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Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region

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Abstract. Fire is a common source of change for the plant species of Mediterranean-type ecosystems, but little is known about the comparative effects of different fire intensities. Accordingly, nine species of small tree (*Acacia binervia*, *Acacia implexa*, *Acacia parramattensis*, *Casuarina littoralis*, *Casuarina torulosa*, *Hakea sericea*, *Jacksonia scoparia*, *Leptospermum trinervium*, *Persoonia linearis*) were studied 1 year after each of two low-intensity prescribed fires and a high-intensity wildfire at a site in the outer western region of the Sydney metropolitan area, south-eastern Australia. All of the species except *H. sericea* proved to be at least partly tolerant of the low-intensity fires (40–80% of their stems surviving the fires), but only *C. torulosa*, *L. trinervium* and *P. linearis* were tolerant of the high-intensity fire (20–30% stem survival). All of the fire-tolerant species had more of their smaller stems killed by the fires, and the high-intensity fire killed larger stems than did the low-intensity-fires. The size of surviving stems was related to the fire-tolerance characteristics for these species, specifically the presence or absence of insulating bark and epicormic or lignotuberous buds, as well as stem height (preventing 100% leaf-scorch). Those species with post-fire shoots at the stem base produced them when the upper part of the stem had been killed, with variable response to the fire intensities in the number of shoots produced. Those species with post-fire epicormic shoots produced them if the stem was alive post-fire, usually with fewer shoots produced after the high-intensity than the low-intensity fire. The number of shoots produced was positively related to the size of the stem for both fire intensities. These different sets of responses to the fire intensities have important implications for the ability to predict community responses to fire based on the study of only a few species, as well for the long-term effects of prescribing a particular fire regime.

Introduction

The world contains many fire-prone regions, and fire is a common source of change particularly for the plant species of Mediterranean-type ecosystems (reviewed by Whelan 1995; Bond and van Wilgen 1996). Fire regimes are usually considered to have three interrelated components that can affect plant population dynamics: fire frequency, season of occurrence, and fire intensity (Whelan 1995). Population changes at short and long intervals are often determined by fire frequency, while intermediate changes are influenced more by season and intensity (Bond and van Wilgen 1996). Thus, knowledge of the responses of plant species to fires is of intrinsic interest, as well as being essential for the scientific management of plant communities (Gill and Bradstock 1992).

For example, two general types of regeneration strategy by plant populations after fire are usually recognised: death of all adult plants during the fire followed by regeneration solely from seeds (fire-sensitive species); and regeneration from protected dormant vegetative buds on adult plants that

survive the fire (fire-tolerant species) (Gill 1981). These two strategies can result in dramatically different population dynamics, and vegetation management for species conservation may need to incorporate these differences into fire-management plans (Bradstock and Auld 1987).

The ecological effects of fire have been particularly well studied for the dry sclerophyll communities of Australia (Gill *et al.* 1981; Pyne 1991). However, while there is an increasing amount of quantitative data on the post-fire behaviour of both fire-sensitive and fire-tolerant species in Australia, there have been relatively few comparative studies of co-occurring species (e.g. Beadle 1940; Hodgkinson and Griffin 1982; Benson 1985; Cowling and Lamont 1987; Delfs *et al.* 1987; Clark 1988; Enright and Lamont 1989; Auld and O'Connell 1991; Lonsdale and Braithwaite 1991; Bradstock *et al.* 1994; Meney *et al.* 1994; Morrison 1995). Such studies are important because the biological comparisons are made under similar environmental conditions, and thus the true local diversity of biological behaviour is established. Furthermore,

variation in behaviour detected among co-occurring species will have important implications for the management of an area. For example, most fire ecology studies have focused on a single species within a community (reviewed by Whelan 1995; Bond and van Wilgen 1996), and it might be inappropriate to predict community responses based on limited study of one or a few species if the species vary considerably.

In addition, there is little knowledge about variability among individuals within a species in response to the various fire characteristics of frequency, season and intensity. Intra-specific variation in fire responses has been reported in several studies (e.g. Pate *et al.* 1991; Gill and Bradstock 1992; Lamont *et al.* 1994; Whelan 1995; Benwell 1998), and may be the result of variation in plant size, intraspecific genetic diversity, or inequality of fire intensity (Gill 1981).

One of the main sources of variability in fire intensity (along with fuel load, fuel type, topography and climatic conditions) is whether it is a prescribed fire or a wildfire. Current fire-management practices in the fire-prone vegetation of south-eastern Australia are based mainly on the concept of hazard reduction by the use of periodic low-intensity fires to maintain the amount of flammable fuel within specified (low) limits (Pyne 1991). These prescribed fires are thus intended to reduce the hazards associated with subsequent non-prescribed fires (wildfires) in the managed area (Gill *et al.* 1981). These fire-management practices are not based on concepts such as maximising or even maintaining species biodiversity, in spite of the fact that these practices can be expected to have a significant effect on the continued long-term survival of plants in the managed area (Whelan and Muston 1991; Williams *et al.* 1994; Morrison *et al.* 1996). Moreover, if a single invariant fire regime is prescribed for an area, then it may favour a subset of the species rather than affecting all of the species in the community as a whole (Morrison *et al.* 1996).

