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Survival of eight woody sprouting species following an autumn fire in Swartboskloof, Cape Province, South Africa

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The survival of *Widdringtonia nodiflora* (L.) Powrie, *Aulax pallasia* Stapf, *Mimetes cucullatus* (L.) R.Br., *Leucadendron salignum* Berg., *Brunia nodiflora* L., *Nebelia paleacea* (Berg.) Sweet, *Penaea mucronata* L. and *Erica coccinea* L. was monitored after an autumn fire in montane fynbos near Stellenbosch in the Cape Province, South Africa. Discriminant and correlation analyses were used to determine the relationships between measures of pre-fire plant size and vigour, the degree of damage caused by the fire, and whether, firstly, plants survived the fire itself, and secondly, the survivors survived the subsequent summer. Pre-fire plant size was important in predicting whether plants survived the fire. Pre-fire plant vigour and the degree of damage caused by the fire were important predictors of whether plants survived the fire and the subsequent summer. Mortality due to the fire and during the following summer was highest for *E. coccinea, P. mucronata, N. paleacea* and *B. nodiflora*. Seedling recruitment varied widely between the different species. The populations of all species except *W. nodiflora* and *A. pallasia* increased as seedling recruitment exceeded adult mortality.

Die oorlewing van *Widdringtonia nodiflora* (L.) Powrie, *Aulax pallasia* Stapf, *Mimetes cucullatus* (L.) R.Br., *Leucadendron salignum* Berg., *Brunia nodiflora* L., *Nebelia paleacea* (Berg.) Sweet, *Penaea mucronata* L. en *Erica coccinea* L. is na 'n herfsbrand in bergagtige fynbos naby Stellenbosch, in die Kaapprovinsie, Suid-Afrika, gemonitor. Diskriminant- en korrelasie-analises is gebruik om die verband tussen plantgrootte en groeikragtigheid voor die brand, beskadiging deur die brand, en oorlewing na vuur asook gedurende die eerste somer na die brand te voorspel. Plantgrootte was belangrik om oorlewing na vuur te voorspel, terwyl beide groeikragtigheid voor die brand en skade as gevolg van die brand belangrik was om oorlewing na vuur en oorlewing gedurende die daaropvolgende somer te voorspel. Mortaliteit as gevolg van die brand en gedurende die somer was die hoogste vir *E. coccinea, P. mucronata, N. paleacea* en *B. nodiflora*. Die aanwas van saailinge van die onderskeie spesies het baie verskil. Aanwas van saailinge het volwasse mortaliteit oortref in al die spesies behalwe *W. nodiflora* en *A. pallasia*.

Keywords: Discriminant analysis, fire, pre-fire size, sprouters, survival.

Introduction

Various hypothetical models have been advanced to explain the relative abundance of seeding and sprouting woody plant species in the fire-prone mediterranean ecosystems of the world (Kruger 1983; Keeley 1986; Bond 1987). No single model, however, satisfactorily accounts for the observed patterns and the differences between analogous communities in the different mediterranean regions (Milewski & Cowling 1985; Bond 1987).

Detailed demographic studies of sprouting species and the factors determining fire survival of established plants and seedling recruitment are needed in order to resolve these questions. Although the percentage of sprouters which survive fires has been described in a number of studies, little is known about the factors determining the survival of individual plants. Noble (1984) found that post-fire success of three species of lignotuberous *Eucalyptus* seedlings depended on pre-fire height, the number of stems and leaves and the size of the lignotuber. The larger and more vigorous individuals had a better chance of survival. Survival was further enhanced by low litter loads and, consequently, low fire intensity.

In general, sprouters with lignotubers experience low mortality in fires and produce few seedlings (Specht, Rayson & Jackman 1958; James 1984; Midgley 1987), hence the net change in population size is negligible. As resources available to a plant are limited, it is presumed that sprouters allocate resources preferentially to vegetative reproduction (Carpenter & Recher 1979; Lamont & Barrett 1988). Thus, there may be an inverse relationship between parent survival and seedling recruitment (Keeley & Zedler 1978).

There is some evidence to suggest that bud-banks in some sprouting species may have a finite life-expectancy (Hobbs & Mooney 1985; Zammit 1988), but there are no data on age- or size-specific sprouting abilities for fynbos shrubs. The seedlings of vigorous sprouters may also be more susceptible to mortality than those of weak sprouters and seeding species (Zammit & Westoby 1988). Juvenile plants of sprouting species may also require relatively long periods between fires in order to become fire-tolerant, hence frequent fires may have a negative influence on population sizes in the long term (Bradstock & Myerscough 1988).

This paper describes a study of the demography of eight woody sprouting species. A planned autumn fire in a fynbos catchment provided an opportunity to assess factors which could determine the fire survival of woody sprouting species. In this study we distinguished between mortality as an immediate result of the fire (assessed at eight months post-fire) and mortality during the first summer drought (assessed at 12 months post-fire). We addressed the following null hypotheses:

(i) Survival is not related to pre-fire size.
(ii) Survival is not related to the pre-fire vigour of the plant.
(iii) Survival is not related to the amount of damage sustained in the fire.
(iv) Survival rates do not differ between species belonging to different growth forms.
(v) The tendency for sprouters to resprout and then die during the first summer is independent of the pre- and post-fire factors assessed above.

