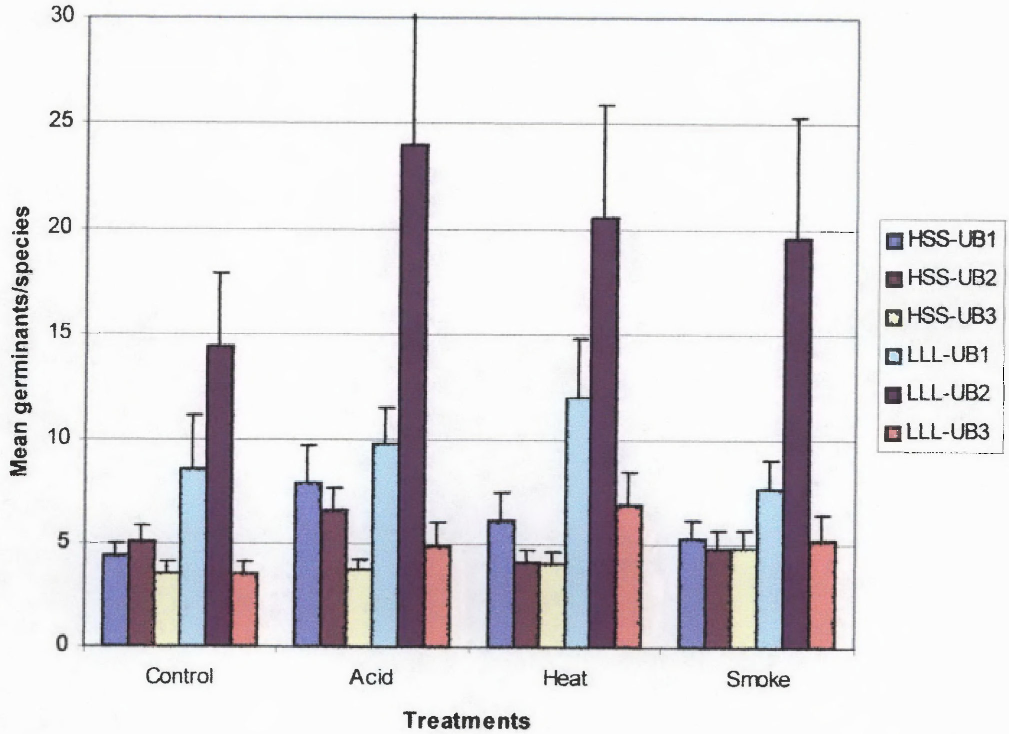


Figure 5.8. Mean germinants (+SE) for each germination treatment by site. Above - comparison of HSS-preburn (B) and HSS-postburn (BP) and below - comparison of HSS-unburnt (C) and LLL-unburnt (UB).

In the forb group, a number of species had high germination levels (over 5 seedlings/m^2). These were *Cardamine paucijuga, Centaurium tenuiflorum, Desmodium varians, Euchiton sphaericus, Haloragis heterophylla, Hypericum gramineum, Poranthera microphylla* and *Pratia purpurascens*. There was a significant difference between the two areas. Those species where germination increased in the LLL-unburnt area included *Eriocaulon scariosum, Epilobium billardierianum, Glycine clandestina, Geranium solanderi, Hypericum gramineum* and *Wahlenbergia communis*. *Gonocarpus micranthus* and *Hypericum japonicum* only germinated in the LLL-unburnt area. Species with greater germination in the HSS-unburnt area were *Centaurium erythraea, Euchiton sphaericus, Poranthera microphylla* and *Pratia purpurascens*.

The split-plot ANOVA showed a significant difference in the soil seed bank of the HSS-unburnt and LLL-unburnt sites and total germination counts (Table 5.1). The HSS-unburnt area, with a history of high NOF and short SIFI, had a significantly different and proportionally smaller seed bank to that of the LLL-unburnt area. The replicate sites within the areas and the plots within each of the sites were also shown to be significantly different. The germination treatments were significantly different, with an interaction between the treatments and area. The LLL-unburnt areas had greater numbers of species and germinants. On average there were 0.86 germinants/m^2 in the HSS-unburnt and 1.73/m^2 in the LLL-unburnt areas.

Table 5.1. Output summary from the split-plot ANOVA between the HSS-unburnt and LLL-unburnt areas and total germination counts. The top three variables are nested - plot within site, site within area. Significant ($P < 0.05$) values indicated with **.

Variables	Degrees of freedom	Sum of Squares	Mean Square	F-value	P-value
Area	1	19.707	19.707	12.857	0.001**
Site	4	70.655	17.664	12.420	0.001**
Plot	72	346.129	4.807	13.462	0.001**
Treatment	3	3.572	1.191	3.334	0.020**
Treatment:area	3	4.052	1.351	3.782	0.011**
Residuals	228	81.417	0.357		

Only three woody genera were recorded in the seed bank experiment (*Acacia*, *Eucalyptus* and *Leptospermum*) and those that occurred were mainly in the LLL-unburnt area. The number of *Acacia* species germinating from the soil from the LLL-unburnt area was high, with almost none germinating in any of the HSS areas. There was one occurrence of an *Acacia irrorata* germinant in the HSS-postburn sites. There was one occurrence of *Leptospermum polygalifolium* seedling in the HSS-unburnt site and all others (10 seedlings) were from the LLL-unburnt area. The ANOVA of the woody plants (Table 5.2) showed the only significant difference to be with *Acacia irrorata* between the HSS-unburnt and LLL-unburnt areas, with significantly more germinants in the LLL-unburnt area. *Acacia irrorata* had higher germination in the heat treatment. Although there were many more *Leptospermum polygalifolium* germinants in the LLL-unburnt area, the difference was not significant. With regard to germination treatments *Leptospermum polygalifolium* had fewer germinants in the heat but more in the smoke treatments.

Table 5.2. Results of the ANOVA of woody plants in the LLL-unburnt and HSS-unburnt areas. Significant differences at P < 0.05 are indicated with **

		Sum squares	Degrees of freedom	Mean Square	Sum square	Degrees of freedom	Mean Square	F-value	P-value
	Species	Effect	Effect	Effect	Error	Error	Error		
Area	*Acacia irrorata*	125.208	5	25.042	156.750	18	8.708	2.876	0.044**
Treatment		25.792	3	8.597	256.167	20	12.808	0.671	0.580
Area	*Leptospermum polygalifolium*	20.208	5	4.042	27.750	18	1.542	2.622	0.060
Treatment		3.792	3	1.264	44.167	20	2.208	0.572	0.640

5.3.3 Fire behaviour

A moderate intensity burn was achieved in all of the burn sites. Calculations of fire intensity for each of the burn sites are given in Table 5.3. The burns were between 510 and 1165 kW/m in the moderate intensity range (510-3000 kW/m) recognised by Cheney (1981) for *Eucalyptus* forests. Flames up to a height of 1.5-2 m accompanied each burn, also within the range for a moderate intensity burn.

