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Ken C. Hodgkinson

Sprouting success of shrubs after fire: height-dependent relationships for different strategies

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Abstract The sprouting success of co-occurring populations of shrub species in a temperate woodland of semi-arid Australia was investigated and related to population survival strategies. Straw was added to 21 × 15 m plots in the woodland, burnt and the pre-fire characteristics of shrubs were used to determine the basis for sprouting success. Species differed widely (4–94%) in sprouting success; a high percentage of established seedlings of all species were killed by fire but survival increased with height reaching a maximum at 25–60 cm (depending on the species). Thickness of bark at stem bases increased with height growth but sprouting success was not related to bark thickness; sprouting success of shrubs at similar thickness varied greatly between species. All species were able to initiate sprouts after cutting through their basal stems, so lack of active meristems was not a limitation. Species differed in the height at which shrubs began flowering but this was always after maximum sprouting success was reached. It is proposed that differences between individual shrubs in supply of nutrients, carbohydrates, and/or water to activated meristems would account for patterns of inter- and intra-specific sprouting success. The data are consistent with recognised fire survival strategies. 'Sprouters', the species relying more on sprouting than recruitment for population persistence, maintained maximum sprouting success with height growth and gained sprouting ability along stems once they reached 1 m in height. In contrast, 'non-sprouters', the species largely relying on recruitment from seed to maintain populations, were either not able to sprout after seedling establishment or steadily lost the ability to maintain sprouts with growth beyond 60 cm and did not develop axillary buds along stems at any height.

K.C. Hodgkinson (✉)
CSIRO Wildlife and Ecology,
PO Box 84, Lyneham, ACT, 2602, Australia
Fax: +61-2-62414-020; e-mail: ken.hodgkinson@dwe.csiro.au

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Introduction

There is a binary response to the passage of fire through a plant community – plants either die or sprout. The proportion of the woody plants which sprout is species dependent and this forms the basis for the primary classification of woody species into 'sprouters' and 'non-sprouters' (Biswell 1974). Other attributes, especially those relating to reproduction and recruitment processes, are now considered along with sprouting for predicting persistence of plant species in fire-prone communities (Gill 1975; Naveh 1975; Keeley and Zedler 1978; Noble and Slatyer 1980). Change in floristic composition can be predicted for many plant communities from these attributes and knowledge about the fire regime.

Sprouting of woody plants is probably an early adaptive trait enabling survival after considerable damage from fire, whereas fire-promoted recruitment is considered a later, or derived, adaptation (Wells 1969). Today, the floras of most fire-prone communities contain woody species across a continuum of sprouting abilities (e.g. Hodgkinson and Griffin 1982). Certain genera such as *Arctostaphylos* (Keeley 1977), *Banksia* (Specht et al. 1958; Bellairs and Bell 1990), *Ceanothus* (Keeley 1977), *Eremophila* (Hodgkinson and Griffin 1982) and *Hakea* (Bellairs and Bell 1990) contain both 'sprouting' and 'non-sprouting' species.

Sprouting after fire damage requires a substantial pre-fire allocation of resources acquired by the plant to grow protective bark and to store reserves within woody structures. Following fire damage, these reserves are mobilised (Bowen and Pate 1993) and, in combination with current assimilates, contribute to growth of new leaves, stems and roots. This prior allocation of resources to ensure fire survival is a major cost for 'sprouters', one not incurred by 'non-sprouters' which thus gain reproduction and growth rate advantages (Bond and van Wilgen 1996). In south-west Australia heathlands, Pate et al. (1990) found that 'sprouters' possessed lignotubers, had slower shoot growth, less extensive root systems (higher shoot:root ratios) and longer juvenile periods than 'non-sprouters' of congeneric shrub species. Shrubs (Pate et al. 1990) and species of Restionaceae (Pate et al. 1991) allocated more assimilate to storage of starch in below-ground organs in 'sprouter' than in 'non-sprouter' congeneric species. These studies provide evidence for a trade-off between allocation to roots for survival from future fire damage in 'sprouters' and to shoots for immediate post-fire germination and seedling growth in 'non-sprouters'.