Materials and Methods

Species selection

The eight species used in the study were: *Widdringtonia nodiflora* (Cupressaceae), *Aulax pallasia* (dioecious, Proteaceae), *Mimetes cucullatus* (Proteaceae), *Leucadendron salignum* (dioecious, Proteaceae), *Brunia nodiflora* (Bruniaceae), *Nebelia paleacea* (Bruniaceae), *Penaea mucronata* (Penaeaceae) and *Erica coccinea* (Ericaceae). Species nomenclature follows that of Bond and Goldblatt (1984). These species were selected for the following reasons:

(i) they are common in the study area which made sample selection easy;
(ii) all the species are common and widespread in the fynbos biome (Bond & Goldblatt 1984), so information gathered from this study can be used in research elsewhere;
(iii) they represent a range of growth forms, from low proteoid and ericoid shrubs to a small tree (Table 1);
(iv) some of the species were used in previous studies in Swartboskloof (*e.g.* Kruger *et al.* 1985; Higgins *et al.* 1987).

Study site

The Swartboskloof catchment is situated within the Jonkershoek Valley (33°57'S, 18°55'E) about 15 km from Stellenbosch, South Africa. The area has been described in detail by McDonald (1988). Swartboskloof has a dry summer and an average daily temperature below 22°C for the warmest month (Wicht *et al.* 1969). The mean annual rainfall is 1700 mm with 60% occurring from May to August (Van Wilgen 1982). The valley has a north-facing aspect, with the valley floor at 285 m and the highest point at 1200 m. Porphyritic Cape granite forms the undulating floor of the valley and the cliffs and ridges are of quartzitic sandstones of the Table Mountain Group. Extensive sandstone talus has accumulated on the slopes and there are several boulder scree areas (Wicht *et al.* 1969; McDonald 1988). Soils derived from granites are finer textured and higher in nutrients than the shallow and more rocky soils derived from the sandstones (Fry 1987).

The dominant vegetation in the study area, situated in the lower part of the catchment, was a tall shrubland dominated by *Protea neriifolia* R.Br. and *P. repens* (L.) interspersed with other tall shrubs, mainly *Cliffortia* species. The understorey at the study sites consisted of low ericoid shrubs, graminoids, restios, forbs and sedges (McDonald 1988). The Swartboskloof catchment was burnt by wildfires in 1927, 1942, 1956 and in a planned fire in March 1987. All the study sites (Table 2) were situated in the area last burnt in 1956 except for the *A. pallasia* study site. This was situated near the eastern boundary in a firebreak, burnt every four to six years, which was also burnt in March 1987.

Table 1 The growth forms and mean pre-fire height of the eight species

Species	Growth form	Mean height (m)
Widdringtonia nodiflora	Small tree	1.68
Aulax pallasia	Proteoid shrub	0.89
Nimetes cucullatus	Proteoid shrub	0.83
Leucadendron salignum	Proteoid shrub	0.79
Brunia nodiflora	Ericoid shrub	1.44
Nebelia paleacea	Ericoid shrub	1.03
Penaea mucronata	Ericoid shrub	0.65
Erica coccinea	Ericoid shrub	0.69

Sampling methods

Individual plants were selected using the wandering quarter method (Catana 1963) and marked with numbered, fireproof wire stakes. Five surveys were carried out, one pre-fire and four post-fire. Fieldwork began in February 1987, one month before the fire, and continued until April 1989, approximately two years after the fire. The following parameters were measured (Table 3):

(i) Plant height — height of the tallest shoot (m).
(ii) Plant canopy — length of the longest axis (m), width at right angles to it (m) and depth (m). The canopy extent

Table 2 Details of the sample sites selected for this study as well as sample size for each species

Species[a]	Sample size	Features of the sample site			Pre-fire community structure
		Aspect	Altitude (m)	Slope (°)	
W. nodiflora	50	North	460	29.5	Tall open shrubland
A. pallasia	25	North-east	420	29.5	Low grassland
M. cucullatus	55	North	460	29.5	Tall open shrubland
L. salignum	100	North	410	11.4	Tall open shrubland
B. nodiflora	25	North	460	29.5	Tall open shrubland
N. paleacea	50	South-west	520	43.0	Tall closed shrubland
P. mucronata	50	North	560	37.4	Tall open shrubland
E. coccinea	50	South-west	520	43.0	Low open shrubland

[a] The full species names are given in Table 1.