Table 5.3. Burn intensity inputs and calculations based on the Byram (1959) equation (equation 1.1). Final inputs to the equation in bold.

Area replicates (sites)	**1**	**2**	**3**	**Unit of measure**
Fuel heat yield (H)	20000	20000	20000	kJ/gm
Fuel weight (*w*)				
Fuel weight on site	1.535	1.269	1.427	g/m^2
Fuel weight straw	0.210	0.210	0.210	g/m^2
Fuel weight post-burn	0.303	0.167	0.183	g/m^2
Total (w)	1.442	1.312	1.454	g/m^2
Rate of spread (*r*)	0.018	0.044	0.021	m/s
Intensity	510.5	1165.1	596.1	kW/m

The underground temperatures during the burn, logged in the first burn site are shown in Figure 5.9. The surface thermistor reached over 100 °C. This was confirmed in the final burn with heat sensitive temperature crayons. Underground, the 5 cm thermistor was slowest to change and reached a maximum temperature of only 22.8 °C. The temperature at 2.5 cm was higher, with a maximum of 29.6 °C. Figure 5.10 shows the burn progressing through site 2.

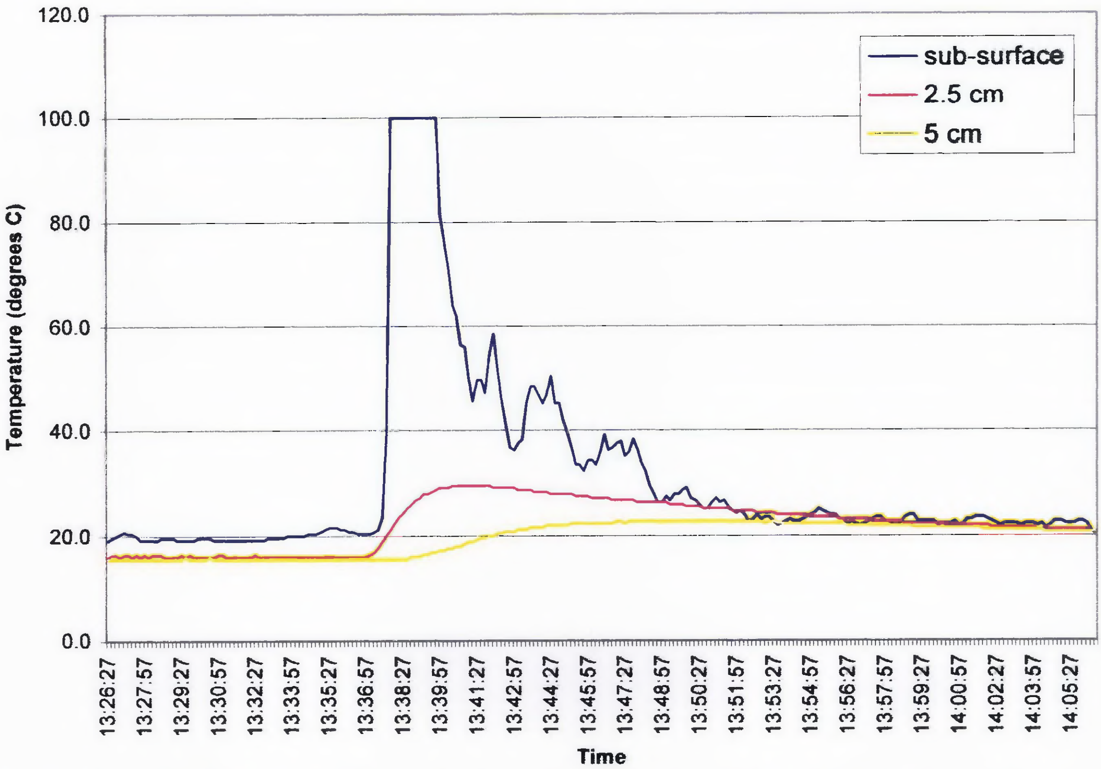


Figure 5.9. Temperature trace from the underground thermistor in site 1, 29 October 1998.

Figure 5.10. Burn progressing in site 2, 29 October 1998.

5.3.4 Comparison of soil seed bank in pre and post-burn areas

Plant responses varied (and are listed by species in Appendix 5.1) between the pre- and post-burn areas. The mean density of the grass group declined following the burn. Prior to the burn, the mean density of grass species was 1.2 germinants/m^2. Following the burn, the mean density was 0.7 germinants/m^2. The abundance of the sedge group increased following the burn. Prior to the burn, densities were 0.6 germinant/m^2, this rose to 0.9 germinant/m^2 following the burn. The three species with the greatest increase in abundance were *Carex breviculmis* (0.8 to 1.8 germinant/m^2), *Juncus* sp. (1.1 to 2.4 germinant/m^2) and *Juncus subsecundus* (3.6 to 5.8 germinant/m^2).

There was an increase in the mean germinant density of the forb group following the burn from 0.5 germinant/m^2 to 0.7 germinant/m^2. Larger increases in abundance were recorded in *Centaurium tenuiflorum* (5.7 to 9.7 germinant/m^2), *Euchiton involucratus* (1.5 to 2.3 germinant/m^2), *Euchiton sphaericus* (2.2 to 3.9 germinant/m^2), *Haloragis heterophylla* (1.9 to 2.2 germinant/m^2), *Hypericum gramineum* (2.3 to 3.5 germinant/m^2) and *Poranthera microphylla* (1.6 to 3.7 germinant/m^2). However, there were also species that recorded sharp declines in abundance due to the burn. These included *Desmodium varians* (4.3 to 3.8 germinant/m^2), *Pratia purpurascens* (3 to 0.3 germinant/m^2) and *Viola betonicifolia* (0.8 to 0.1 germinant/m^2).

The results of the repeated-measures ANOVA showed there was no significant difference between the pre and post-burn areas and total germination counts. There was a significant difference between the HSS-preburn and HSS-postburn sites and within the plots within the sites. There was no significant difference between the treatments or the interaction between the treatments and areas. This was found for the sites, treatments and interaction between the site and treatment (Table 5.4).