Therefore, the work reported here seeks to compare some of the population responses to both low-intensity prescribed fires and high-intensity wildfires of a range of co-occurring species of small tree (woody perennials) from a dry sclerophyll forest of the Sydney region, in south-eastern Australia. In particular, the following questions were addressed with respect to different fire intensities:

- (1) Which of the species are fire-tolerant as adult individuals, and what characteristics allow them to be so?
- (2) For those species with some degree of fire-tolerance, what is the minimum stem size necessary for post-fire survival?
- (3) For those species that can regenerate post-fire shoots from dormant buds (e.g. James 1984), what is the pattern of post-fire shoot production from these epicormic and/or stem basal buds?

Materials and methods

The work was carried out on the 'Yarrawood' property of the University of Technology Sydney, at Yarramundi in the outer western region of the

Sydney metropolitan area. The vegetation is a sclerophyllous open forest dominated by large trees of *Eucalyptus punctata*, *E. fibrosa*, *E. eximia* and *E. oblonga* (vegetation type 10ar[iii] of Benson 1992), occurring on both sandstone and shale substrates. The vegetation is thus not uniform throughout the area, but varies with soil type (sand versus clay) and aspect (Benson 1992). Most of the species are distributed disjunctly on the 40 ha of the property, depending on their habitat preferences.

Our study was a non-manipulative 'natural' (opportunistic) experiment. We appreciate that this is not an ideal form of experimental design for attributing cause-and-effect in scientific studies, which would instead involve a symmetrical repeated-measures analysis of a spatially and temporally replicated BACI (Before-After, Control-Impact) design (e.g. Green 1993). However, the practicalities of studying the effects of a high-intensity wildfire, whose location and timing cannot be controlled, meant that we had very little alternative but to adopt the sampling design that we have used, especially as there were no unburnt plants in the vicinity with which to compare our samples.

Our sampling strategy consisted of stratifying the property into different study areas based on the recent (*c.* last 30 years) fire history. The majority of the vegetation has been subjected to prescribed fires since the late 1960s, although on the western end of the property the most recent fire previous to our study was a high-intensity wildfire in 1968. About half of the property was burnt by a low-intensity prescribed fire in the autumn of 1991, and most of the rest was burnt by a low-intensity prescribed fire in the autumn of 1992 (the areas burnt did not overlap). Both fires varied spatially in intensity, with scorch height varying from 2 to 4 m. Study samples were taken from these two areas 12 months after each of the respective fires (i.e. in April of 1992 and 1993). All of the samples from these two years were combined for the data analyses, as no consistent differences in response by the species were noted (Morrison 1995).

All of the vegetation on the property was burnt by a high-intensity wildfire in the summer of 1994. Although there was presumably some spatial variation in fire intensity, all of the plants were subjected to 100% leaf-scorch (i.e. scorch height 10–15 m). Study samples were collected 3 months after the fire (i.e. in April of 1994) for those species in which all of the stems were killed by the fire, since stem death could be accurately determined at this early stage. Study samples were collected 15 months after the fire (i.e. in April of 1995) for those species in which some stems survived the fire, since this delay was necessary to ensure that all live shoots would have resprouted.

Individuals were sampled by locating as many individuals of the small tree species as possible in each of the different study areas. Small tree species were defined as those species that have adult individuals whose stems usually grow to be more than 2 m tall on the 'Yarrawood' property. For each individual plant, the following characteristics were recorded: whether the stem was dead or alive (i.e. whether it had clear evidence of green shoots, either surviving pre-fire shoots or new post-fire shoots); stem circumference at 1 m height (to the nearest centimetre); number of post-fire aerial (epicormic) shoots; number of post-fire shoots at the stem base (either from a lignotuber or from the bottom 30 cm of the trunk, depending on the species). Individual plants were chosen for sampling only if their post-fire stem was more than 1 m tall, or they had clear evidence of post-fire shoot regeneration (if there was no stem > 1 m tall then the circumference was recorded as 0 cm).