Table 3 Details of the sampling of each species[a]

Variables	Species: *W. nodiflora*	*L. salignum*	*M. cucullatus*	*A. pallasia*	*B. nodiflora*	*N. paleacea*	*E. coccinea*	*P. mucronata*
Height	BA	BA	BA	BA	BA	BA	BA	BA
Canopy width, length and depth	BA	BA	BA	BA	BA	BA	BA	BA
Lignotuber area	—	—	B	—	—	B	B	B
Cover	A	BA	BA	BA	A	BA	BA	BA
Vigour	BA	BA	BA	BA	BA	BA	BA	BA
Fuel index	B	B	B	B	B	B	B	B
Fire damage	A	A	A	A	A	A	A	A
Number of:								
flowering shoots	—	A	A	A	—	—	—	—
dead shoots	A	A	A	A	A	A	A	A
live shoots	BA	BA	BA	BA	BA	BA	BA	BA
Flowered in 1986	—	B	B	B	B	B	—	B
Basal resprouts	—	—	B	—	B	B	B	B
Sex	—	B	—	B	—	—	—	—
Number of cone crops	B	—	—	—	—	—	—	—

[a] B: Sampling carried out only before the fire; A: only after the fire; BA: both before and after the fire.

was calculated as the area of a circle using the mean canopy diameter.

(iii) Lignotuber size — length and width (mm). Lignotuber area was calculated as the area of a circle using the mean lignotuber radius. *L. salignum* has a horizontal underground stem so the number of live shoots at ground level was used as a surrogate measure for lignotuber size. The same procedure was applied to *A. pallasia*, the only difference being that this species has an underground lignotuber. The lignotuber area of some of the large *M. cucullatus* plants could not be measured accurately without disturbing the plants. A linearized exponential regression was fitted using the natural logarithm of the number of live shoots (x) and lignotuber size (y) of the measured plants. The lignotuber area was then calculated from the number of live shoots. The number of live, dead and flowering stems were counted.

Visual estimates were made of the following:

(i) Canopy cover — this was estimated either as the number of clipboards (0.079 m^2) that would be covered by foliage or as a percentage of the canopy extent. Pre-fire canopy extent for two species was not measured owing to time constraints in the case of *B. nodiflora* and the difficulty of estimating this accurately for tall trees in the case of *W. nodiflora*.

(ii) Plant vigour — this was estimated on a scale of one to five where one: >75% of shoots dead; two: 75 – 50% of shoots dead; three: 49 – 25% of shoots dead; four: <25% of shoots dead; and five: no dead or dying shoots.

(iii) Fuel index — an estimate of the quantity of potential fuel (litter, fine twigs, etc.) surrounding the individual plant on a scale of one to three where one indicates low and three indicates high.

(iv) Fire damage — the degree of damage during the fire on a scale of one to three where one indicates leaves and fine twigs burnt off, two indicates leaves burnt off but not fine twigs, and three, little or no leaf material burnt off.

We noted whether the mature plants had flowered the previous season and whether there were new sprouts or shoots from the lignotuber or base of the plants. Both items were used as additional indices of vigour (Table 3).

The number of live and dead seedlings and adult plants of each species were counted two years after the fire, on 10 × 5 m plots situated along the wandering quarter lines. A plot sample was used because the number of seedlings per tagged plant could not be accurately determined owing to the closeness and often overlapping canopies of neighbouring plants. Part of the *B. nodiflora* sample site was burnt again in December 1989 so the number of seedlings of this species could not be determined.

Statistical analyses

We employed two approaches as many of the variables measured before the fire were not independent of each other. For the univariate analyses, we used Spearman's rank correlations (r_s) throughout because the variables tended to be non-normally distributed and a number were integer scores. The multivariate analyses of survival were done with a stepwise discriminant analyses (STEPDISC procedure, SAS 1985) as this allowed for the non-independent nature of the variables. Discriminant analyses (DISCRIM procedure, SAS 1985) were also done to test the ability of a linear model to separate and correctly classify surviving and dead plants. Survival at eight months and one year were analysed separately in order to see whether different factors determined (i) immediate post-fire survival and (ii) subsequent dieback during the summer drought.

Results

The fuel index was not correlated with the degree of fire damage sustained by the plants or independently (partial correlations) with the survival or regrowth of the plants and it was omitted from the analyses.

Patterns in pre-fire population structure

A number of the variables measured before the fire were correlated. Most of these correlations were simply consequences of geometric relationships involving size, for example the correlation of height with canopy extent, lignotuber area and also number of cone crops in *W. nodiflora*. The more important correlations were those affecting vigour and presence of basal sprouts. Vigour was not correlated with size in *W. nodiflora, L. salignum, M. cucullatus, A. pallasia* and *P. mucronata*, but it was negatively correlated in *B. nodiflora* (height: $r_s = -0.43$, $P < 0.01$), *N. paleacea* (height: $r_s = -0.34$, $P < 0.01$; lignotuber area: $r_s = -0.26$, $P < 0.05$) and *E. coccinea* (lignotuber area: $r_s = -0.32$, $P < 0.05$). Vigour was also negatively correlated with the presence of basal shoots in *M. cucullatus* ($r_s = -0.26$, $P < 0.05$) and *N. paleacea* ($r_s = -0.31$, $P < 0.05$) but positively in *E. coccinea* ($r_s = 0.28$, $P < 0.05$). Flowering in the previous season was positively correlated with size, for example *M. cucullatus* (height: $r_s = 0.68$, $P < 0.01$), *N. paleacea* (height: $r_s = 0.60$, $P < 0.01$) and *E. coccinea* (height: $r_s = 0.53$, $P < 0.01$) but not in *P. mucronata, W. nodiflora* and *L. salignum*. There were no significant differences between male and female plants of *A. pallasia* but male *L. salignum* plants had larger canopies and were more vigorous than the females. For *P. mucronata*, the presence of basal shoots was correlated with size (canopy extent: $r_s = 0.36$, $P < 0.05$). The degree of fire damage was negatively correlated with pre-fire size, particularly height, a natural consequence of the greater exposure of short plants to combustion during the fire. This made it difficult to separate the influence of the degree of fire damage and pre-fire size in the analyses.