Table 5.4. Output summary from the repeated-measures ANOVA between the HSS-preburn and HSS-postburn area and sites within the areas, with total germination counts. Significant variables ($P < 0.05$) indicated with **.

Variable	Degrees of freedom	Sum of Squares	Mean Square	F-value	P-value
Area	1	2.424496	2.424496	2.139603	0.145
Site	4	15.4050	3.851250	3.398705	0.009**
Plot	72	267.4027	3.713926	11.01785	0.001**
Treatment	3	1.61730	0.539105	1.599330	0.190
Treatment:area	3	0.86970	0.289899	0.860020	0.462
Residuals	228	76.8549	0.337083		

For the woody species there was an increase in *Eucalyptus* germination counts in the HSS-postburn area, increasing from 0.03 to 0.14 germinants/m^2. *Acacia irrorata*, *Eucalyptus nobilis* and *E. dalrympleana* were found in the sites before and after the burn and the results of the ANOVA

(Table 5.5) are shown, indicating none of them were significantly different. There was a decline in *Eucalyptus* germination for all treatments when compared with the control, however none of the treatment effects were significantly different. No *Acacia* seeds germinated from the soil prior to the burn but one seedling germinated post-burn with the heat germination treatment.

Table 5.5. Results of the woody plant ANOVA for area and treatment between the HSS-preburn and HSS-postburn areas. Significant species (P < 0.05) indicated with **.

		Sum squares	Degrees of freedom	Mean Square	Sum square	Degrees of freedom	Mean Square		
Species	Variable	Effect	Effect	Effect	Error	Error	Error	F-value	P-value
Acacia irrorata	Area	1.833	5	0.367	3.500	18	0.194	1.886	0.147
	Treatment	1.000	3	0.333	4.333	20	0.217	1.538	0.235
Eucalyptus nobilis	Area	5.833	5	1.167	8.000	18	0.444	2.625	0.060
	Treatment	2.833	3	0.944	11.000	20	0.550	1.717	0.196
Eucalyptus dalrympleana	Area	0.208	5	0.042	0.750	18	0.042	1.000	0.446
	Treatment	0.125	3	0.042	0.833	20	0.042	1.000	0.413

5.3.5 Comparison of the above-ground vegetation and soil seed bank

There were marked differences between the above-ground vegetation and stored soil seed bank particularly between HSS and LLL NOF areas. Table 5.6 shows the number of species found in the above-ground vegetation compared to the soil seed bank. Out of a total of 189 species sampled in both the above-ground vegetation and the soil seed bank, only 22% occurred in both.

Table 5.6 Species richness in above-ground vegetation and seed bank (treatments combined).

Present in:	**Total species**
Above-ground vegetation only	100 (53%)
Seed bank only	47 (25%)
Both above-ground vegetation and seed bank	42 (22%)

Table 5.7 shows the relative proportion of above-ground vegetation and species in the LLL-unburnt and HSS-unburnt sites. Few species (8.7%) in the HSS-unburnt sites were germinated from the seed bank.

Table 5.7 Proportion of plant species in the above-ground vegetation and seed bank and in the LLL-unburnt and HSS-unburnt sites.

	Above-ground vegetation	**Seed bank**
Total species	142	92
Proportion of total in LLL-unburnt sites	33.1%	31.5%
Proportion of total in HSS-unburnt sites	36.6%	8.7%
Proportion of total in both areas	30.3%	59.8%

Differences between the areas were found in the 10 most abundant species. In the HSS-unburnt area, the seed bank and above-ground vegetation shared five of the top 10 most abundant species (Table 5.8). In the LLL-unburnt area only two of the 10 most abundant species were in common to the soil seed bank and above-ground vegetation. The dominance of the 'sedge and rush' group and the reduced importance of the grass species were observed in the 10 most abundant species in the unburnt area.

Table 5.8. Comparison of the 10 most abundant species in the seed bank and above-ground vegetation between the HSS-unburnt and LLL-unburnt area.

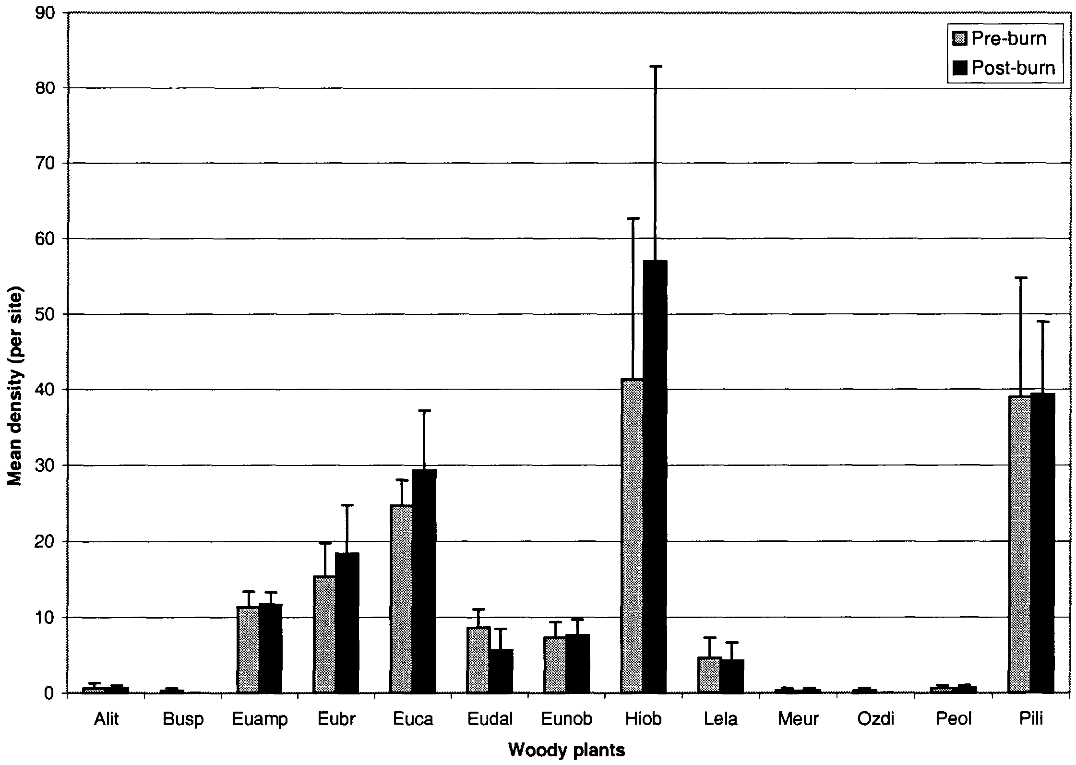
	HSS-unburnt area Seed bank **Species**	**Mean germinants/m^2**	Above-ground vegetation **Species**	**Frequency/site**
1	*Microlaena stipoides*	3.43	*Desmodium varians*	3.0
2	*Poa sieberiana*	3.20	*Pratia purpurascens*	3.0
3	*Haloragis heterophylla*	3.20	*Sorghum leiocladum*	2.9
4	*Centaurium erythraea*	2.71	*Haloragis heterophylla*	2.9
5	*Desmodium varians*	2.68	*Imperata cylindrica*	2.9
6	*Pratia purpurascens*	2.32	*Poa sieberiana*	2.9
7	*Imperata cylindrica*	2.19	*Geranium solanderi*	2.8
8	*Juncus subsecundus*	2.12	*Themeda australis*	2.6
9	*Digitaria* sp.	2.09	*Pimelea linifolia*	2.4
10	*Sporobolus creber*	1.96	*Euchiton coarctatum*	2.2
	LLL-unburnt Seed bank **Species**	**Mean germinants/m^2**	Above-ground vegetation **Species**	**Frequency/sites**
1	*Juncus subsecundus*	13.39	*Geranium solanderi*	2.9
2	*Bulbostylis densa*	10.81	*Pratia purpurascens*	2.9
3	*Poa sieberiana*	10.02	*Viola betonicifolia*	2.9
4	*Cyperus sanguinolentus*	9.60	*Imperata cylindrica*	2.8
5	*Juncus* sp.	7.41	*Poa sieberiana*	2.8
6	*Carex breviculmis*	7.35	*Desmodium varians*	2.7
7	*Eleocharis gracilis*	6.92	*Glycine clandestina*	2.1
8	*Hypericum japonicum*	6.43	*Dichondra* sp. *A*	2.0
9	*Desmodium varians*	3.17	*Pteridium esculentum*	1.8
10	*Gonocarpus micranthus*	3.00	*Stylidium graminifolium*	1.8