This trade-off is apparent in well-established individuals but its ontogeny is poorly understood, especially since juveniles of both 'sprouters' and 'non-sprouters' show low survival after fire damage, whereas 'sprouters' gain and then may lose survival ability as they develop (Hobbs and Mooney 1985; Hodgkinson 1986). The basis for these rises (and falls) in sprouting ability is poorly defined but clearly change in the distribution of shoot meristems amongst plant parts may be involved (Gill 1995).

Using the height-specific survivorship curves described by Hodgkinson (1986), Bond and van Wilgen (1996) proposed four broad patterns for sprouting of shrub species. These may however only represent 'nodes' of a continuum. In this paper, relationships between sprouting success and location and shrub height are compared amongst co-occurring shrub species in a fire-prone semi-arid woodland community in eastern Australia. It is proposed that (1) recently established individuals, of all species, will not sprout because they lack suitably located meristems; (2) the rate of change in sprouting success will be associated with ontogenetic development and therefore linked with reproduction, and (3) species which develop and maintain high sprouting success will eventually sprout from positions along stems rather than exclusively from stem bases. This would be a mechanism for quickly regaining an efficient and elevated leaf surface after fire damage.

Materials and methods

Study site

The site was 115 km south of Bourke in New South Wales on the pastoral property 'Oakvale' (146°30′ E, 30°55′ S) and within an extensive area of semi-arid woodland (Harrington et al. 1984). It is near the centre of a large pediplain and at an elevation of 250 m. Soil type is a massive red earth (Stace et al. 1968) or typic durargid (Soil Survey Staff 1975), with no A2 horizon and an indurated layer of stone or bedrock at 60–80 cm (Johns 1984). Topography is very gently undulating, with rises 0.5–1 km apart and slopes of 1–1.5%.

Vegetation is a poplar box (*Eucalyptus populnea* F. Muell.) woodland (Beeston et al. 1980) which occurs between the latitudes of 21 and 35° S in eastern Australia (Harrington et al. 1984). Vegetation at the site is described by Harrington (1979). Briefly, trees of *E. populnea* (26 ha^{-1}) are on the slopes and depressions and of *E. intertexta* R.T. Baker (10 ha^{-1}) are on the ridges. Tree canopies cover 13% of the ground surface and beneath each is a shrub thicket dominated by *Eremophila mitchellii* Benth. and *Geijera parviflora* Lindl. Intervening 'interthicket' areas are dominated by *Acacia aneura* F. Muell. ex Benth., *Senna artemisiodes* ssp. *filifolia* Randell, *S. artemisiodes* (Gaud. ex D. C.) Randell ssp. *artemisiodes* and *Eremophila bowmanii* F. Muell. var. *bowmanii*. The shrubs *Eremophila sturtii* R. Br. and *Dodonaea viscosa* (L) Jacq. ssp. s*patulata* (Smith) J.G. West commonly occur in both 'thickets' and 'interthickets'. Shrub density is about 4800 ha^{-1}.

Pioneer pastoralists (1850 onwards) described these woodlands as being 'open', with a herbaceous layer dominated by warm-season (C4) perennial grasses (Anon 1901, Harrington et al. 1979). Fewer fires and persistent grazing by domestic and native herbivores have shifted the vegetation to shrub dominance. Annual forbs and grasses now dominate the herbaceous layer that produces 0 to only 150 g m^{-2} year^{-1} (Harrington and Johns 1990). The shift has reduced the one in 5 years chance of fire in these woodlands to one in 15–20 years (Walker 1981).

Annual rainfall and potential evaporation (US class A pan) average 350 mm and 2900 mm, respectively, in the area and rainfall is evenly distributed. The coefficient of variation for monthly rainfall ranges from 70% (July) to 180% (February). Redistribution of water is common in the landscape, with more water being stored under 'thicket' than 'interthicket' areas following rainfall events (Johns 1984).

