Contrasting effects of fire severity on regeneration of the dominant woody species in two coastal plant communities at Wilsons Promontory, Victoria

J.W. Morgan[1] *and C. Nield*

Department of Botany, La Trobe University, Bundoora, VIC 3086, AUSTRALIA
[1]Author for correspondence: J.Morgan@latrobe.edu.au

Abstract**:** Following wildfire in 2005 at Wilsons Promontory, Victoria, we asked how fire severity affected the post-fire regeneration of dominant woody species in two coastal plant communities. We documented the effects of fire severity (unburned, low, high) on stand mortality and seedling regeneration in shrublands dominated by the obligate seeder *Leptospermum laevigatum* (Myrtaceae) and woodlands dominated by the resprouting *Banksia integrifolia* var. *integrifolia* (Proteaceae). *Leptospermum laevigatum* is a range-expanding native species that has encroached into grassy *Banksia* woodland and hence, we were also interested whether fire severity affects post-fire succession in encroached and un-encroached stands. Fire severity impacted on all measures of post-fire recovery examined: stand mortality, seedling germination, seedling survival, seedling growth. High fire severity (complete canopy consumption) led to 100% mortality of both species. Despite variable responses at the stand level, mean *Leptospermum laevigatum* seedling establishment, growth and survival all increased with increasing fire severity in shrublands, thus ensuring shrublands are replaced. *Banksia integrifolia* recruitment, however, was minimal in all stands and not fire-cued. Increasing fire severity enabled *Leptospermum laevigatum* to recruit into woodland sites from where it was previously absent and this establishment, coupled with the loss of overstorey *Banksia* trees, may rapidly transform woodlands into shrublands. Hence, fire severity-induced population responses were observed and these imprints are likely to affect longer-term succession by reinforcing site occupancy of the encroaching *Leptospermum laevigatum* while simultaneously leading to the potential decline of *Banksia* woodlands.

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Introduction

Large fires do not burn homogeneously; most fires result in a mosaic of unburned and burned patches of varying size, shape and intensity (Turner *et al.* 1997, Chafer *et al.* 2004, Williams *et al.* 2006, Bradstock 2008). Plant population responses to fire are therefore likely to vary with fire severity, which should affect post-fire plant community recovery and subsequent succession (Morrison & Renwick 2002).

Fire severity, the impact of fire, is often assessed as the extent of canopy consumption and it is increasingly seen as an important determinant of how plant populations respond to fire (Chappell & Agee 1996, Pausas *et al.* 2003, Vivian *et al.* 2008). For example, adult plant mortality (Williams *et al.* 1999, Wright & Clarke 2007), seedling recruitment (Anderson & Romme 1991, Hodgkinson 1991, Moreno & Oechel 1991, Turner *et al.* 1999, Vivian *et al.* 2008), and ecosystem productivity (Christensen *et al.* 1989) have all been shown to vary with fire severity. Differences in fire severity may affect competitive interactions among plants in the post-fire environment (Ducey *et al.* 1996) and this may have important consequences for successional trajectories of plant communities (e.g. Ashton 1981, Ashton & Martin 1996, Turner *et al.* 2003), although these longer-term impacts have been less well-studied.

One particularly important interaction between fire and plant population response concerns range expanding species. Three classes of response to fire might be observed. Positive fire-range expansion relationships might be expected where fire promotes migration in obligate seeders that are constrained by competitors rather than climate (Vivian *et al.* 2008, Landhausser *et al.* 2010). Here, fire severity may play a key role by affecting the extent of post-fire competitive release that advantages expanding species (Johnstone & Chapin 2003). Neutral fire-range expansion responses, regardless of fire severity, would be expected where current species distributions are in equilibrium with climate. Negative fire-range expansion relationships might exist where fire-sensitive species (e.g. rainforest species) are excluded from burnt areas, with mortality increasing with fire frequency and/or severity (Fairfax *et al.* 2009).