5.3.6 Post-fire regeneration in high fire frequency areas

Woody shrub and tree species rapidly regenerated after the burn, but the more obvious effect was the overall increase in forb and grass species. After one month, the majority of woody shrubs and small trees were regenerating with new vegetative growth. The mean density of the small (< 2 m) trees and shrubs before and after 12 months is shown in Figure 5.11.

The smaller trees and shrubs increased over the 12 months, with the mean number of individuals per site increasing from 155 (±13) to 175 (±29). An increase in mean density was found in *Hibbertia obtusifolia*, *Eucalyptus caliginosa* and *E. bridgesiana*. The number of *Eucalyptus dalrympleana* plants declined. *Bursaria spinosa* did not regenerate following the burn, but the density of this species was very low (2 plants) and both were small individuals (5 cm height). One *Leucopogon lanceolatus* died, but the majority regenerated rapidly and vigorously following the burn.

The density of the woody plants in the HSS-unburnt area (Figure 5.12) showed little change throughout the year. Change was apparent due to mortality but the loss of individuals was minor. Overall, the mean woody plant density was 150 stems (±11)/0.1 ha site before the burn, compared to 145 stems (±12)/0.1 ha after 12 months. The larger trees (> 2 m) were generally unaffected by the burn. They showed a slight increase in height and DBH over the year attributed to natural growth.



F igure 5.11. The mean density of small (< 2 m height) woody trees and shrubs in the burnt area, before the burn (pre) and 12 months following the burn (post-burn). Abbreviations refer to: Alit = *Allocasuarina littoralis*, Busp = *Bursaria spinosa*, Euamp = *Eucalyptus amplifolia*, Eubr = *E. bridgesiana*, Eudal = *E. dalrympleana*, Eunob = *E. nobilis*, Hiob = *Hibbertia obtusifolia*, Lela = *Leucopogon lanceolatus*, Meur = *Melichrus urceolatus*, Ozdi = *Ozothamnus diosmifolius*, Peol = *Persoonia oleoides* and Pili = *Pimelea linifolia.*

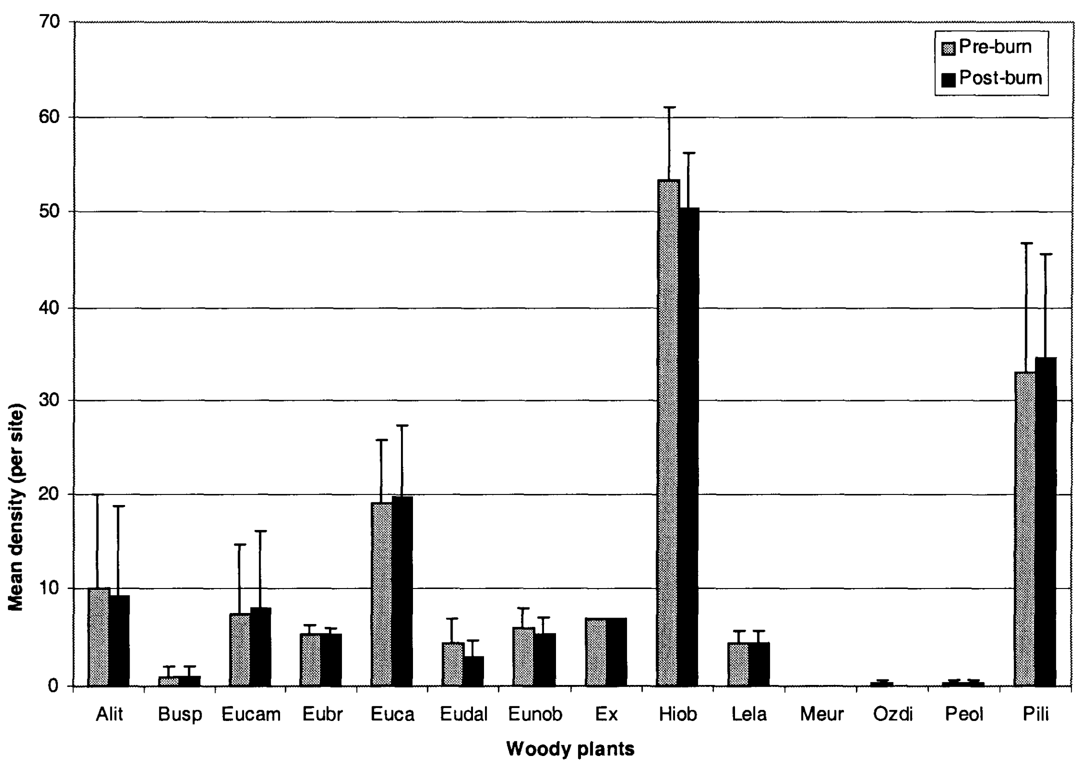


Figure 5.12. Mean density of trees and shrubs (< 2 m) in the HSS area before the burn (pre-burn) and 12 months (post-burn). Abbreviations for species as in Figure 5.11, plus Ex = *Exocarpos cupressiformis.*