Plot selection

Within a 108-ha exclosure, fenced in 1977 to exclude sheep, cattle, goats and pigs but not kangaroos, there were two areas of *E. intertexta* and two of *E. populnea*. The areas of each species were irregular in shape but contiguous. Species composition of the shrub layer was similar between the areas (Harrington et al. 1981). Within each of the four areas, 24 trees were selected along transects. From each selected tree, a 15 × 21 m plot was laid out, which included at one end the tree with its associated 'thicket' and at the other end an 'interthicket' area. The trees selected were near access tracks laid out with regular spacing and each tree had similar and moderate densities of *E. mitchellii* in their 'thicket' and of *S. artemisiodes* in their surrounding 'interthicket' areas. 'Interthicket' areas were variable in shrub density, so plots were orientated to contain moderate densities of shrubs.

Treatments

Within each of the four areas, 24 treatments were randomly allocated to the plots; 8 were controls and 16 were experimental fires. The fires were applied (beginning October 1977) in either the spring, summer, autumn or winter, with one of two fuel levels (300 and 800 g m^{-2} of added straw) and in one of two consecutive years. Each control plot was established at the same time that two of the plots in the same area were burned.

Experimental fires

The plots allocated to fire treatments were burnt once. Before burning, wheaten straw was spread uniformly over each plot to be burnt and the 3 m surrounds, to augment the low quantity of tree litter and standing forbs. Plots were ignited at one end with a drip-torch and the prevailing wind carried a head-fire through each plot. Air temperature (wet and dry bulb) before and after each fire was measured using a ventilated Assman psychrometer.

The fire-line intensity for each plot was calculated using the formula:

$$I = Hwv$$

where I is fire-line intensity in kW m^{-1}, H is the heat yield of the fuel (in kJ kg^{-1}), w is the dry weight of the straw and litter in kg m^{-2} and v is the fire-line velocity in m s^{-1} (Byram 1959). The calorific value of the straw was 17 800 kJ kg^{-1} (determined in a bomb calorimeter), and correcting for the latent heat absorbed when the water of reaction is vaporised (1 263 kJ kg^{-1}) yielded 16 540 kJ kg^{-1} for the value of H. About 80% of the straw combusted and the fuel weight was corrected for incomplete combustion. A proportion of the litter beneath the straw combusted but at a slower rate and mostly after the flame front had passed. For this reason, litter was not accounted for in the intensity measurements. Fire velocity was determined by averaging the time taken for the fire front to travel 3-m intervals in each plot.

Experimental cutting

At the time of burning the four low-fuel plots in July of the first year, shrubs in areas near to each burnt plot were cut down. Ten juveniles (5–75 cm high) and 10 adults (100–430 cm high) of each of five species (*A. aneura*, *D. viscosa*, *E. mitchellii*, *E. sturtii* and *S. artemisiodes*) were selected from each area. Shrubs were cut down by sawing through the main stems 2–3 cm above the soil surface. In all, 200 shrubs were cut down (5 species × 2 size classes × 4 areas × 5 replicates).

Measurements

Dawn xylem water potential (dawn ψ_x)

Within an hour of dawn on the days of fire, xylem water potentials were determined on six species in a representative area using a pressure bomb (Scholander et al. 1965). Measurements were made on shoots from six randomly selected shrubs of major species. Terminal shoots of 7–10 cm length were cleanly cut from shrubs and lower leaves were trimmed so that about five leaves remained on each shoot.

Litter fuel

The amount of ground litter (tree bark, small branches, shrub and tree leaf) in each quadrat was visually estimated using a modified dry-weight-rank method (t'Mannetje and Haydock 1963). The biomass of annual and other herbaceous plants was negligible (<0.005 kg m^{-2}) on both occasions.