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A common form of range expansion in southern Australia is the encroachment by indigenous obligate seeder shrubs into coastal grassland, heathland and woodland communities (Bennett 1994, Lunt 1998, Costello *et al.* 2000, Moxham *et al.* 2009, Lunt *et al.* 2010). This is primarily thought to occur because of the change in disturbance regimes that have characterized coastal ecosystems over the last five decades, particularly the absence of frequent fire and increasing disturbance associated with grazing. Shrub encroachment can exert strong negative ecosystem effects on native communities (Costello *et al.* 2000, Price & Morgan 2008) and hence, the re-introduction of fire is thought crucial for recovering the structure, if not composition, of these coastal systems (Molnar *et al.* 1989). There is little evidence, however, of whether fire severity is an important determinant of post-fire recovery of encroached stands, and whether these outcomes are likely to be positive, negative, or neutral with regards to dominant woody species responses. Such information is necessary if land managers are to re-institute fire in coastal landscapes with the aim of favoring native communities over encroaching shrubs.

In 2005, wildfire at Wilsons Promontory National Park, Victoria created a landscape with strong patchiness in burn severity across a range of coastal woodland communities that have been variously impacted by the native, range-expanding coastal shrub *Leptospermum laevigatum*. This fire provided a landscape template to ask questions about the role of fire severity on initial post-fire recovery of dominant species in encroached and un-encroached systems. In particular, we asked:

(1) does fire severity impact regeneration of the structural dominants in (a) the extensive shrublands dominated by *Leptospermum laevigatum* compared to (b) the more restricted *Banksia integrifolia* grassy woodlands that are now imbedded in the shrublands?

(2) can range-expanding species such as *Leptospermum* exploit differences in fire severity to expand into previously unoccupied plant communities such as *Banksia* woodland?

To answer these questions, we surveyed the stand dynamics and seedling regeneration patterns of the dominant woody species in *Leptospermum* shrublands and *Banksia* woodlands in areas unburned and compared this to the responses of vegetation affected by low and high fire severity.

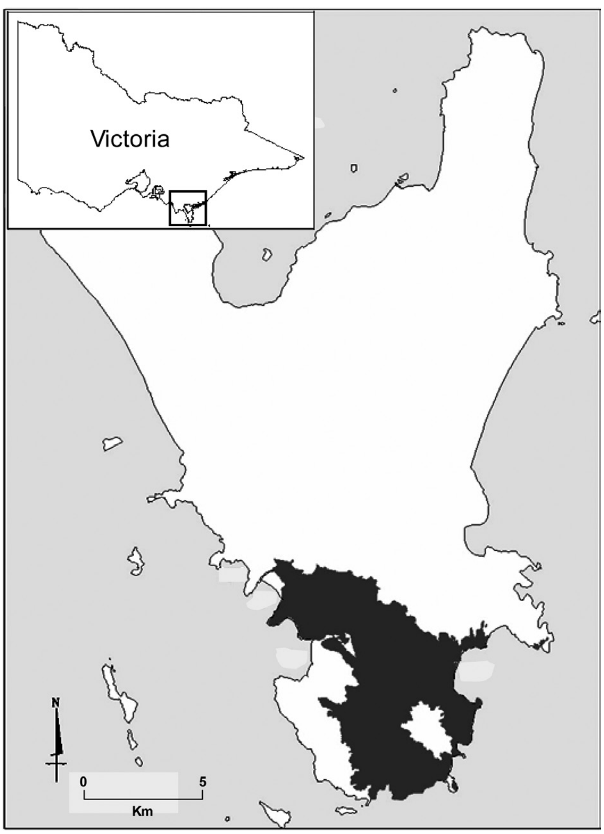

Fig. 1. Location of the 2005 wildfire (darkened area) in Wilsons Promontory National Park, Victoria.

Methods

Study area

Wilsons Promontory National Park forms the southernmost part of the Australian mainland. The climate is temperate and modified by maritime influences resulting in seasonally well-distributed temperatures and rainfall. Mean annual maximum temperature is 16.3 ºC and mean annual minimum temperature is 11.2 ºC. Mean annual rainfall is approximately 1060 mm, with maximum rainfall occurring in July (mean 121 mm) and minimum rainfall occurring in February (mean 46 mm) (Wilsons Promontory Lighthouse, Bureau of Meteorology, *unpublished data*).