The proportion of the grass, sedge and rush and forb groups, as a ratio of initial site cover, at each time period after the burn is summarised in Figure 5.13. A proportion of one indicates that the species cover had not changed from before to after the burn. Most of the forb species regenerated rapidly after the experimental burns, and by 12 months the cover had exceeded the pre-burn level. In contrast, grasses were still less abundant in cover than before the burns. The sedge and rush group were the most rapid to regenerate following the burns. At one-month, the sedge and rush group cover was 18% of the pre-burn levels. *Lomandra* species dominated and rapidly regenerated from insulated underground roots. By six months the sedge and rush group cover was 74% of pre-burn levels, by 12 months *Carex* species were prominent. The sedge and rush group had the highest proportion of species not sampled in the site prior to the burn, notably *Carex* species and *Schoenus apogon*.

A temporal sequence of the regeneration of site 3 from the burn to 12 months is shown in Figure 5.14 - 5.18 demonstrating the rapid regeneration of predominantly forbs and grasses.

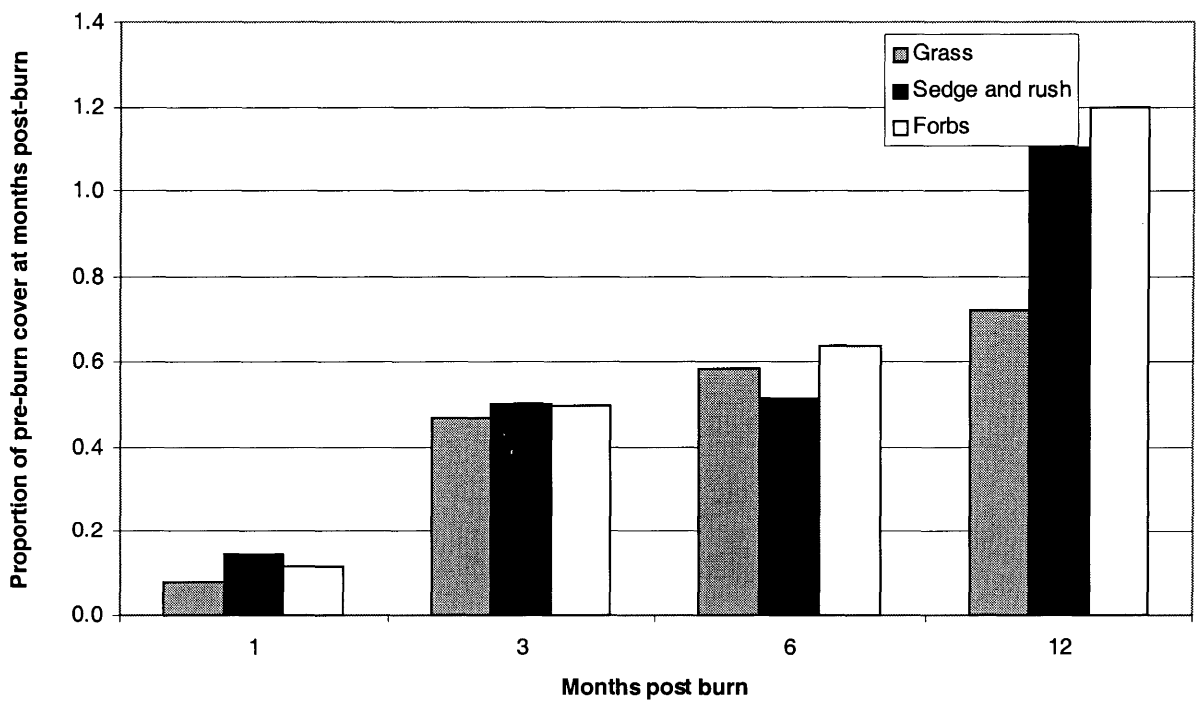


Figure 5.13. Post-burn plant cover at each time period as a proportion of the pre-burn cover, for the grass, sedge and rush, and forb groups.

Figure 5.14. Site number 3 immediately following the burn, 5 November 1998.

Figure 5.15. Site number 3, 1 month after the burn, 7 December 1998

Figure 5.16. Site number 3 approximately 3 months after the burn, 17 March 1999

Figure 5.17. Site number 3 approximately 6 months after the burn, 16 June 1999.

Figure 5.18. Site number 3 approximately 12 months after the burn, 20 November 1999.

Prior to the burn, all of the sites were dominated by four main grass species (*Imperata cylindrica*, *Poa sieberiana*, *Themeda australis* and *Sorghum leiocladum*). This changed in the 12 months following the burn. Prior to the burn, these species comprised 93% of the total grass cover and almost two-thirds of the total herbaceous cover. However, these species were slow to regenerate. Although present at all sites, they were still well below the cover values prior to the burn at 12 months following the fire. *Imperata cylindrica* was the exception. This species was vigorously growing at one month following the burn and at 12 months was at 60% of the pre-burn cover. Despite the slow response of the dominant grasses, other native species regenerated rapidly. Of these *Cymbopogon refractus*, *Dichelachne micrantha*, *Echinopogon caespitosus* and *Microlaena stipoides*, by 12 months had increased to almost 10 times their total cover prior to the burn.