As noted above, non-manipulative experiments are subject to several problems related to the lack of explicit control over the experimental conditions. In particular, confounding sources of variation are often difficult to deal with. For our sampling program, it was necessary to assume that stem death was always a response to the most recent fire; this is likely to be true for most of the species, as the previously dead stems are usually consumed by the fires (particularly wildfires). We also needed to assume that no individual with a live stem more than 1 m tall was completely consumed by the most recent fire, and that stem growth since the fire was randomised across all samples and produced

variability that was no larger than the variability due to measurement precision. These assumptions are probably reasonable, based on our knowledge of the area. However, in this type of study it is clearly better to label live individuals before the fire and then check for post-fire death (cf. Noble 1984); this is impossible for high-intensity fires, as these are not planned events. Our estimates of the number of deaths are thus probably best treated as minimum estimates.

Also, it should be noted that many of the individuals sampled after the high-intensity fire had also been subjected to one of the previous low-intensity prescribed fires, while others had not (i.e. those in the area at the western end of the property). This is thus a potentially confounding factor, in that the plants burnt by the prescribed fires have also been subjected to a higher fire frequency in recent years; but it does allow a comparison of these plants with plants that had not been burnt since the 1968 wildfire (assuming that the frequency distribution of the size of the individuals was similar in both areas prior to the fires). Finally, the season of the fires is inextricably confounded with the fire intensities, because the prescribed fires occurred in early autumn while the wildfire occurred in mid-summer. However, summer and autumn fires often have similar effects on the floristic composition of the dry sclerophyll communities of the Sydney region (D. A. Morrison, unpubl. data).

It was not possible to use many of the standard (e.g. regression) statistical tests to analyse the data, because the error distribution was often bimodal. Consequently, non-parametric tests were used for all of the analyses. These are potentially weaker and less informative than parametric tests, and they thus provide conservative analyses of the patterns in the data. We preferred to use this more cautious approach in order to reduce the probability of Type I errors.

Stem mortality for the two fire intensities was compared by using log-likelihood ratio contingency tests for each species (Wilkinson 1989). The stem circumferences of individuals in the different samples were compared using log-likelihood ratio contingency tests on the frequency histograms for each species (Wilkinson 1989). The median stem circumference necessary for post-fire survival (i.e. the stem size at which the probability of the stem surviving the fire is 0.5) was estimated by the trimmed Spearman–Kärber method for each species (Hamilton *et al.* 1977). The numbers of shoots produced by individuals with live and dead stems were compared by using log-likelihood ratio contingency tests on the frequency histograms for each species, as above. The relationships between stem circumference and the number of post-fire shoots for each species were assessed by using Spearman rank-order correlation coefficients (Wilkinson 1989). For all of the statistical tests significance was tested at $P = 0.005$, to allow for the fact that several non-independent tests are being carried out on the same data—there were up to 10 tests per data set, and so the Bonferroni adjustment was $P = 0.05 \div 10$ (Wilkinson 1989).

Results

Nine species of small trees were common enough on the ‘Yarrowood’ property to be studied (Table 1). There were six other small tree species recorded, for which fewer than 50 individuals were located. There was considerable variation within and among these nine species in their responses to the different fire intensities.

Of these nine species, only *H. sericea* had all of the stems killed after both the high-intensity and low-intensity fires (Table 2), suggesting that all of the other species have some degree of tolerance to fires as adults. All of the other species showed significantly different responses to the fire intensities, with more stems being killed after the high-intensity fire compared with the low-intensity fire (Table 2). Only three species, *C. torulosa*, *L. trinervium* and *P. linearis*, had some stems survive 100% leaf-scorch (i.e. the high-intensity fire); the other five species, *A. binervia*, *A. implexa*, *A. parramattensis*, *C. littoralis* and *J. scoparia*, had 20–60% of their stems killed by the low-intensity fire but all of their stems killed by the high-intensity fire (Table 2).

For all of the eight species with some adult fire-tolerance, smaller stems were more likely to be killed after both the low- and high-intensity fires (Tables 3, 4), compared with larger stems; but the minimum stem size necessary for post-fire survival varied widely between these species (Table 2). More of the relatively larger stems were killed after the high-intensity fire compared with the low-intensity fire for most of the species (Tables 3, 4), except for *H. sericea* (where all of the stems were killed by the low-intensity fire) and *J. scoparia* (where most of the stems were killed by the low-intensity fire). Furthermore, for *C. littoralis*, *J. scoparia* and *L. trinervium* after the high-intensity fire, the stems that had previously been subjected to a low-intensity fire were killed at relatively larger stem sizes than those stems that had not recently been burnt (Table 4).