Soil moisture

Immediately prior to burning each plot, surface soil (0–5 mm) was taken from two random locations in 'thicket' and 'interthicket' areas of each plot and sealed in cans for later determination of gravimetric soil water with oven drying.

Shrub height, fire damage and sprouting success

All shrubs within the fire and control plots, together with those selected for cutting, were labelled before treatments began with a numbered aluminium disc attached to a wire pin (about 40 cm long). The pins were thrust into the ground next to bases of individual shrubs. The species, height (maximum foliage height above ground) and quadrat location was recorded for each.

Twelve months after the fires, each numbered shrub was assessed for fire damage and sprouting success. Sprout height above ground was measured on surviving shrubs. It was assumed that if a shrub had no living or recently dead sprouts then it had failed to survive the fire damage. The proportion of the original stem that was dead or consumed by the fire was easily estimated and this was used as an index of fire damage. This was possible even though the fire had occurred 12 months earlier. Most shrubs were defoliated by fire and the degree of stem reduction was largely a function of shrub size. Survival and height of live shrubs in control plots were assessed at the same time.

Sprouting success was analysed in several ways. First, the percentage of the population of each species present at the time of the low-fuel winter fires that sprouted in burned and unburned treatments during the next 12 months was calculated. Standard errors were calculated from survival data from each plot. Second, sprouting success for species within certain height ranges was calculated from shrubs cut or burned in July of the first year and standard errors were calculated from plot percentages. Third, for the low-fuel winter fires, individuals were placed in a height class and the sprouting percentage of each class was calculated. Height classes contained different numbers of individuals (the minimum acceptable class size for inclusion in the analysis was set at ten individuals) and there were differences between species in the height range used in some of the upper classes. The sprouting percentages were plotted against the logarithms of the median height of each class. The relationships between these two parameters appeared to be linear but, for the majority of species, with an abrupt change in the slope of the linear relationship within the range of heights measured. Piecewise linear regression models provided the best fits to these data. They enabled the relationships to be described and the break points to be estimated. The survivorship of the shrub species in fires of different fuel levels and in different seasons will be reported separately.

Flowering and shrub height

In October 1981 when there had been adequate rainfall for continuous growth through the autumn/winter/spring period, individual shrubs were examined for floral structures. Individual shrubs in 16 control plots were measured for height and the presence of floral structures was noted. The data were sorted into height groups of 50-cm increments and the percentage of the plants which were flowering in each was calculated.

Stem sprouting

Location of sprouts (stem, base, root) after fire damage was determined for all shrubs in the 64 fire plots. Shrubs with at least complete leaf scorch and with the majority of their small-diameter stems not consumed by the fire were selected for the analysis. Percentage of shrubs sprouting along stems was calculated for shrubs arranged in height classes of 10 cm. Numbers of individuals in each height class varied (but was ten or more) and the relationship between percentage sprouting along stems and shrub height was examined by linear regression analysis.

Sprouting of felled shrubs

After being cut down, sprouting of individuals was assessed 3, 4, 5, 6, 7, 10 and 13 months later. Shrubs were deemed alive if viable sprouts were visible. Comparative sprouting of burnt shrubs of the same species and similar size was obtained from nearby plots burnt at the same time.

Bark thickness

Twenty to 30 individuals of five species, with heights spanning the range for each species, were selected along a linear transect within the study site. The height of each shrub was measured and a small section of bark and wood was cut from the stem base. Wood internal to the cambium layer was carefully peeled away from each section and bark thickness was measured with callipers. The relationship between shrub height and bark thickness for each species was determined by linear regression.