The forb species' regeneration over the 12 months is given for each species in Table 5.9. Most prominent in the burn sites at one month following the burn were the weed *Hypochaeris radicata* and the native ground cover *Pratia purpurascens*. At three months, the vanilla lily (*Arthropodium milleflorum*) was prominent and obvious, along with the two common ground covers on the Tablelands, *Desmodium varians* and *Glycine clandestine*. Other common herbaceous species at three months were *Oxalis* sp., *Vernonia cinerea* and *Zornia dyctiocarpa* var. *dyctiocarpa*. At three months, the total cover of the forbs was 51% of the pre-burn level. This increased marginally (66%) by 6 months, as it was then late autumn. By 12 months the forb cover was greater than the pre-burn level (120%). The large increases were evident predominantly in the Asteraceae species of *Euchiton involucratus*, *Helichrysum rutidolepis* and *Solenogyne bellioides*, and *Hypericum* *gramineum* and *Poranthera microphylla*. There were some species not sampled in the sites prior to the burn area (*Asperula conferta, Cirsium vulgare, Glycine tabacina, Hydrocotyle* sp., and *Kennedia rubicunda*) although they were observed in the surrounding vegetation. A temporal sequence of one 1 m^2 plot from 1 to 12 months after the burns are shown in Figures 5.19-5.22.

Table 5.9. Mean plant cover (±SE) for forb species over the monitoring periods

Months post-burn	Pre-burn		1		3		6		12	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Species Name										
Acaena nova-zelanderiae	1.33	0.88	0.23	0.15	0.67	0.44	1.00	0.58	2.67	1.76
Ajuga australis	0.50	0.41			0.25	0.20	0.25	0.20	1.50	0.41
Asperula conferta									1.00	0.00
Bracteantha bracteata	2.00	0.00								
Centaurium erythraea	2.00	0.00								
Circium sp.									2.00	0.00
Conyza bonariensis	3.00								3.00	0.00
Desmodium varians	7.00	1.53	0.53	0.15	7.80	2.80	9.33	1.86	9.67	0.67
Dichondra repens	3.67	2.03	1.00	0.53	2.10	1.22	2.73	1.67	4.33	2.40
Euchiton sp.	5.67	0.88	0.60	0.30	0.97	0.52	1.17	0.44	3.33	1.86
Euchiton sp.*1.*									3.00	0.00
Euchiton involucratum									3.33	1.33
Galium propinquum	2.00	1.15	0.30	0.12	1.20	0.90	1.90	1.07	2.83	1.17
Geranium solanderi	6.33	2.33	1.03	0.48	3.10	2.06	4.07	2.63	8.50	3.33
Glycine sp.	3.00	2.08	0.27	0.17	0.43	0.38	0.73	0.64	0.67	0.67
Glycine clandestina	1.00	1.00	0.10	0.10	1.00	1.00	2.33	1.20	2.00	1.53
Glycine tabacina									2.00	0.00
Gonocarpus sp.	1.00	0.00	0.20		0.20	0.00	0.50	0.00	1.00	0.00
Gonocarpus tetragynus	4.50	2.86			3.15	2.57	3.75	3.06	4.50	3.67
Haloragis heterophylla	4.00	1.15	0.70	0.20	3.60	1.52	4.10	1.71	6.17	1.36
Helichrysum rutidolepis	5.00	0.00	0.50	0.00	3.00	0.00	3.00	0.00	11.00	0.00
Hydrocotyle sp.									0.50	0.00
Hypericum gramineum									3.00	0.00
Hypochaeris radicata	4.33	1.86	1.13	0.68	3.00	1.00	3.17	1.17	5.67	3.84
Kennedia rubicunda					1.50	0.00	1.50	0.00		
Opercularia aspera	6.00	0.00	0.40	0.00	1.50	0.00	2.00	0.00	4.00	0.00
Opercularia hispida	6.00	0.00	0.15	0.04	1.40	0.24	2.10	0.73	2.75	0.61
Oreomyrrhis eriopoda	0.50	0.41	0.05	0.04	0.50	0.41	0.50	0.41	0.50	0.41
Oxalis pernnans			0.10	0.00	0.10	0.00	0.20	0.00	0.50	0.00
Oxalis sp.	1.00	0.82	0.10	0.00	1.25	0.20	1.50	0.41	1.00	0.00
Picris sp.									2.00	0.00
Polygala japonica	1.00	1.00			0.90	0.35	1.40	0.67	1.33	0.67
Poranthera microphylla									6.00	1.73
Pratia purpurescens	6.67	2.33	2.63	1.55	4.53	1.94	5.63	2.38	9.33	3.67
Ranunculus lappaceus					0.20	0.00	0.50	0.00	1.00	0.00
Rubus parvifolius	2.00	2.00	0.67	0.67	2.33	2.33	3.00	2.08	2.00	2.00
Senecio sp.	8.33	2.73	1.00	0.36	1.83	0.38	2.30	0.35	7.33	2.33
Solenogyne bellioides	2.00	0.00	0.30	0.00	0.80	0.00	1.40	0.00	4.00	0.00
Solenogyne sp.	2.50	0.41	0.25	0.20	1.80	0.24	2.70	0.57	4.25	0.61

Trachymene sp. nov.			0.20	0.16	0.50	0.41	1.50	0.41	1.50	1.22
Veronica calycina	1.00	0.58			0.40	0.31	0.50	0.29	1.17	0.17
Vernonia cinerea			0.03	0.03	1.43	0.81	1.57	0.72	0.33	0.33
Viola betonicifolia	3.00	2.52	0.40	0.31	1.53	0.75	2.33	0.44	2.83	1.59
Wahlenbergia communis					0.10	0.08	0.25	0.20	1.00	0.00
Zornia dyctiocarpa					2.67	0.73	2.80	0.62		

There was some evidence of disturbance in the sites during the 12-month period. Ant mounds were particularly evident in the second burn site one month after the burn. Also, kangaroo grazing was observed. There was little change in the HSS-unburnt area over the 12 months.

Figure 5.19. A plot (1 m^2) in site 3 prior to the burn. The same plot is shown in Figures 5.20-5.22. The intervals on the rod are 10 cm, 28 October 1998.

5.3.7 Mode of regeneration of woody species

All the woody species burnt in the experimental fire regenerated from underground lignotubers, epicormic shoots or basal stem buds. The responses for each species are summarised in Table 5.10. There was insufficient evidence to classify *Bursaria spinosa* or *Ozothamnus diosmifolius* as only two plants were burnt of each and none survived the fire. Figure 5.23 shows the *Hibbertia obtusifolia* resprouting, Figure 5.24 the *Leucopogon lanceolatus* resprouting and Figure 5.25 the *Eucalyptus caliginosa*.

Table 5.10. The fire response classification of woody trees and shrubs following 100% scorch in the burns, as determined at 12 months post-burn. Fire response class is from the National Fire Response Database (Gill and Bradstock, 1992) where 5 is a species that resprouts from basal sprouts and 6 is a species that resprouts from epicormic shoots.