All four of the species that are capable of producing new post-fire shoots at the stem base preferentially did so when the upper stem had been killed after both the low- and high-intensity fires (Tables 3, 5). *Jacksonia scoparia* and *L. trinervium*

Table 1. Species of single-stemmed small trees studied, and their fire-regeneration characteristics

Species	Family	Maximum height (m)	Stem aerial buds	Stem basal buds	Root buds
<i>Acacia binervia</i> (H.L.Wendl.) J.F.Macbr.	Mimosaceae	10	—	—	—
<i>Acacia implexa</i> Benth.	Mimosaceae	6	—	—	suckers
<i>Acacia parramattensis</i> Tind.	Mimosaceae	7	—	—	—
<i>Casuarina littoralis</i> Salisb.	Casuarinaceae	8	—	—	—
<i>Casuarina torulosa</i> Aiton	Casuarinaceae	8	epicormic	stem base	—
<i>Hakea sericea</i> Schrader	Proteaceae	3	—	—	—
<i>Jacksonia scoparia</i> R.Br.	Fabaceae	3	—	stem base	suckers
<i>Leptospermum trinervium</i> (Smith) J.Thompson	Myrtaceae	4	epicormic	lignotuber	—
<i>Persoonia linearis</i> Andrews	Proteaceae	4	epicormic	lignotuber	—

Table 2. Stem survival (including the log-likelihood ratio contingency tests) and median stem size (circumference) that must be reached before the stem is capable of surviving a low- or high-intensity fire for the small tree species

For stem survival, numbers are mean (sample size); for stem circumference, numbers are median (95% confidence limits—note that they are asymmetrical)

Species	Stem survival (%)		Contingency test		Stem circumference (cm)			
	Low-intensity	High-intensity	<i>G</i>	<i>P</i>	Low-intensity		High-intensity	
<i>Acacia binervia</i>	74.8 (218)	0.0 (170)	281.66	<0.001	(22.2)	24.9 (28.0)	—	
<i>Acacia implexa</i>	61.0 (292)	0.0 (206)	258.66	<0.001	(6.9)	7.7 (8.5)	—	
<i>Acacia parramattensis</i>	82.6 (138)	0.0 (358)	407.25	<0.001	(8.0)	8.6 (9.3)	—	
<i>Casuarina littoralis</i>	66.4 (321)	0.0 (297)	386.07	<0.001	(15.2)	16.7 (18.5)	—	
<i>Casuarina torulosa</i>	65.9 (170)	26.4 (474)	82.24	<0.001	(10.6)	11.9 (13.4)	(22.8)	25.0 (27.3)
<i>Jacksonia scoparia</i>	38.5 (205)	0.0 (356)	182.72	<0.001	(12.5)	13.7 (15.0)	—	
<i>Hakea sericea</i>	0.0 (60)	0.0 (226)	—	—	—		—	
<i>Leptospermum trinervium</i>	71.5 (274)	19.7 (917)	248.56	<0.001	(5.7)	6.3 (6.9)	(11.3)	12.4 (13.5)
<i>Persoonia linearis</i>	56.2 (217)	27.3 (410)	50.15	<0.001	(5.7)	6.4 (7.2)	(14.2)	15.6 (17.2)

Table 3. Stem circumference, number of basal (lignotuber or stem base) shoots per stem and number of epicormic shoots per stem for the relevant small tree species following a low- or high-intensity fire

Numbers in table are median (inter-quartile range—note that they are asymmetrical)

Species	Low-intensity fire						High-intensity fire						
	Alive stems			Dead stems			Alive stems			Dead stems			
Stem circumference (cm)													
<i>Acacia binervia</i>	(38.0)	51.0	(69.0)	(17.0)	23.0	(31.5)	— ^A				(27.0)	44.0	(59.0)
<i>Acacia implexa</i>	(7.5)	10.0	(13.0)	(5.5)	7.0	(9.0)	— ^A				(7.0)	9.0	(12.0)
<i>Acacia parramattensis</i>	(12.0)	15.0	(18.0)	(7.5)	8.5	(9.0)	— ^A				(10.0)	14.0	(18.0)
<i>Casuarina littoralis</i>	(24.0)	33.0	(40.0)	(9.0)	14.0	(18.0)	— ^A				(16.0)	23.0	(34.0)
<i>Casuarina torulosa</i>	(17.0)	21.0	(27.0)	(5.0)	8.0	(12.0)	(21.0)	26.0	(31.5)		(13.0)	17.0	(21.0)
<i>Jacksonia scoparia</i>	(12.0)	15.0	(19.0)	(8.0)	10.0	(13.0)	— ^A				(7.0)	9.0	(12.0)
<i>Hakea sericea</i>	— ^A			(8.0)	11.0	(13.0)	— ^A				(8.0)	11.0	(14.0)
<i>Leptospermum trinervium</i>	(9.0)	12.0	(15.0)	(4.0)	5.0	(6.5)	(9.5)	13.0	(18.0)		(5.0)	7.0	(9.0)
<i>Persoonia linearis</i>	(10.0)	12.0	(15.0)	(4.5)	6.0	(7.0)	(13.5)	17.5	(24.0)		(7.0)	10.0	(13.5)
Number of basal shoots per stem													
<i>Casuarina torulosa</i>	(0.0)	0.0	(0.0)	(1.0)	3.0	(5.0)	(0.0)	2.0	(3.0)		(2.0)	3.0	(5.0)
<i>Jacksonia scoparia</i>	(0.0)	0.0	(0.0)	(0.0)	0.0	(2.0)	— ^A				(0.0)	0.0	(0.0)
<i>Leptospermum trinervium</i>	(0.0)	0.0	(0.0)	(2.0)	6.0	(8.0)	(0.0)	1.0	(3.0)		(2.0)	3.0	(5.0)
<i>Persoonia linearis</i>	(0.0)	0.0	(1.0)	(3.0)	4.0	(7.0)	(0.0)	1.0	(3.0)		(3.0)	5.0	(7.0)
Number of epicormic shoots per stem													
<i>Casuarina torulosa</i>	(0.0)	0.0	(0.0)	(0.0)	0.0	(0.0)	(24.0)	11.0	(36.0)		(0.0)	0.0	(0.0)
<i>Leptospermum trinervium</i>	(6.0)	11.0	(16.0)	(0.0)	0.0	(0.0)	(3.0)	6.0	(15.0)		(0.0)	0.0	(0.0)
<i>Persoonia linearis</i>	(13.0)	20.0	(30.0)	(0.0)	0.0	(0.0)	(5.0)	10.0	(22.0)		(0.0)	0.0	(0.0)