In April 2005, approximately 13% (6143 ha) of the national park was burnt from a fire that originated at Tidal River (39° 00 S, 146° 25’ E). The fire burnt from the west coast, across Mt Oberon to the east coast, and down to the southern coast in an area not burnt since 1951 (Fig. 1). No significant predictive models were found to explain variation in fire severity with vegetation type, slope, aspect or stand density (C.Nield *unpublished data*). Rather, local weather patterns seemed to play a more important role in determining local fire severity patterns within- and between-communities.

Study species and site selection

We focused on two coastal vegetation types that were common on the calcareous dunes in the Norman Bay and Oberon Bay area, and where fire severity mosaics were clearly obvious. Closed shrubland dominated by *Leptospermum laevigatum* and woodland dominated by *Banksia integrifolia* var. *integrifolia* were selected for comparative purposes to assess the effect of fire severity of stand mortality and seedling recruitment. We chose these vegetation types, in part because of management concerns about the extent and dynamic of these communities. *Leptospermum* is an expanding shrub species at Wilsons Promontory, having encroached from near-primary dune systems into hinterland vegetation over the last 50 yrs in the absence of fire (Burrell 1981, Bennett 1994, Ashton & van Gameren 2002). Here, it forms near mono-specific closed shrublands and threatens local diversity by competitive dominance (Parsons 1966, Ashton & van Gameren 2002). Re-introduction of fire is thought crucial as a management technique to reduce its occupancy and there is some indication of success where this has been applied (Molnar *et al.* 1989). By contrast, *Banksia integrifolia* var. *integrifolia* is in decline at Wilsons Promontory (Bennett & Attiwill 1996) and the extent of the grassy woodland community it dominates has been reduced, in part, due to *Leptospermum* encroachment in the absence of fire (Bennett 1994). Most remaining un-encroached *Banksia integrifolia* woodland occurs as 'islands' surrounded by a matrix of *Leptospermum* shrubland, as was the case in this study.

Leptospermum laevigatum (Myrtaceae) is an obligate seeding shrub to 5–10 m tall with annual seedfall. Successful seed regeneration is minimal or absent in undisturbed mature stands (Ashton & van Gameren 2002), but prolific after fire or soil disturbance (Burrell 1981). *Banksia integrifolia* var. *integrifolia* (Proteaceae) is a non-bradysporous tree to 25 m, shedding seeds annually as soon as the follicle matures, with germination in late-winter (Price & Morgan 2003). Hazard & Parsons (1977) suggest that whilst thick bark may provide protection against fire, survival depends on tree age and fire intensity.

Study sites were stratified first by (a) dominant species (*Banksia*, *Leptospermum*) and then by (b) fire severity (unburned, low, high). Sites were distributed across the range of topographic positions occupied by the species within the burnt area. Fire severity was determined in August 2005 (approx 3.5 months after fire) according to the criteria outlined in Table 1. We used visual estimates of fire severity rather than *post-hoc* measures such as twig diameter (e.g. as used by Williams *et al.* 2006) primarily because the vegetation was too tall to employ these quantitative measures. Sites were selected according to accessibility, fire severity patch size (minimum 50 x 50 m), fire severity patch homogeneity, and the absence of previous disturbance such as walking tracks or fire breaks. In total, eight *Leptospermum* stands (3 unburned, 2 low severity, 3 high severity) and nine *Banksia* stands (3 unburned, 3 low severity, 3 high severity) were chosen for study. *Banksia* woodlands had no *Leptospermum* present as mature plants but were surrounded by dense *Leptospermum* shrublands.

Table 1. Visual criteria used to assign shrubland and woodland stands at Wilsons Promontory, Victoria to fire severity classes.