The size distribution of all the sampled populations was strongly skewed toward the smaller plants. There were also gaps in the size distributions of all species, except *E. coccinea, L. salignum* and *A. pallasia*, suggesting that at least two cohorts were represented and that the plants must have longevities spanning at least the period of the last three fires, about 60 years.

Stem recruitment

The number of stems for each species except *A. pallasia* increased after the fire (Table 4). The number of new sprouts was significantly and positively correlated with plant size for all species with the exception of *W. nodiflora* and *E. coccinea*. Pre-fire height was positively correlated with the number of post-fire shoots in *E. coccinea* ($r_s = 0.48$, $P < 0.01$) and for *W. nodiflora* the strongest correlations were with pre-fire height ($r_s = 0.69$, $P < 0.01$) and lignotuber area: $r_s = 0.73$, $P < 0.01$). *B. nodiflora* and *N. paleacea* both had the greatest gains in shoot numbers, followed by *W. nodiflora*. *E. coccinea* had the lowest number of pre-fire stems with most plants having a single dominant shoot.

The number of post-fire stems was positively correlated with pre-fire size, including the number of stems in all species. When the shoot recruitment was expressed as a ratio it was still correlated with size in most species except for *A. pallasia* and *B. nodiflora* where there was no significant correlation. For most, the shoot recruitment ratio was negatively correlated with the pre-fire shoot numbers, plants with four stems having relatively more sprouts. The number of flowering shoots two years after the fire was positively correlated with the pre-fire size for *L. salignum* ($r = 0.29$; $P = 0.009$), *M. cucullatus* ($r = 0.48$; $P = 0.01$) and *A. pallasia* ($r = 0.78$; $P = 0.0001$). A few *L. salignum* and *M. cucullatus* plants had flowered within 12 months of the fire.

Survival patterns

Fire survival was above 85% for all except two species, *E. coccinea* and *P. mucronata*, with 56 and 62% survival, respectively (Table 5). Mortality during the first summer was high for several species, notably *B. nodiflora* where 32% died, 64% of those that had survived the fire. *M. cucullatus, E. coccinea* and *P. mucronata* also had a high percentage mortality during the first summer, this trend continuing over the next 12 months. No *N. paleacea* plants died during the first summer but seven plants (18% of the fire survivors) died between one and two years after the fire. All the *A. pallasia* plants survived the fire and the first summer, but one juvenile died between one and two years after the fire.

The first post-fire surveys were carried out in April 1987, about one month after the fire. Some of the plants which had not sprouted at this stage, sprouted before the next survey in November, eight months after the fire. This late sprouting was not correlated with any of the measured traits but did influence the ability of plants of some species to survive the subsequent summer or up to two years after the fire. All the

Table 4 Mean stem recruitment of eight woody sprouting species eight months after a March fire

Species	Number of stems: pre-fire	post-fire	Post-fire / pre-fire	Correlation between pre- and post-fire numbers
W. nodiflora	3.44	46.36	13.48	0.17
L. salignum	3.96	21.44	5.41	0.41**
M. cucullatus	15.15	81.16	5.36	0.72**
A. pallasia	33.48	18.28	0.55	0.82**
B. nodiflora	3.92	106.48	27.16	0.48*
N. paleacea	3.88	95.71	24.67	0.34*
E. coccinea	1.66	15.68	9.45	−0.18
P. mucronata	5.08	71.93	14.16	0.48**

* $P < 0.05$, ** $P < 0.01$.

Table 5 The net survival of eight sprouting species after a March fire

Species	Pre-fire sample size	Percentage survival up to: 8 months	1 year	2 years
W. nodiflora	50	94.0	86.0	86.0
L. salignum	100[a]	99.0	87.0	80.0
M. cucullatus	54[b]	90.7	66.7	53.7
A. pallasia	25[c]	100.0	100.0	96.0
B. nodiflora	25	88.0	56.0	52.0
N. paleacea	50	90.0	90.0	74.0
E. coccinea	50	62.0	46.0	30.0
P. mucronata	50	56.0	46.0	36.0

[a] 50 male and 50 female plants.
[b] One plant was excluded because it was not burnt during the fire.
[c] 13 male, nine female and three juvenile plants.

B. nodiflora and *A. pallasia* plants had sprouted at one month, as had all but two *M. cucullatus* and most plants of the other species except *N. paleacea*. *N. paleacea* was the slowest to sprout with only 40% of the plants having sprouted four months after the fire. In *E. coccinea*, three of the four late sprouters subsequently died as did all five late-sprouting *N. paleacea* plants and all three late-sprouting male *L. salignum* plants. Late sprouting did not seem to influence the subsequent survival of *M. cucullatus*, *W. nodiflora* and female *L. salignum* plants. Plants of several species showed signs of partial die-back after the first summer. The shoots of one *M. cucullatus*, two *B. nodiflora* and one *W. nodiflora* plant died back completely during the first summer but the plants resprouted during the subsequent winter.