^ANo live stems were found.

produced fewer shoots per stem after the high-intensity fire than after the low-intensity fire, while *C. torulosa* produced more (Tables 3, 5). After the low-intensity fire, all of the species showed a moderate negative relationship between the number of shoots produced per stem and the size of the stem, but this relationship was reduced after the high-intensity fire (Table 6). After the high-intensity fire, the stems that had previously been subjected to a low-intensity fire pro-

duced the same number of shoots as did the stems that had not recently been burnt (Table 5).

All three of the species that are capable of producing new post-fire epicormic shoots usually did so if the stem was alive post-fire (Table 3), except for *C. torulosa*, which produced no epicormic shoots after the low-intensity fire. *Persoonia linearis* and *L. trinervium* produced fewer shoots per stem after the high-intensity fire than after the low-inten-

Table 4. Results of the log-likelihood ratio contingency tests for the comparison of the frequency histograms of stem circumference after a low- and high-intensity fire for the small tree species

Species	Alive v. dead stems after the low-intensity fire		Alive v. dead stems after the high-intensity fire		Dead stems after the low-intensity v. high-intensity fires		Dead stems after the high-intensity fire in the previously-burnt v. unburnt areas	
	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>
<i>Acacia binervia</i>	118.95	<0.001	— ^A		69.59	<0.001	— ^B	
<i>Acacia implexa</i>	44.76	<0.001	— ^A		33.31	<0.001	— ^B	
<i>Acacia parramattensis</i>	83.27	<0.001	— ^A		39.65	<0.001	3.92	0.417
<i>Casuarina littoralis</i>	205.16	<0.001	— ^A		109.58	<0.001	30.27	<0.001
<i>Casuarina torulosa</i>	110.83	<0.001	130.39	<0.001	79.94	<0.001	4.98	0.419
<i>Hakea sericea</i>	— ^A		— ^A		2.73	0.256	— ^C	
<i>Jacksonia scoparia</i>	43.07	<0.001	— ^A		5.41	0.067	11.16	0.004
<i>Leptospermum trinervium</i>	129.65	<0.001	228.88	<0.001	18.25	<0.001	13.82	0.003
<i>Persoonia linearis</i>	66.24	<0.001	112.68	<0.001	35.63	<0.001	10.01	0.040

^ANo live stems were found in the burnt area.

^BNo stems were found in the previously unburnt area.

^CAll stems in the previously burnt area were dead prior to the high-intensity fire.

Table 5. Results of the log-likelihood ratio contingency tests for the comparison of the frequency histograms of number of basal (lignotuber or stem base) shoots per stem after a low- and high-intensity fire for the relevant small tree species

Species	Alive v. dead stems after the low-intensity fire		Alive v. dead stems after the high-intensity fire		Dead stems after the low-intensity v. high-intensity fires		Dead stems after the high-intensity fire in the previously-burnt v. unburnt areas	
	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>	<i>G</i>	<i>P</i>
<i>Casuarina torulosa</i>	102.68	<0.001	82.05	<0.001	40.92	<0.001	1.67	0.947
<i>Jacksonia scoparia</i>	50.18	<0.001	— ^A		131.47	<0.001	— ^B	
<i>Leptospermum trinervium</i>	52.36	<0.001	168.45	<0.001	73.00	<0.001	17.14	0.047
<i>Persoonia linearis</i>	123.42	<0.001	213.39	<0.001	9.08	0.169	14.80	0.097

^ANo live stems were found in the burnt area.