Severity Class	Description
Unburnt	No sign of fire evident
Low	Surface burn only: ground layer mostly consumed, canopy remains largely intact or with light scorching at most, leaf litter present
High	Crown fire: ground layer completely consumed, canopy also completely consumed, leaf litter absent

Effects of fire severity on stand dynamics, seedling recruitment and growth

At each of the 17 stands, one plot was established within which all subsequent data were collected. Woodland plots were larger (30 x 20 m) than shrubland plots (20 x 20 m) to account for the more open structure of the former communities. All individuals of the target species were assessed for survival in each stand at 6 months after fire by assigning them as dead (no green shoots or canopy evident, bark lifted away from the trunk) or alive (obvious signs of resprouting from epicormic shoots, green canopy). For *Banksia*, girth over bark at breast height (GBBH) was measured for all individuals in each stand, while girth at 15 cm was measured for *Leptospermum* (because of low frequent branching) for a maximum of 30 plants per stand. Plants in unburned control plots were scored and measured in the same way.

Leptospermum seedling density was recorded in both shrubland and *Banksia* woodland stands in ten permanent 25 x 25 cm quadrats in the main plot. Within each quadrat, the total number of *Leptospermum* seedlings was counted at November 2005. Emergence did not occur until August/September 2005 but we waited until November before counting seedlings to ensure correct identification. *Leptospermum* seedling growth and survival were monitored over the first summer by tagging a maximum of 10 seedlings per quadrat in December 2005 and measuring their height at monthly intervals until March 2006. Seedling height was measured from the soil to the tip of the longest branchlet, and survival was determined by a visual estimation of leaf condition. Seedlings that died were assigned a probable cause of death: (a) desiccation (leaves intact but browned-off), (b) herbivory (seedling clearly nipped off), (c) unknown (seedling disappeared without a trace).

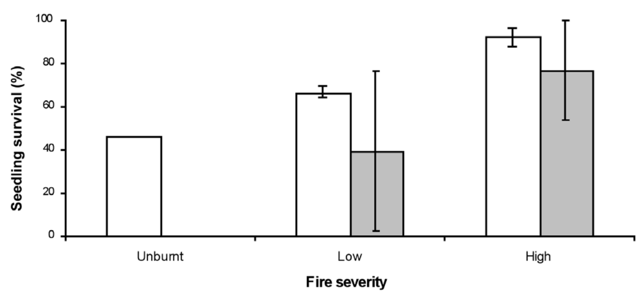

Fig. 2. Mean percent survival (± 95% CI) of tagged *Leptospermum laevigatum* seedlings at March 2006 in shrubland (□) and woodland (■) stands in relation to fire severity (unburnt, low, high) at Wilsons Promontory, Victoria. Note: there was no germination in unburnt *Banksia* woodland.

Table 2. Mean (± 95% CI) stand attributes (density, girth), and effect of fire severity of survival of *Leptospermum laevigatum* in shrublands and *Banksia integrifolia* in woodlands at Wilsons Promontory, Victoria. GBBH = girth over bark at breast height

Species	Attribute	Unit	Fire Severity		
			Unburnt	**Low**	**High**
Leptospermum	Stand density	Shrubs ha^{-1}	4967 ± 3757	5050 ± 6958	5167 ± 1059
	Basal girth	cm	44 ± 11	38 ± 24	25 ± 1
	Mortality	% of stand	7 ± 7	92 ± 17	100
Banksia	Stand density	Trees ha^{-1}	233 ± 105	339 ± 171	389 ± 202
	GBBH	cm	176 ± 20	127 ± 27	118 ± 53
	Mortality	% of stand	20 ± 8	88 ± 14	100

Table 3. Mean (± 95% CI) seedling density (per ha) of *Leptospermum laevigatum* and *Banksia integrifolia* var. *integrifolia* at November 2005 in response to fire severity and stand type at Wilsons Promontory, Victoria.

Stand type	Species	Fire severity		
		Unburnt	**Low**	**High**
Shrubland	*Leptospermum*	180,000 ± 350,000	770,000 ± 470,000	10,040,000 ± 12,330,000
Woodland	*Banksia*	78 ± 152	50 ± 98	89 ± 174
Woodland	*Leptospermum*	0	580,000 ± 610,000	2,010,000 ± 1,050,000

Banksia seedling density was so low that the whole 600 m^2 woodland plot was surveyed for recruitment. In December 2005, a 30 minute search of the plot area was undertaken at each stand and the total number of seedlings encountered was recorded. There were too few seedlings across the stands to follow survival and growth.