Family Name	**Species Name**	**Mode of Regeneration**	**Fire response class**
Epacridaceae	*Melichrus urceolatus*	Resprouter	5
Proteaceae	*Persoonia oleoides*	Resprouter	5
Myrtaceae	*Eucalyptus amplifolia*	Resprouter	5
Myrtaceae	*Eucalyptus bridgesiana*	Resprouter	5
Myrtaceae	*Eucalyptus caliginosa*	Resprouter	5,6
Myrtaceae	*Eucalyptus dalrympleana*	Resprouter	5
Myrtaceae	*Eucalyptus nobilis*	Resprouter	5
Dilleniaceae	*Hibbertia obtusifolia*	Resprouter	5
Thymelaeaceae	*Pimelea linifolia*	Resprouter	5
Casuarinaceae	*Allocasuarina littoralis*	Resprouter	5
Epacridaceae	*Leucopogon lanceolatus*	Resprouter	5

Figure 5.20. Plot in site 3 (as in Figure 5.19) sampled 1 month following the burn, 7 December 1998.

Figure 5.21. Plot in site 3 (as in Figure 5.19) sampled approximately 3 months following the burn, 17 March 1998.

Figure 5.22. Plot in site 3 (as in Figure 5.19) sampled approximately 12 months following the burn, 20 November 1999.

Figure 5.23. *Hibbertia obtusifolia* resprouting from the base, 2 weeks following the burn.

Figure 5.24. *Leucopogon lanceolatus* resprouting from the base, 2 weeks following the burn, alongside the stem of the dead mature plant behind.

Figure 5.25. *Eucalyptus caliginosa* resprouting from a lignotuber 2 months after the burn.

5.4 Discussion

The most significant result from this study was the low occurrence of woody shrub and tree species in both the above-ground vegetation and stored soil seed bank in the high fire frequency (HSS) area. This suggested that past fire frequency had reduced woody plant species composition and abundance. The low abundance of existing species and the possible depletion of soil seed reserves due to a HSS fire regime have implications for the long-term persistence of woody species in these sites.

5.4.1 Fire frequency and the soil seed bank - woody plants

This study demonstrated that fire frequency influenced the composition and abundance of the soil seed bank. This adds to the evidence in Chapter 4 that fire frequency had significant impacts on vegetation composition. In particular, high NOF and short SIFI significantly reduced the soil seed bank, particularly of woody trees and shrubs in this part of the study region. Areas with low fire-frequency, represented by the LLL-unburnt sites, maintained a stored seed bank of woody shrubs. These sites tended to have higher numbers of woody shrubs, including *Acacia irrorata* and *A. melanoxylon* demonstrating that these species maintain viable but dormant seed banks when given adequate fire-free intervals for maturation. In contrast, the sites with a history of high NOF and short SIFI had few seeds of woody species that germinated. These sites had lower numbers of germinants in the soil and reduced numbers of species, particularly woody species. It would appear that the high frequency of fire was not allowing sufficient time between fires for woody plants to grow to maturity and contribute to the soil seed bank. Thus, fire frequency also affects the richness and abundance of the soil seed store.

An interesting result was that of *Leptospermum polygalifolium* that was found in the seedbank in the LLL-unburnt sites. While the comparison with the HSS-unburnt site was not statistically significant due to the small number of germinants, the germination of these seedlings show there are some seed in the soil. This species generally holds seed in canopy-borne capsules. The occurrence of the germinants may be due to recently shed seed mixing from the surface soil or it may demonstrate that while *Leptospermum polygalifolium* stores seed in canopy-borne capsules some seed may also be retained in the soil. The data here are too sparse to draw conclusions but warrant further investigation.

5.4.2 Fire frequency and the soil seed bank - ground cover

In each category of grass, sedge and rush, and forbs, more seedlings germinated from the seed bank in the LLL-unburnt areas. The significantly higher overall germination numbers in the LLL-unburnt sites indicate frequent fires can lower the number of potential germinants stored of all plant growth forms in the soil seed bank.

5.4.3 Soil seed bank - germination treatments

Various germination treatments had a role in promoting germination in these Northern Tablelands plant species. Some species demonstrated a response to a specific treatment. The response of *Acacia* species, to heat observed in this study, has been well documented by a number of authors (Shea et al., 1979; Warcup, 1980; Auld, 1986b; Auld and O'Connell, 1991). Floyd (1976) studied the wet sclerophyll forests of northern NSW and his work indicated that *Acacia irrorata* required heating of approximately 70°C. Similarly in this study, the heat treatment (80 °C) was successful in promoting germination of *Acacia irrorata, A. melanoxylon* and other Fabaceae species.

Gibberellic acid produced the greatest germination response. However, germination of *Themeda australis* decreased due to acid, demonstrating a detrimental effect of this growth hormone for some species.

Germination of *Eucalyptus* species declined in all treatments compared to controls, suggesting that *E. caliginosa*, *E. dalrympleana* and *E. nobilis* do not require specific germination treatments. In contrast, germination of *Leptospermum polygalifolium* significantly increased with smoke application. In similar studies, the compounds in smoke have been found to significantly increase germination levels (e.g. Dixson et al., 1995; Read et al., 2000). With the protection afforded from fire by the *Leptospermum* woody capsule, this suggests that heat and smoke may interact to assist germination. Overall, the germination of Juncaceae and Cyperaceae species in response to heat was found to be lower, despite relatively high germination in the post-burn sites. Warcup (1980) recorded high germination of Juncaceae and Cyperaceae with lower temperatures. This suggests the temperature of the experimental burns was not sufficient to reduce germination of these species.

There is increasing evidence that germination response is enhanced by a combination of treatments such as smoke and heat (Kenny, 2000; Izhaki et al., 2000).

5.4.4 Soil seed bank and above-ground vegetation

The species richness of the above-ground vegetation differed from the soil seed bank. The differences between the two were predominantly in the sedge and rush group and the exotic forbs. These opportunistic species take advantage of the post-fire conditions of increased light and nutrients to reproduce rapidly. The large increase in the common weed species *Hypochaeris radicata*, at one month following the burn and its subsequent decline suggests it germinated, grew and matured rapidly following the fire. Some of the species that were not sampled in the above-ground vegetation but appeared in high numbers in the seed bank were observed in the surrounding vegetation. These included the common species, *Epilobium billardierianum* and *Cirsium vulgare*. Variation between the above-ground vegetation and the soil seed bank has been found in other studies. In rehabilitated mine sites, the composition of the above-ground vegetation and the soil seed bank was found to be similar (Grant and Koch, 1997). In contrast, in soil seed banks in forests in Western Australia a high degree of difference to the existing vegetation was found (Ward et al., 1997). In this study, a high proportion of the woody species occurring in the above-ground vegetation, but not the seed bank, were species that stored seed in the canopy including *Allocasuarina littoralis*, *Banksia integrifolia* and *Hakea microcarpa*. All of these species have the capacity to regenerate from vegetative material as well as from stored canopy-borne seed.