^BNo stems produced basal shoots.

sity fire, while *C. torulosa* produced more (Tables 3, 7). For all three species the number of shoots produced was positively related to the size of the stem after both the low- and high-intensity fires (Table 6). After the high-intensity fire, the stems that had been subjected previously to a low-intensity fire produced the same number of shoots as did those stems that had not been burnt recently (Table 7).

Discussion

This study is unique in investigating variation both among and within locally co-occurring species in survival and resprouting after two different fire intensities. The nine co-occurring species of small trees studied display a wide range of responses to the two types of fire encountered at 'Yarrowood', both within and between species. There is thus

considerable local diversity of regeneration behaviour in response to fires.

Fire tolerance of adults

Only *H. sericea* appears to be incapable of surviving low-intensity fires as adult plants (i.e. it is absolutely fire-sensitive), thus relying entirely on regeneration of new individuals from its serotinous canopy-stored seedbank for continuation of the populations. There is expected to be a higher death rate of seeds after more intense fires, because the seeds are protected only by the relatively thin walls of the woody fruits (Bradstock *et al.* 1994). However, no seedlings of this species were observed to become established after the second prescribed fire (which was the only one that affected the single population of this species on the 'Yarrowood'

Table 6. Relationship (Spearman rank correlation) between stem circumference and number of basal (lignotuber or stem base) and epicormic shoots per stem for the relevant small tree species following a low- or high-intensity fire

Species	Low-intensity fire		High-intensity fire	
	Circumference v. basal	Circumference v. epicormic	Circumference v. basal	Circumference v. epicormic
<i>Casuarina torulosa</i>	-0.500	— ^A	-0.132	0.509
<i>Jacksonia scoparia</i>	-0.299	— ^A	— ^A	— ^A
<i>Leptospermum trinervium</i>	-0.363	0.734	-0.175	0.535
<i>Persoonia linearis</i>	-0.385	0.696	-0.198	0.549

^ANo shoots were produced.

Table 7. Results of the log-likelihood ratio contingency tests for the comparison of the frequency histograms of number of epicormic shoots per stem after a low- and high-intensity fire for the relevant small tree species

Species	Alive stems after the low-intensity v. high-intensity fires		Alive stems after the high-intensity fire in the previously-burnt v. unburnt areas	
	G	P	G	P
<i>Casuarina torulosa</i>	293.04	<0.001	— ^A	
<i>Leptospermum trinervium</i>	25.77	<0.001	14.80	0.005
<i>Persoonia linearis</i>	38.87	<0.001	5.19	0.268

^AToo few live stems were found in the previously unburnt area.

property), although a small number of juveniles were found 1 year after the wildfire in the area that had not previously been burnt since 1968 (Buckney and Morrison, unpubl. data). Local extinction of a fire-sensitive species will occur if an interfire interval (the time between successive fires) is shorter than the time taken for the individuals to reach first reproduction (the primary juvenile period) (reviewed by Whelan 1995), and this may well be the case for this species in the part of 'Yarrowood' subjected to prescribed burns.

Casuarina torulosa, *L. trinervium* and *P. linearis* all showed that some (c. 25%) of their stems are capable of surviving 100% leaf-scorch (i.e. are absolutely fire-tolerant). Actual individual death could not be properly quantified for these species (because pre-fire individuals were not tagged and then monitored post-fire), but only for *P. linearis* did all of the individuals located (a total of 410) have post-fire shoots (there were five individuals for *C. torulosa* and 14 for *L. trinervium* without post-fire shoots, out of a total of 474 and 917, respectively). However, all of these species can be classified as fire-tolerant, by using the 'general rule' (fewer than one-third of individuals killed by the fire) of Gill and Bradstock (1992).

The remaining five species all showed some stem tolerance of low-intensity fires but not of high-intensity fires. For *A. binervia*, *A. parramattensis* and *C. littoralis* stem death is

equivalent to death of the individual, indicating that they are all fire-sensitive (because there is 100% individual death when the population is subjected to 100% leaf-scorch). However, for the low-intensity fires, where many of the individuals were only partly scorched, there was only c. 25% death of the individuals. Death of the individuals could not be determined for *A. implexa* and *J. scoparia*, as these two species have root suckers, and identifying individuals is thus problematic, but only 40–60% of the stems were killed by the low-intensity fire. The physiology and ecology of root-suckering in relation to fire is a neglected area of research (cf. Lamont 1988).

It is quite common for species to display variable survival rates even within the one fire (e.g. Beadle 1940; Hodgkinson and Griffin 1982; Clark 1988; Lamont and Markey 1995), as shown by these small tree species, presumably as a result of variation in both fire intensity and size-related fire resistance of the individual plants (Hodgkinson and Griffin 1982; Benson 1985; Clark 1988; Morrison 1995).