Data analysis

Due to large within-stand variation in most parameters and low stand replication, we assessed differences in mean stand density, mean stand girth, effects of fire severity on mean stand seedling density (at November 2005), and mean percent seedling survival (of tagged individuals at March 2006) as the percentage change between fire severity class stands and by examining overlap of 95% confidence intervals (Cumming & Finch 2005). Hence, for a comparison of two independent means, $p < 0.05$ when the overlap of the 95% CIs is no more than about half the average margin of error, i.e., when proportion overlap is about 0.50 or less; $p < 0.01$ when the two CIs do not overlap (Cumming & Finch 2005). For *Leptospermum* in shrubland and *Banksia* woodland, monthly seedling height (mean height of tagged seedlings per stand) was compared across fire severity classes using repeated measures ANOVA, comparing the effect of severity and time, and the interaction between severity and time on seedling growth.

Results

Stand structure and mortality

Leptospermum stand density was high (mean ≈5000 plants $hectare^{-1}$) and variable, but not significantly different across fire severity classes (Table 2). Fire resulted in very high mortality of *Leptospermum*; all plants in the high fire severity stands were dead after fire, while a few plants in the low severity stand survived the fire event (Table 2). Background levels of mortality in unburned sites, by comparison, were low (Table 2).

Banksia trees were large (mean >115 cm GBBH) and occurred at similar densities in all fire severity stands (Table 2). Mean tree mortality was high at both low and high fire severity (88% and 100% respectively, Table 2). A considerable proportion of the trees were dead in unburned stands (mean 20%, Table 2).

Seedling recruitment

Mean *Leptospermum* seedling density was highly variable across stands (Table 3) but fire severity had a clear impact on seedling establishment with a ≈1200% increase in mean seedling density in the high fire severity stands relative to low fire severity stands (Table 3).

Banksia seedlings were patchily distributed in all woodland stands, with no seedlings in six of the nine stands (two in each fire severity class) and there was no evidence that fire positively affected seedling regeneration (Table 3).

Leptospermum seedlings were observed after fire in previously unoccupied *Banksia* woodland stands. Fire severity had a clear effect on their establishment (Table 3). No seedlings were observed in unburned *Banksia* stands, but mean seedling density increased significantly (by 247%) with increasing fire severity (Table 3).

Seedling survival

Percent survival of tagged *Leptospermum* seedlings in shrublands at March 2006 was high and increased significantly with fire severity (i.e. increased by an average of 39% in high versus low fire severity stands; Fig. 2). The cause of death of seedlings differed according to fire severity. In unburned and high fire severity stands, mortality appeared to be due to desiccation, whereas in the low fire severity stands, herbivory was the major cause of death (Table 4).

Leptospermum seedling survival in *Banksia* woodland was not significantly different between low and high fire severity stands due to high stand variation, and was lower and more variable than in shrubland stands (Fig. 2). The cause of seedling mortality differed according to fire severity in a way that was similar to that seen in the shrublands (Table 4). In the low fire severity stands, herbivory was the most obvious cause of mortality whereas seedlings in the high fire severity stands died mainly due to the effects of desiccation (Table 4).

Table 4. Potential cause of mortality of Leptospermum laevigatum seedlings in shrublands and woodlands at Wilsons Promontory, Victoria in relation to fire severity. Note: there was no germination of Leptospermum in unburnt Banksia woodland.

Stand	**Fire severity class**	**Cause of mortality** (as a % of those seedlings that died)		
		Herbivory	Desiccation	Unknown
Shrubland	Unburnt	7	79	14
	Low	78	11	11
	High	0	88	12
Woodland	Low	57	29	14
	High	9	88	3