Results

Fire and post-fire conditions

The fire front engulfing the shrubs was of low intensity in both years (Table 1). The air temperature in 1978 was about 7°C lower than in 1979 and this contributed to a slower rate of fire spread (*v*) and hence lower fire-line intensities (*I*). Spatial variability in fire-line intensity may have been high, depending on the proportion of ground litter combusted. The maximum estimated litter plus straw was 900 and 3 000 g m^{-2} for 'interthicket' and 'thicket' respectively. Assuming 80% combustion, *I* at $v_{\max}$ (2.58 m min^{-1}) reached 100 and 300 kW m^{-1} in limited areas of 'interthicket' and 'thicket', respectively.

The higher water content of the soil in 1978 was associated with the 0.8–1.0 MPa difference in the dawn ψ_x of shrubs. This was due to the 53 mm of rain that fell over 7 days during the fortnight preceding the fires in July 1978; no rain fell over the equivalent period in 1979. Post-fire rainfall was higher in 1978 than in 1979 but similar to the long-term average of 350 mm $annum^{-1}$.

Sprouting success of shrub species

The sprouting success of shrubs in this woodland differed considerably among species (Table 2). Sprouting success ranged from 4% (*A. aneura* in year 1) to 94% (*Eremophila longifolia*); other species occupied intermediate positions, indicating there was a continuum of sprouting success amongst the shrub flora.

Nearly all shrubs survived the ensuing 12 months if they were not burnt; only in two species, *S. artemisiodes* and *E. longifolia*, was there significant mortality in both years (Table 2). The mortality was 8–11% and occurred amongst recently established seedlings. Except for one species (*E. longifolia* in year 1), plant survival was always lower after fire than in control (no-fire) plots.

Shrub survival was generally higher after fire in 1978 than in 1979 (Table 2) and this was particularly evident for *A. aneura*, *E. longifolia* and *G. parviflora*.

Table 1 Fire, plant and environment parameters measured on plots burned in winter (July). Air temperature and fire parameters are means of four plot measurements with the range given in parentheses. Standard errors of means are given for dawn xylem water potential and soil water content

Parameter	Burned 15 July 1978	Burned 18 July 1979
Air temperature at burning (°C)	13.2 (12.8–14.0)	20.4 (18.9–21.6)
Fire-line velocity (m s^{-1})	0.031 (0.28–0.035)	0.039 (0.036–0.043)
Fire-line intensity (kW m^{-1})	122 (111–139)	154 (143–171)
Combustible ground fuel (straw, bark, leaves, branches of 15 mm diameter) (kg m^{-2})	0.78 (0.62–1.12)	0.75 (0.54–1.15)
Dawn xylem water potential (MPa)		
Acacia aneura (*n* = 6)	−1.4 ± 0.3	−2.4 ± 0.3
Eremophila mitchellii (*n* = 6)	−1.7 ± 0.2	−2.5 ± 0.2
Senna artemisiodes (*n* = 6)	−1.7 ± 0.2	−2.6 ± 0.1
Surface soil water content at 0–5 mm (%)		
Thicket (*n* = 8)	16.8 ± 2.8	7.7 ± 4.4
Interthicket (*n* = 8)	10.9 ± 2.3	2.6 ± 0.9
Post-fire rainfall (mm)		
July–September	119	59
October–December	92	61
January–March	68	139
April–June	158	77
Total for year	**437**	**336**

Table 2 Initial density (after Table 7 in Harrigton 1979) and survival (%) of each population of species 12 months after being burned in July or not burned. Standard errors (*n* = 4) follow each mean (*N*/*A* not applicable)

	Density (ha^{-1})	Burned		Unburned	
		1978	1979	1978	1979
Acacia aneura	470	25 ± 4	4 ± 1	100	98 ± 2
Dodonaea viscosa	583	59 ± 7	50 ± 5	99 ± 1	99 ± 1
Eremophila bowmanii	245	92 ± 3	90 ± 3	100	100
E. longifolia	N/A	94 ± 3	67 ± 7	91 ± 3	91 ± 3
E. mitchellii	618	75 ± 4	81 ± 3	98 ± 1	96 ± 2
E. sturtii	401	81 ± 6	88 ± 2	100	100
Geijera parviflora	159	71 ± 5	43 ± 5	97 ± 4	100
Myoporum desertii	128	69 ± 6	61 ± 8	93 ± 3	100
Senna artemisiodes	2185	42 ± 2	37 ± 2	92 ± 2	89 ± 2