Stem size necessary for fire tolerance

For all of the study species, it was the smaller stems that were more likely to be killed by both low and high fire intensities, as has also been reported for some large-tree species (Noble 1984; Strasser *et al.* 1996). Furthermore, for those

species with relatively low death rates after the low-intensity fires, the higher intensity of the wildfire killed larger stems than did the prescribed fires. Individual stems must thus attain a certain minimum stem size before they are fire-tolerant (i.e. so that the temperature of the meristem tissue is not raised to lethal levels), and this size is presumably related to several growth characteristics that may protect the living tissue of the plant from the heat of the fire (Gill 1981). First, as secondary growth progresses, bark is formed on the outer surface of the trunk, which may provide a protective insulating layer (the periderm protecting the cambium) that becomes increasingly effective as the stem ages. Second, as the stem height increases, an increasingly greater proportion of the foliage may be held above the scorch height of the flames. Third, there may be protected dormant vegetative buds, either on the aerial parts of the stem itself or at its base, and the degree to which these buds are protected may increase as the stem ages (James 1984).

Leptospermum trinervium and *P. linearis* have relatively short stems (c. 4 m), with both aerial (epicormic) and basal (lignotuberous) dormant vegetative buds that are protected, as well as quite specialised insulating flakey bark. Stems of these species can survive the fires at quite small sizes (6–7 cm circumference at 1 m height for the low-intensity fires, 12–16 cm for the high-intensity fire). It thus appears that the bark and the dormant buds are important in allowing the stems of these species to survive fires, as even the low-intensity fires can cause 100% leaf-scorch for these short stems.

Casuarina torulosa has relatively tall stems (c. 8 m) with both aerial (epicormic) and basal dormant vegetative buds that are protected. Only larger stems of this species can survive the fires (12 cm circumference for the low-intensity fires, 25 cm for the high-intensity fire). It thus appears that the stem height and the dormant buds are important in allowing the stems of this species to survive fires, as the low-intensity fires do not usually cause 100% leaf-scorch for these tall stems.

Jacksonia scoparia has short stems (c. 3 m) with only basal (non-lignotuberous) dormant vegetative buds that are protected. Stems of this species must also be larger (14 cm circumference) before they can survive the low-intensity fires, and did not survive the high-intensity fire. Thus, this species has only a partial tolerance mechanism. This suggests that the basal buds are not well protected, and, given that about 60% of the stems were killed after the low-intensity fires, it may be lack of 100% leaf-scorch that allows some of these stems to survive.

The remaining species, *A. binervia*, *A. implexa*, *A. parramattensis* and *C. littoralis*, do not have any protected vegetative buds, nor have they any specialised insulating bark. None of these species had stems that were capable of surviving the wildfire, but they all showed partial tolerance of the prescribed fires. This partial tolerance appears to be related to stem height, with the taller species requiring larger stem sizes to survive the low-intensity fires: *A. implexa*

(c. 6 m tall, 8 cm stem circumference), *A. parramattensis* (c. 7 m, 9 cm), *C. littoralis* (c. 8 m, 17 cm), *A. binervia* (c. 10 m, 25 cm). Stem height thus appears to be important in allowing the stems of these species to survive fires, as the low-intensity fires do not necessarily cause 100% leaf-scorch for these taller stems.

No growth data exist for any of these species, but if they did then it would be possible also to calculate the length of time necessary for the stems of each of these species to become fire-tolerant (assuming that stem size is related to stem age). This time is clearly important for vegetation management purposes if an interfire interval is shorter than the time required for a species to become fire-tolerant then new individuals will not be recruited to the population and local extinction will result (Whelan 1995).

Furthermore, the stems of *C. littoralis*, *J. scoparia* and *L. trinervium* that had previously been subjected to a prescribed fire were killed by the wildfire at relatively larger stem sizes than those stems that had not recently been burnt. There is thus the potential for a cumulative effect of fires on the populations of these species—even if some of the stems do survive a particular fire this does not guarantee their survival of subsequent low-intensity fires, as they may be predisposed to mortality from subsequent fires.

Production of post-fire shoots

All four of the species with protected buds at the stem base (*C. torulosa*, *J. scoparia*, *L. trinervium* and *P. linearis*) do not usually produce new shoots unless the upper part of the stem has been killed, irrespective of whether these shoots are from lignotuberous buds or not; and thus these basal shoots may be viewed as a back-up mechanism that is only employed by the individuals when the protection of the stem itself from the heat of the fire fails (James 1984). There was considerable variability in response to the different fire intensities, with two species (*J. scoparia* and *L. trinervium*) producing fewer shoots after the high-intensity fire compared with the low-intensity fire, one (*C. torulosa*) producing more, and one (*P. linearis*) with no difference. The number of shoots produced is usually negatively related to the size of the stem for the low-intensity fires but not for the high-intensity fire.