The discriminant analyses generally fared poorly (Table 6) although less than 30% of the plants were mis-classified, *i.e.* classed as live when actually dead or vice-versa. The percentages of mis-classifications rose as the proportion of plants that had died increased. In most cases, more of the dead plants were incorrectly classified than the live plants. The few *W. nodiflora*, *L. salignum* and *N. paleacea* plants that died were all incorrectly classified.

Factors influencing short-term survival

Eight months after the fire the survival of *B. nodiflora* was correlated with the damage sustained in the fire and pre-fire flowering whereas for *N. paleacea*, survival was not related to any of the measured variables (Table 6). The three *N. paleacea* plants that died had fire damage indexes of two and three while both *B. nodiflora* plants killed during the fire had the highest fire damage indexes (Figure 1). These two *B. nodiflora* plants were also small and were the only ones that did not flower in 1986 (Table 6; Figure 1). Vigour was not a significant predictor of survival for *N. paleacea* but all of the plants killed had a lignotuber area less than 10 000 mm^2 (mean radius < 56 mm).

Tall *L. salignum* plants were less likely to be killed by the fire, and most of the dead plants had a lower than average height (Figure 2). Vigour was not an important predictor of fire kill in male or female *L. salignum* plants. Male *L. salignum* plants were, however, generally more vigorous with 24% of the males and 8% of the females having a vigour index of five. For *M. cucullatus*, vigour was important (Table 6) and most of the plants that died had low vigour scores (Figure 3). All the *L. salignum* plants killed during the fire had fire damage scores of two and three, while *M. cucullatus* plants that were killed were all in fire damage class three.

The survival of *W. nodiflora* was not significantly related

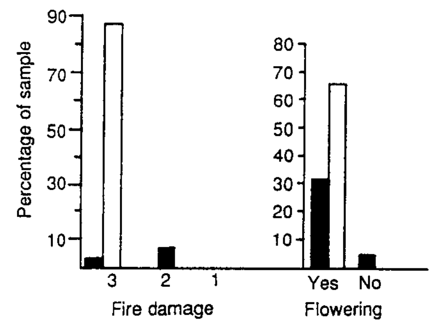

Figure 1 Percentage survival of *B. nodiflora* plants eight months after the fire in different fire damage classes (3, least damaged; 1, most damaged), and according to whether they flowered in 1986. Shaded bars represent plants that died.

Table 6 Results of a stepwise discriminant analysis of factors influencing species survival[a]

Variable	*W. nodiflora*	*L. salignum*	*M. cucullatus*	*B. nodiflora*	*N. paleacea*	*E. coccinea*	*P. mucronata*
	Species						
Eight months after the fire							
Height	0.07	0.05[b]	0.01	0.08	0.01	0.14[c]	0.05
Vigour	0.00	0.00	0.26[c]	0.00	0.02	0.10[b]	0.27[c]
Number of live shoots	0.05	0.02	0.00	0.05	0.00	0.13[b]	0.14[c]
Fire damage	0.00	0.04	0.08[b]	0.64[c]	0.00	0.08[b]	0.09[b]
Basal sprouts	—	—	0.02	0.01	0.04	0.03	0.08[b]
Flowered 1986	—	—	0.00	0.39[c]	0.00	0.07	0.01
Canopy extent	0.04	0.02	0.01	0.03	0.00	0.05	0.07
Sexual maturity	0.09[b]	—	—	—	—	—	—
Average squared canonical corr.	0.09[b]	0.05[b]	0.26[c]	0.64[c]	—	0.36[c]	0.36[c]
Eight to twelve months after the fire							
Vigour	0.00	0.04[b]	0.09[b]	0.12	0.03	0.05	0.04
Flowered 1986	—	—	0.00	0.08	0.02	0.00	0.00
Fire damage	0.01	0.01	0.14[c]	—[d]	0.05	0.14[b]	0.13
Basal shoots	—	—	0.02	0.06	0.02	0.00	0.06
Average squared canonical corr.	—	0.04[b]	0.21[c]	0.27[b]	0.05	0.14[b]	0.20

[a] *A. pallasia* was excluded as no plants died during this period. The values are the initial R-square for each variable. A dash indicates that the variable was not measured for that species.
[b] $P < 0.05$.
[c] $P < 0.01$.
[d] All plants with a fire damage score greater than one were killed by the fire.

to any of the variables recorded except for maturity (Table 6). This was largely due to the extremely high survival rates of this species. All three *W. nodiflora* plants killed had a lignotuber area less than 1 000 mm^2 and two of these plants were juveniles.