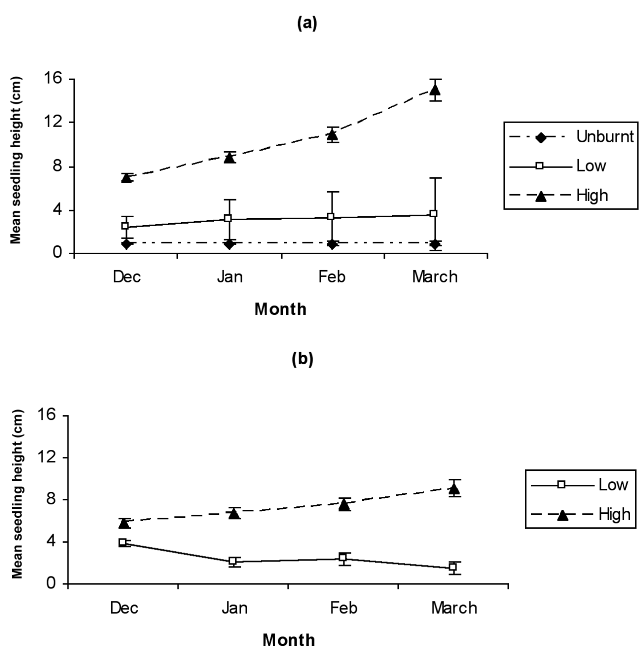

Fig. 3. Mean (± 1 SE) *Leptospermum laevigatum* height of seedlings in (a) shrubland and (b) woodland with respect to fire severity (unburnt, low, high) and month (7–11 months post-fire). Note: there was no germination in unburnt *Banksia* woodland.

Seedling growth

The mean height of *Leptospermum* seedlings in shrublands increased significantly with fire severity (F = 39.88, P< 0.001) and remained significant over the sampling period (F = 39.93, P<0.001) (Fig. 3). The growth of *Leptospermum* seedlings was also significantly affected by the interaction between fire severity and time (F = 15.52, P<0.001), with seedlings in the high severity sites outperforming others, particularly later in the season. Seedling that did emerge in the unburned sites showed no evidence of net growth over the sampling period (Fig. 3).

The mean height of *Leptospermum* seedlings in *Banksia* woodland stands was not significantly affected by fire severity (P = 0.103) or time (P = 0.85), but was significantly affected by a severity and time interaction (F = 2.35, P<0.05, Fig. 3). Hence, while fire severity did not significantly affect mean growth, the treatments did differ over time. The high fire severity stands were the only sites to show a net increase in seedling height over the four month sampling period (Fig. 3).

Discussion

Fire severity is an under-studied aspect of the response of natural vegetation to wildfire but appears to play a crucial role in post-fire recovery in many ecosystems (e.g. Turner *et al.* 1999, Ooi *et al.* 2006, Vivian *et al.* 2008). Post-fire successional processes are likely to be affected by fire severity because of its impact on stand mortality and seedling regeneration (Moreno & Oechel 1991, Turner *et al.* 1999). It is clear that at Wilsons Promontory, differences in fire severity have led to changes in the initial recovery in shrublands and woodlands by affecting adult mortality and recruitment dynamics of the dominant species. This may have set the template for long-lasting structural change in these coastal communities.

Fire severity played out in three obvious ways. In both shrublands and woodlands, increasing fire severity led to increased stand mortality, with 100% mortality observed in both shrublands and woodlands at high fire severity where canopies were consumed by fire. For *Leptospermum laevigatum*, an obligate seeder, this was not unexpected. Even where fire only scorched the canopy rather than consumed it, there was sufficient heating to cause near total adult mortality. However, for *Banksia integrifolia* var. *integrifolia*, a tree thought to be capable of resprouting after fire, this was more surprising. The literature suggests that *Banksia integrifolia* var. *integrifolia* resprouts by epicormic shoots after fire, although Hazard & Parsons (1977) note that this may depend on fire severity. We now have sound evidence that canopy-consuming fires can cause complete stand mortality in this species. Low fire severity (i.e. ground fire) also led to high stand mortality (i.e. mean 88%) and this may be because many trees were old (as evidenced by mean stand GBBH >125 cm) and showing signs of senescence (Bennett & Attiwill 1996).