Those species with protected epicormic buds (*C. torulosa*, *L. trinervium* and *P. linearis*) almost invariably produce post-fire shoots if the stem is still alive and has been subjected to 100% leaf-scorch, and the number of shoots produced is positively related to the size of the stem. Therefore, these aerial shoots may be viewed as part of an active post-fire regeneration strategy by the stem rather than as merely a means of surviving the fire, as the canopy is actively replaced or augmented depending on whether it was completely destroyed by the fire or not. No epicormic shoots were produced by the *C. torulosa* plants after the prescribed fires, presumably because these taller stems were not subjected to

complete leaf-scorch. Fewer epicormic shoots were produced by the *L. trinervium* and *P. linearis* plants after the wildfire compared with the prescribed fires, presumably reflecting greater damage to the buds by the higher fire intensity.

After the wildfire, none of the species produced different numbers of shoots on those individuals that had previously been burnt by prescribed fires compared with those that had not, even though *L. trinervium* did have different sizes for death of the stems. This implies that there is not necessarily any cumulative effect on shoot production of a sequence of fires.

Management

Variation in behaviour detected among co-occurring species will have important implications for the biodiversity management of an area. The management will be affected by both the variation within species and the variation between species reported here, as well as by the different responses to the different fire intensities.

First, it is important for resource management purposes to emphasise the different responses of the plant species to the two different fire intensities. Given that many of the individuals can survive the low-intensity fires but not the high-intensity fires, the population dynamics of the different species will diverge after a prescribed fire in comparison to those following a wildfire. For example, the subsequent size structure of the populations will be markedly different, and so will the response (i.e. stem survival) to later fires. If new individuals of these small tree species are not recruited to the populations, but the adult individuals continue to survive prescribed fires, then the populations will eventually become senescent. None of the largest stems was killed by either of the prescribed fires, suggesting that the populations had not yet reached this senescent stage before the wildfire.

Consequently, it may be reasonable to conclude that the current local fire regime has had a significant impact on the relative abundances of these species, and will continue to have the same effect for as long as the current fire management practices continue. The long-term effects of prescribing a particular fire regime (e.g. a particular fire intensity), and maintaining this prescription closely, can thus be considerable. It is clear from our results that any particular fire intensity affects some species more than it does others, and there is thus the danger that prescription of an invariant fire regime will favour a particular subset of the species within a community. This will inevitably lead to the diminution of the local biodiversity (e.g. species richness).

Second, land managers often use 'fire response categories' in an attempt to predict community responses to particular fires (Bradstock and Auld 1987). These management tools place each plant species in a particular category according to the perceived generalised response of the species to fires. However, it is clear from the data presented here that there can be no simple classification scheme of plant responses to fires that comprehensively covers the potential range of post-fire behaviour. Most of the species studied at

'Yarrowood' showed variability between individuals in their response to the low-intensity fires, and all of the species showed considerably different responses to the high-intensity fire. It is therefore necessary to consider the type of fire being studied before species are assigned to particular categories (cf. Gill and Bradstock 1992). In particular, to predict the fate of a population in response to a fire it is necessary to know whether the individuals have been subjected to 100% leaf-scorch (which will depend on the fire intensity and the height of the stems), rather than simply considering whether the species is potentially fire-tolerant or fire-sensitive; and it may be necessary to have some knowledge of the characteristics of the prior sequence of fires for accurate predictions of behaviour.

Third, the fact that the nine species studied here have different responses to the different fires has important implications for the ability to predict community responses to fire based on the study of only a few species. This is often the case when using fire response categories, because most fire ecology studies have focused on a single species within each response category (Whelan 1995; Bond and van Wilgen 1996). On the basis of the results presented here, it is clearly inappropriate to predict community responses from a limited study of one or a few species, because the species are likely to vary considerably even within a category.

Finally, from a management viewpoint, it is also important to note that the prescribed fires may have had little effect on the occurrence or intensity of the subsequent wildfire. The low-intensity burns had a relatively low scorch height (2–4 m), leaving a considerable fuel load still in the canopy of the surviving stems of the taller species, even for those species that were not tolerant of 100% leaf-scorch. This fuel load was soon augmented by the active regrowth by the surviving stems of the shorter species with protected buds (Morrison 1995). Consequently, the wildfire was able to pass through the crown of the forest 1.7 and 2.7 years (depending on the area of the property) after the prescribed fires, even though the fuel load in the understorey was relatively small (Buckney and Morrison, unpublished data). It is thus likely that prescribed burns of low intensity at fixed intervals may be an inadequate fire-control measure in dry sclerophyll forests (cf. Morrison *et al.* 1996).

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