The survival of *E. coccinea* and *P. mucronata* was related to vigour, fire damage and the number of live shoots (Table 6). For *E. coccinea*, height was also an important predictor of survival and for *P. mucronata*, the presence of basal shoots. Relationships were, however, not simple. Most of the *E. coccinea* plants, both dead and alive, were fairly vigorous and generally small (Figure 4), whereas for P. *mucronata* the majority of those that died were slightly less vigorous than the survivors (Figure 5). In both *E. coccinea* and *P. mucronata*, vigour classes one to three suffered 48 and 53% mortality, respectively, versus 16% for vigour classes four and five. Plants with a lignotuber area of less than 1 000 mm^2 were more likely to be killed (39 and 43%, respectively) than larger plants (7 and 23%, respectively). Plants with basal shoots were more likely to be killed by the fire (63 and 56%, respectively). Fire survival was therefore associated with a variety of factors acting together.

Factors influencing survival of the first summer

Survival of the first summer for both *B. nodiflora* and *N. paleacea*, was not correlated with any of the measured variables (Table 6). Both *N. paleacea* plants that died had a fire damage index greater than one. Mortality for *B. nodiflora* was independent of size (lignotuber area: $r = -0.19$; $P = 0.39$). Eighty-two percent of the plants in vigour classes one and two survived compared with 52% of those with a vigour of three or four. Neither of the *B. nodiflora* plants that had basal shoots prior to the fire died, versus 43% of those without basal shoots that died.

Survival for *N. cucullatus* and *L. salignum* was dependent on vigour (Table 6). Forty-three percent of the *M. cucullatus* plants with a vigour index of three or four died versus 14% of class five (Figure 3). The *L. salignum* plants that died, had vigour ratings of two, three and four (Figure 2). Survival for *M. cucullatus* was also related to fire damage (Table 6) — 50% of the plants with a fire damage class of two died versus 21% of plants in class one (Figure 3).

Survival for *E. coccinea* was dependent on fire damage (Figure 4), but for *P. mucronata* none of the measured variables was significantly correlated with survival after fire. Fifty percent of the surviving *E. coccinea* and 39% of the *P. mucronata* plants in fire damage class one died versus 22 and 25% of those severely burnt. Seventy-eight percent of

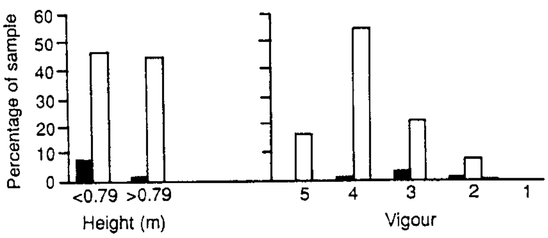

Figure 2 Percentage survival of *L. salignum* plants in different height classes eight months after the fire and different vigour classes (1, low vigour; 5, high vigour) one year after the fire. Shaded bars represent plants that died.

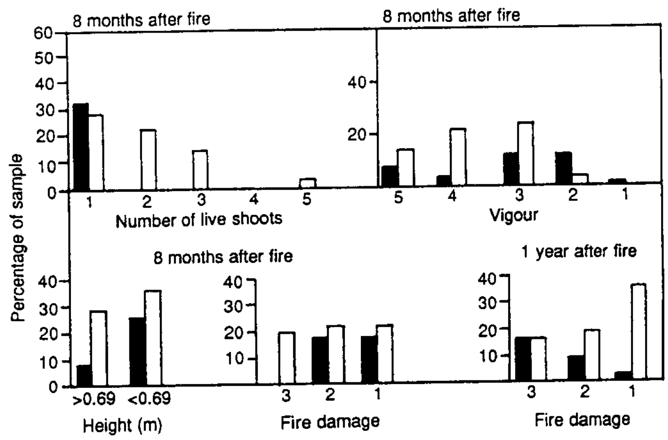

Figure 4 Percentage survival of *E. coccinea* plants in different height, vigour (1, low vigour; 5, high vigour) and number of live shoot classes eight months after the fire and in different fire damage classes (3, least damaged; 1, most damaged), both eight and twelve months post-fire. Shaded bars represent plants that died.

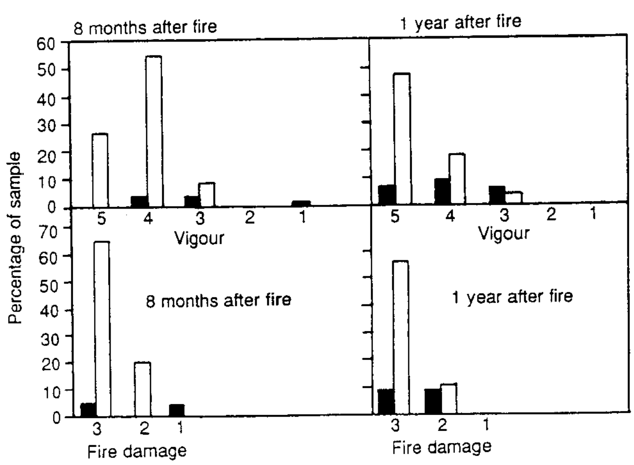

Figure 3 Percentage survival of *N. cucullatus* plants in different vigour (1, low vigour; 5, high vigour) and fire damage (3, least damaged; 1, most damaged) classes both eight months and one year after the fire. Shaded bars represent plants that died.