Secondly, fire severity significantly affected seedling regeneration of *Leptospermum laevigatum* in shrublands, but not *Banksia integrifolia* in woodlands. The post-fire recruitment of *Leptospermum laevigatum* has been well-documented (Burrell 1981, Bennett 1994, Ashton & van Gameren 2002), although the effects of fire severity have not been previously observed. Germination under the unburnt shrubland canopy does occur (Ashton & van Gameren 2002), and seedlings grew very slowly, reached minimal height, had high mortality, and are unlikely to contribute to the population. With increasing fire severity, seedling regeneration, despite high variability at the stand level, increased dramatically. The availability of bare ground and high light conditions (Burrell 1981), as well as fire-induced mass seedfall from woody capsules that can survive high temperatures for short durations (Judd 1993), are likely to have maximised seed availability, germination and survival in high fire severity stands. In low fire severity stands, by comparison, bare ground is likely lower (due to incomplete litter consumption), canopy interception of light higher (due to the scorching rather than consumption of foliage), and initial seed release may have been lower; this may explain the lower levels of germination observed there.

For the non-bradysporous *Banksia integrifolia* var. *integrifolia*, seedling regeneration can occur in the inter-fire period (Price & Morgan 2003, Gent & Morgan 2007). While fire could aid seedling germination and initial survival by the removal of competitors and the increase in light availability, it has been suggested that in harsh environments like coastal dunes, facilitation by the unburnt ground layer vegetation may play an important role in *Banksia* establishment (Price & Morgan 2003). Hence, it was perhaps not unexpected that post-fire seedling densities were low and not promoted by fire *per se*. Additionally, the poor health of the adult population may have contributed to low seed rain post-fire (Price & Morgan 2003) and hence, restricted opportunities for seedling germination in the post-fire environment.

Thirdly, increasing fire severity positively affected the growth of *Leptospermum laevigatum* seedlings over the first growing season in shrublands. Inter- and intra-specific overstorey competition has been shown to suppress *Leptospermum* seedling regeneration through competition for light and soil moisture (Ashton & van Gameren 2002). High fire severity had the most impact on canopy and branch reduction in shrublands, and this likely eliminated competition in the post-fire environment to a greater extent than occurs following low fire severity, which left a scorched (but intact) canopy which continued to intercept light. Higher post-fire soil fertility with high fire severity has been observed elsewhere (Pausas *et al.* 2003) and this may also contribute to faster growth in *Leptospermum* seedlings (Burrell 1981). Vivian *et al.* (2008) found similar positive effects of fire severity on initial seedling growth for the obligate seeding tree *Eucalyptus delegatensis*, hinting that fire severity plays a critical role for establishment of those species strongly constrained by competitive processes rather than climate. In *Banksia* woodland, however, fire severity had less impact on growth of *Leptospermum* seedlings. While seedlings initially grew taller in high fire severity stands, this growth was not maintained, perhaps because herbaceous competitors in the understorey were fast to recover, regardless of fire severity.

The increase in mean density, survival and growth of *Leptospermum* seedlings with increasing fire severity was clear, yet this trend differs from that observed for shrubs in semi-arid woodland (Hodgkinson 1991, Pausas *et al.* 2003) and trees in northern hemisphere forests (Anderson & Romme 1991, Chappell & Agee 1996, Turner *et al.* 1999). In these systems, highest recruitment occurs after low to moderate severity fire, perhaps because of the consumption of canopy seed in high severity fires. This disparity may be due to differences in seed properties in the different ecosystems, or it may just reflect the subjective nature of the fire severity classifications used. In a comparative sense, fire severity in shrubland at Wilsons Promontory may have been at the lower end of the fire severity continuum relative to forest or woodland canopy fires, allowing high proportions of *Leptospermum laevigatum* seed to survive even after 'high severity' fire. However, in a relative sense, the high fire severity stands we identified in shrublands at Wilsons Promontory experienced fire orders of magnitude higher than the low severity fires, and it is suspected to be at the upper end of the fire intensities that would occur in these communities. Hence, the general responses to fire severity in coastal shrublands would still appear to differ from those observed elsewhere.