Table 3 Percentage of shrubs sprouting after cutting off the shoot 2–3 cm above the soil or burning shoots. Treatments were applied in winter (July) to both juveniles and adults. Survival was assessed 12 months later. Shrubs that had been cut down were assessed monthly during the first 6 months to determine the percentage which sprouted. Standard errors follow each mean

Species	Height range (cm)	Cut (n = 20)		Burned (n = 20–130)
		1–6 months	12 months	12 months
Juveniles				
Acacia aneura	(12–50)	80 ± 10	35 ± 11	28 ± 12
Dodonaea viscosa	(5–50)	95 ± 5	85 ± 8	65 ± 11
Eremophila mitchellii	(10–75)	100	95 ± 5	93 ± 5
E. sturtii	(5–55)	100	95 ± 5	94 ± 3
Senna artemisiodes	(15–60)	100	75 ± 10	52 ± 4
Adults				
A. aneura	(170–260)	80 ± 10	25 ± 10	–
D. viscosa	(130–400)	100	75 ± 8	52 ± 10
E. mitchellii	(150–430)	95 ± 5	95 ± 5	90 ± 4
E. sturtii	(130–280)	100	95 ± 5	90 ± 4
S. artemisiodes	(100–170)	95 ± 5	95 ± 5	18 ± 4

Sprouting after cutting or fire

Nearly all individuals, irrespective of size (juveniles and adults), initiated sprouts from stumps during the period 2–6 months after cutting through stems near the ground surface (Table 3). The exception was *A. aneura*, where 20% of the juvenile and adult shrubs failed to sprout. However, some species were unable to sustain viability and growth of sprouts. Sprout mortality was high for *A. aneura* (45–55%) and low for *E. mitchellii* and *E. sturtii* (0–5%).

Sprouting after fire damage was similar to that following the cutting treatment for *E. mitchellii* and *E. sturtii* but was lower (by 77% for adult *S. artemisiodes*) for the remaining species.

Shrub height and sprouting success

Data presented in Table 2 are the mean proportions of the established populations of each shrub species that sprouted after fire damage and, as such, mask differences due to shrub height (or age). In Fig. 1a–e, the relationships are given between sprouting percentage and height class plotted on a natural-logarithm scale. This presentation expands the narrow height range (0–25 or 60 cm depending on the species) over which sprouting percentage rapidly increases. Plotted in this way, two linear regression lines adequately fit the data for each species; a quadratic relationship was found to be inappropriate. Shrub heights and sprouting relationships were the same, or very similar, for 1978 and 1979, except for *A. aneura*, for which separate lines are fitted for each year.

Three distinct patterns of sprouting in relation to shrub height are apparent amongst the five species. In pattern one, sprouting success is low and remains so for shrubs of increasing height (*A. aneura* in year 1, Fig. 1a). In pattern two, sprouting success increases with shrub height, peaks and then decreases with increased shrub height (*D. viscosa* and *S. artemisiodes*, Fig. 1b and c respectively). In pattern three, sprouting success increases with height but then remains high after the peak is reached (*E. mitchellii* and *E. sturtii*, Fig. 1d and e respectively).

Sprouting success of the smallest (5 cm high) and presumably youngest individuals differed amongst species. *E. mitchellii* and *E. sturtii* seedlings had relatively high sprouting success (35 and 45%, respectively) compared with the other three species (25% or less).

Peak sprouting success was reached when individuals were 60, 27, 25 and 25 cm high for *D. viscosa*, *E. mitchellii*, *E. sturtii* and *S. artemisiodes*, respectively.