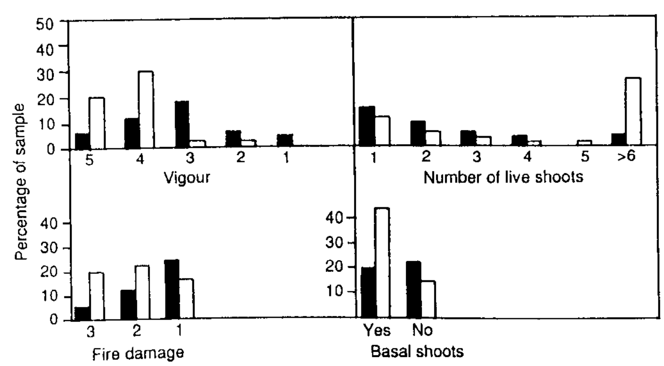

Figure 5 Percentage survival of *P. mucronata* plants in different vigour (1, low vigour; 5, high vigour), fire damage (3, least damaged; 1, most damaged) and number of live shoot classes, and the percentage survival of plants with or without new basal shoots (before the fire) eight months after the fire. Shaded bars represent plants that died.

the *P. mucronata* and 36% of the *E. coccinea* plants with a vigour index of three to five died versus 19 and 26%, respectively, of the less vigorous plants. Fifty-five percent of *P. mucronata* and 25% of the *E. coccinea* plants with lignotuber areas less than 1 000 mm^2 died versus 8 and 35% of the larger plants. In general, the plants which, predictably, survived the fire were more likely to die during the first summer and there was an inverse relationship between factors predicting fire survival and first summer mortality for *E. coccinea* and *P. mucronata*.

Seedling recruitment

Seedling recruitment varied widely between the different species (Table 7). Only one of the *A. pallasia* plants in the tagged sample died versus 33% of those in the plot sample. The populations of all species except *W. nodiflora* increased as seedling recruitment exceeded adult mortality.

Discussion

At the beginning of this study five null hypotheses were put forward on factors that could predict post-fire survival. The first of these, that survival is not related to pre-fire size, was supported by the results for some species, primarily those which had more than 85% post-fire survival. Pre-fire size is a significant predictor of survival for *E. coccinea, P. mucronata* and *L. salignum*, when measured as the number of shoots and the height of the individual. Noble (1984) also found that large individuals (*Eucalyptus* spp.) were more likely to survive fire. He also found, however, that these individuals had a low number of stems before the fire. In our study, both *E. coccinea* and *P. mucronata* plants with a greater number of stems had a better chance of survival. Stohlgren and Rundel (1986) also found that larger individuals had a lower fire-caused mortality. Surprisingly, lignotuber area was not significantly related to survival for any of the species that we studied. Zammit (1988), however, found that the survival of plants with the smallest lignotubers was influenced by the time that had elapsed since the fire and by the direct effects of the fire.

The second hypothesis, that survival was not related to vigour, was supported by the results for some species, for example *W. nodiflora* and *N. paleacea*. It was not supported by the ericoid shrubs, where the more vigorous individuals had the best chance of survival.

Our results did not support the third hypothesis that survival is not related to the amount of damage sustained in the fire. In all species where survival was related to fire damage, the less damaged individuals had a better chance of survival. This concurs with Noble's (1984) results with *Eucalyptus* species.

The fourth hypothesis, that survival rates do not differ between species belonging to different growth forms, was not supported by our results. The average survival rate for the ericoid shrubs was consistently lower than for either the proteoid shrubs or the small tree. However, S. Gous (pers. commun. 1990) found a significant difference between the survival rates of *B. nodiflora* and *N. paleacea*, both ericoid shrubs (more of the *N. paleacea* shrubs survived). The mean fire survival of the proteoid shrubs was higher than that of *W. nodiflora* to begin with, but a greater proportion of the proteoid shrubs, notably *M. cucullatus*, had died one and two years after the fire.

The fifth hypothesis, that the tendency for sprouters to resprout and then to die during the first summer is independent of the measured pre- and post-fire factors, is supported for some species only. Vigorously growing proteoid shrubs had a better chance of surviving the first summer and the least fire-damaged individuals of *M. cucullatus* and *E. coccinea* had a better chance of survival. Late sprouting did influence the ability of some species to survive the summer. Noble (1984) recorded that 11 individuals (8% of his sample) died back after sprouting later than the others and three of these (2%) died in the following summer. The other species that recovered rapidly, namely, *L. salignum* and *M. cucullatus*, had high survival rates. The other two species with relatively high mortality, *P. mucronata* and *E. coccinea*, recovered slowly. It is possible that mortality during the summer was caused by secondary factors such as pathogens.