While many of the general effects of fire severity we observed on mortality and recruitment are well known, we also found that fire severity impacted upon post-fire recovery in two less obvious ways. Fire severity had an indirect impact on the cause of *Leptospermum* seedling mortality in both shrublands and woodlands. After low severity fire, slugs, caterpillars and other insects colonised the post-fire regrowth in large numbers and were seen actively feeding on seedlings (author. *pers. obsv.*). By contrast, in high fire severity shrubland stands, seedlings died due to desiccation over the summer months, presumably because there was little shading from regrowing vegetation. Surprisingly, mortality of *Leptospermum* in the high severity sites was low, despite seedling density being highest there, indicating that mortality was not density-dependent as is often observed (Hodgkinson 1991, Harms *et al*. 2000). Rather, in the open, well-lit, sandy soils, seedlings that were not well protected by near neighbours were most likely to be affected by heat and drought stress.

Fire severity also provided differential opportunities for *Leptospermum* to establish in previously un-encroached *Banksia* woodland stands. No *Leptospermum* seedlings were observed in unburnt woodland, presumably because of high vegetation cover and a lack of bare ground (i.e. the absence of regeneration niches) (Burrell 1981, Bennett 1994). By contrast, fire provided opportunities for *Leptospermum* seedling germination in woodland by removing canopy and groundlayer competitors, as well as a temporary increase in soil nutrients (Burrell 1981). Enhanced seed supply was provided by 'spillover' dispersal from adjoining shrubland stands that were burned (i.e. the mass ratio effect; Grime 1998). Seedling germination, establishment and growth were all higher at high fire severity where bare ground was higher and it is possible that high fire severity has led to the establishment of *Leptospermum* founder populations that may lead to a vegetation state change in *Banksia* woodland.

Predictions for long-term vegetation development from initial fire responses

Variation in fire severity has the ability to initiate changes in stand composition and structure, and may generate a number of alternative successional pathways in plant communities (Turner *et al.* 1997, 1999, 2003). The high *Leptospermum. laevigatum* seedling density promoted by high severity fire will most likely result in the complete re-occupation of the shrubland sites by a dense *Leptospermum laevigatum* stand. In the years following fire, as the canopy closes over and litter levels build up, small-scale species coexistence is predicted to decline (Costello *et al.* 2000, Price & Morgan 2008). By contrast, in shrubland exposed to low fire severity, seedling recruitment was lower and may result in more open, mixed stands with lower densities of *Leptospermum laevigatum* and a higher number of coexisting species. If fire was re-introduced into these sites at high frequency, before *Leptospermum laevigatum* seedlings attain reproductive age (≤ 5 years) (Bennett 1994), it may be possible to reduce or even remove *Leptospermum laevigatum*, and push the system away from its current state.

The widespread senescence of *Banksia integrifolia* stands, the high levels of fire-induced tree mortality, low and patchy seedling recruitment after fire, as well as high density of *Leptospermum laevigatum* seedlings in woodlands after fire, all point towards a complete state change of burnt *Banksia* woodlands at Wilsons Promontory. The encroachment of woodland by *Leptospermum laevigatum* in the absence of fire has been of ongoing concern to park managers aiming to maintain biodiversity and increase habitat heterogeneity; the 2005 fire seems likely to have only exacerbated that concern. The poor pre-fire health and widespread senescence of *Banksia integrifolia* var. *integrifolia* populations may have increased their sensitivity to fire *per se* and it is hard to see how re-implementing fire (as a regime) will restore these communities to their former state. The consequences of the loss of this 'foundation species' (*sensu* Ellison *et al.* 2005) are likely to be felt in the decades to come.

Conclusion

The establishment, growth and survival of *Leptospermum laevigatum* seedlings in shrubland and woodland were clearly promoted by fire. The post-fire environment of high light, bare soil and the lack of canopy and groundcover competition likely provided the temporary opportunity necessary for abundant recruitment of this encroaching species. Hence, one-off fires of any severity are unlikely to eliminate this species from plant communities into which it has substantially encroached. Rather, high fire severity in shrublands is likely to promote or reinforce the dominance of *Leptospermum*. By contrast, *Banksia integrifolia* var. *integrifolia* mortality was high, seedling recruitment was minimal and not promoted by fire, and it is likely that stand-level changes in dominance may occur in woodlands as a consequence of both fire and subsequent shrub encroachment, with subsequent important effects on habitat heterogeneity and ecosystem function. Restoring this community is likely to be challenging, and the use of fire in this process is likely to have variable outcomes depending on tree age, health and landscape context.

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