5.4.5 Fire intensity and pre and post-burn areas

A small but non-significant difference in the soil seed bank due to the moderate intensity burn was found in the comparison of the pre and post-burn areas. Only one *Acacia irrorata* seed germinated from these areas and this was in an HSS-postburn site. While this isn not statistically significant it could indicate the potential for more to exist, although present conditions do not appear suitable for 'in-situ' germination. A more likely explanation is that there are very few *Acacia* seeds remaining in the HSS area. High numbers of germinants of the sedge and rush group were found in the post-burn area, indicating seed remained viable following the burn. Likewise, there were low grass numbers in the post-burn area. Some of the seed in the post-burn area were being heated twice, in the experimental burn and then the heat treatment. This combination may have been particularly detrimental to grass species.

The abundance of *Eucalyptus* species in the post-burn samples was due to the moderate-intensity burn undertaken a week prior to the collection of soil. Massive seed fall following fire has been observed for *E. delegatensis*, with seed fall increasing 70-fold in the weeks following full crown scorch (O'Dowd and Gill, 1980). Seed fall from *Eucalyptus* species may depend on the intensity of the fire, with low intensity fires producing no increase over natural and normal dissemination rates (Bassett and Geary, 1996). The adaptive advantage of this response has been hypothesised as either the saturation of the post-burn site with seed to reduce the impact of predation, or the increase in seedling germination and survival probability due to dispersal into favourable post-fire conditions (O'Dowd and Gill, 1980). The total number of *Eucalyptus* germinants could have been even higher if soil collection had occurred immediately following the fire, rather than a week later, as abundant ant activity was observed on all plots following the fire. The rapid harvesting of seeds by ants has been found to greatly reduce seeds available for germination (Harrington and Driver, 1995).

The burns were not as intense as originally planned, but the addition of the straw did increase below-ground temperatures. The burns were of moderate intensity as defined by Cheney (1981), but the measured below-ground temperature traces suggested the temperature rise was below that required to break seed dormancy in hard seeded *Acacia* species. In the Sydney region, a temperature greater than 60°C was required to break dormancy in most legume species (Auld and O'Connell, 1991). Bradstock and Auld (1995) discussed the difference between actual fire intensity and the heat transferred to the soil and concluded it was the amount of heat in the soil that had the greater impact on plant persistance and higher soil temperatures caused greater plant morality. The addition of the straw increased the residence time of the flame on a micro-scale, so over the whole site it is suggested there were more locations where a higher intensity could have been reached. However, there was still a lack of germination of *Acacia* species in the site following the burn. It would appear that low seed numbers, frequent low intensity burns and possibly animal disturbance restricted their regeneration.

5.4.6 Post-fire regeneration

Monitoring of the burn area for 12 months after the fire showed regeneration of all woody species from vegetative material and the continued increase in cover of the grasses, sedge-group and forbs. A sequence of the initial and rapid regeneration of grass species (native species not dominant prior to the pre-burn), some forb weeds such as *Hypochaeris radicata* and the regeneration of the majority of the *Eucalyptus* species was based primarily on species in the site prior to the burn. Through time, the grass abundance gradually increased along with an even more rapid increase in the forb-group species. By 12 months, the original native grass species were becoming more dominant, the cover of the forbs was high and the majority of the woody shrubs and trees species were continuing to regenerate. Twelve months after the burn there were still small but observable differences between the HSS-unburnt and burn areas. As the majority of the species had regenerated, the composition had returned to pre-burn levels but cover remained low. With more time, this is likely to return to the same pre-burn levels.

The vast majority of species surveyed in the site prior to the burn, were also found in the sites following the burn. While there was a moderate increase in species, those additional species were found in areas adjacent to the burn plots. Some species, for example the native grasses that dominated the cover prior to the burn, were still of low plant cover at 12 months, when compared to prior to the burn. This is probably a function of the time since the fire. A number of studies have noted the rapid regeneration of plants in the 1-2 years following fire (e.g. Purdie, 1977a; 1977b; Fox and Fox, 1987; Moreno and Oechel, 1991) and Posamentier et al. (1981) studied the vegetation trends in Nadgee Nature Reserve for 6 years following a burn and found the changes in the first two years related to time, as opposed to environmental factors after that.

5.4.7 Regenerative mechanisms

The experimental burn provided information on the mode of regeneration of 11 woody species. All species (excluding *Bursaria spinosa* and *Ozothamnus diosmifolius*), regenerated from woody lignotubers or vegetative buds. This dominance of 'resprouters' indicated that the post-burn community was largely comprised of woody species that survived the fire and regenerated rapidly by vegetative means. As the burn was only undertaken in the HSS area, it is possible that frequent fires had already removed seeder species that may have once occurred. Only those with the capacity to resprout have been able to survive the history of frequent fires. Resprouter species only need to produce sufficient seed to offset mortality of parent plants. In contrast, seeder species, without soil-stored seed, rely entirely on seed produced in the years between disturbance for their survival (Meney et al., 1997). These seeder species need either large persistent seed banks or large annual seed production to enable population expansion post-fire (Meney et al., 1994).

The results from this study strongly indicate that the vegetation of the burnt areas will return to a similar structure and composition as was found prior to the burn. The greater number of seeds in the seed bank of sites in the low fire frequency areas provides evidence that the past fire frequency has reduced the seed bank, especially of woody plants. This suggests a future management plan of less frequent fires with longer inter-fire intervals, would be worthwhile.

Future information requirements in this area include further research into the responses to the fire regime of individual species such as *Leptospermum polygalifolium*. This would identify those species exhibiting particular responses to fire that may need attention for fire management planning. Future monitoring of the burn sites could be used to establish if the sites regenerate to the full compliment of species found prior to the burn or if other species regenerated in the moderate intensity burn. This, plus further information on the mode of regeneration following fire, would provide input into fire management planning to ensure the persistence of a range of species. Information on plant regenerative mechanisms was required in this study for species in GFRNP and will be addressed further in Chapter 6.