Mortality as a result of the fire differed markedly between species as found in other studies (*e.g.* Keeley & Zedler 1978). Noble (1984), however, found that the three *Eucalyptus* species he studied had similar survival rates. All the *A. pallasia* plants growing in the firebreak survived, which is not surprising as the site is burnt regularly (every four to six years) and the remaining plants have a high fire-tolerance. As a result, one would expect the use of pre-fire

Table 7 Seedling recruitment of seven sprouting species two years after a March fire[a]

	Species						
Category	*W. nodiflora*	*L. salignum*	*M. cucullatus*	*A. pallasia*	*N. paleacea*	*E. coccinea*	*P. mucronata*
Seedlings							
live	3	42	20	0	12	8	42
dead	1	0	0	0	0	0	0
Adults							
live	5	14	16	11	18	22	22
dead	0	3	3	0	1	6	6
Total number of seedlings per							
live and dead parent	0.80	2.47	1.05	0.00	0.63	0.29	1.50
dead parent	—	14.00	6.67	—	12.00	1.33	7.00

[a] The data are counts of the numbers of plants in each category in a 5 × 10 m plot at each site.

measurements to assess post-fire survival to be less successful as indicators of post-fire survival for this species. The proteoid shrubs and *W. nodiflora* had a higher rate of survival than the ericoid shrubs except in the case of *N. paleacea* 12 months after the fire. More than 50% of both the *E. coccinea* and *P. mucronata* plants died during the summer. Size-related mortality between species can only really be viewed in terms of smaller plants sustaining a greater degree of damage in the fire because of thinner bark, smaller volume to absorb heat, or fewer dormant buds or any combination of these factors.

Resistance to fire is a function of the degree of bud protection by the bark or the soil or both (Gill 1981). The insulating capacity of the bark is dependent on its thickness, its structure, density, moisture content and composition (Gill 1981; Rundel 1981; De Ronde 1982). The insulating capacity of bark is high (Gill 1981) and hence is considered by many authors to be the most important factor for survival (Rundel 1981). Bark thickness does, however, vary both within and between species (Gill 1981; Rundel 1981). Bowman and Kirkpatrick (1986) found a relationship between bark thickness, height and fire survival of *Eucalyptus delegatensis*. *E. coccinea* has a relatively thin layer of bark on the exposed area of its lignotuber (<2 mm) compared with a plant like *L. salignum* (>6 mm, Le Maitre, unpublished data) and this may contribute to its high mortality rate. As shoot diameter increases, bark thickness increases in *L. salignum* (Kruger & Bigalke 1984).

Some of the inter-specific variation in the percentage survival of the first summer after the fire may be due to the plant's ability to tolerate drought. The presence or absence of growth rings may give an indication of susceptibility to draught (Carlquist 1978). Neither *B. nodiflora* nor *N. paleacea* have growth rings, although this does not necessarily mean that drought conditions are absent (Carlquist 1978). Survival is high for *N. paleacea* and low for *B. nodiflora* during the summer. However, it appears that both species are not particularly vulnerable to drought. According to Carlquist (1978), the wood anatomy indicates that members of the Bruniaceae are adapted to drought. No work has been done on *E. coccinea* as yet. No growth rings are apparent for *P. mucronata* either, although xeromorphy is higher (138) than for both *B. nodiflora* and *N. paleacea* (92) (Carlquist 1978). Sprouters generally have deeper main root systems, and hence may be less affected by seasonal drought (Specht & Moll 1983) — the deeper the root system the higher the chance of survival (Ahlgren 1960 in Hinn & Wein 1977). Root depth influences the availability of water and the amount of stored carbohydrates and hence ability to sprout (Hobbs & Mooney 1985). The proteoid roots of the proteoid shrubs substantially increase the root surface area available for water and nutrient absorption (Higgins *et al.* 1987) and may play an important role in post-fire survival.

Population size increased for all but two species. These increases may not, however, be significant if subsequent survival rates of the seedlings are poor. Adult mortality for *A. pallasia* was minimal and there was no seedling recruitment after the fire. This could be the result of the *A. pallasia* plants being in the firebreak where there is little chance to accumulate seeds. However, these data were recorded two years after the fire and many seedlings could already have died. Seedling recruitment was high for *W. nodiflora* but a high proportion of the seedlings died during the first summer (Le Maitre, pers. obs.). Midgley (1987) also found a low mortality for *W. nodiflora* of 1% in a fire of medium intensity and no mortality in an intense fire. Conversely, Scriba (1976) found no seedling recruitment for *W. nodiflora* and a 28% mortality in a sheltered rocky area compared with 85% on an exposed slope area. Studies have shown that sprouting species with high adult mortality produce a greater number of seedlings than those with low adult mortality (Keeley & Zedler 1978; Keeley 1986; Bradstock 1990; Le Maitre & Midgley 1992). These findings were supported in this study for all the species except *E. coccinea*. Hence, a greater fire-caused mortality seems to be balanced by a higher probability of seedling establishment.

Noble's findings were clear-cut: plants with large, vigorous lignotubers in sites of low litter load and low fire intensity had a higher chance of survival. The results of this study were more complex. Several factors are reasonable predictors for most species but some idiosyncratic results were obtained as well. Our results suggest that there is no simple way of predicting survival for the particular species studied. Further studies may be able to build on these insights and reliable models of response of sprouters to fire may develop. Future studies could benefit by focusing on fewer species but more individuals; by concentrating on a more accurate quantification of plant size, vigour and bark thickness and of fire intensity in the immediate vicinity of each plant; and, lastly, by deliberately manipulating fire intensity.

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