Shrub height and flowering

The heights at which shrubs reached peak sprouting success was within the juvenile phase (Fig. 2). Within the higher 51–100 cm height class, some individuals had become reproductive but the percentage differed widely amongst the species. There was also considerable variation amongst species in the height class at which peak flowering was reached; *E. mitchellii* was notable in that the highest flowering percentage was reached when shrubs were 3 m or more in height.

Shrub height and stem sprouting

Three shrub species at the site were found to sprout from epicormic buds located beneath bark along stems when plants had grown beyond a threshold height; all other shrub species sprouting after fire damage did so only from the stem base. For the former three species (*E. mitchellii*, *E. sturtii* and *G. parviflora*), the extent of fire damage to shoots and the height of individuals governed the expression of this trait.

Stem sprouting capability was destroyed when a crown fire developed in shrub foliage, and survivors resprouted from ground level or below. Sprouting occurred along stems only when all the leaves were at least singed. The data in Fig. 3 include only those shrubs whose total foliage was singed but not consumed.

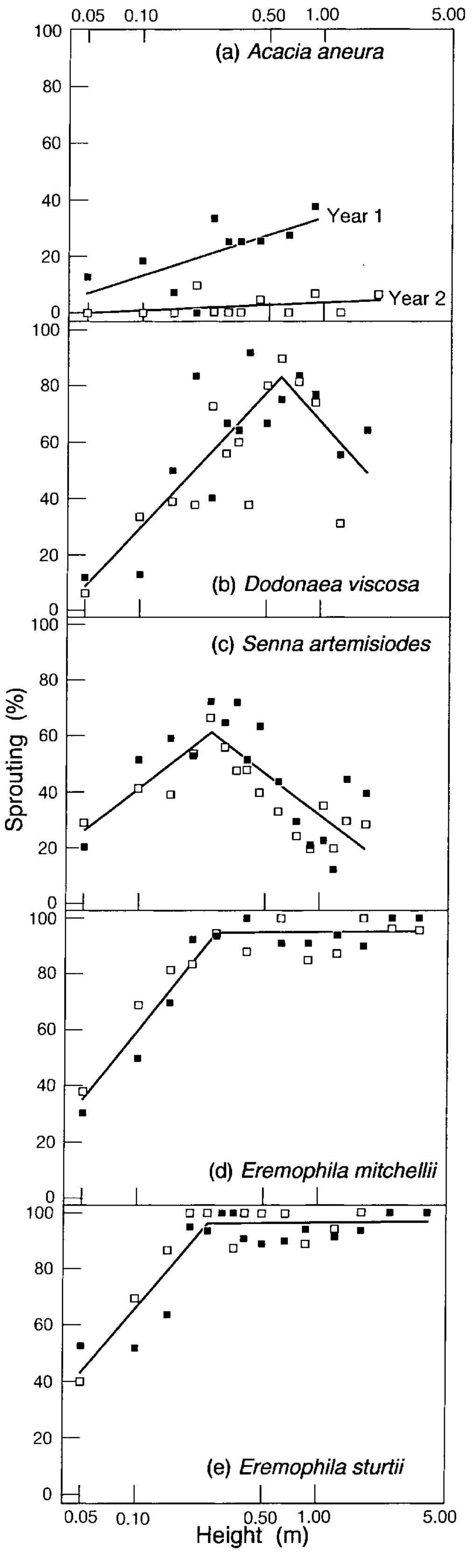

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Fig. 1a–e Sprouting percentage of shrubs in height classes of five species which sprouted after low-intensity winter fire in 1978 (■) or 1979 (□). The height for each point is the median of the range of plant heights in that class. The lines were determined by piecewise linear regression, and the estimated breakpoints were 0.6 m (**b**), 0.27 m (**c**), 0.25 m (**d**) and 0.25 m (**e**). Population size in 1978 and 1979 was respectively, 105 and 181 (**a**), 55 and 122 (**b**), 624 and 540 (**c**), 149 and 246 (**d**), and 283 and 199 (**e**)

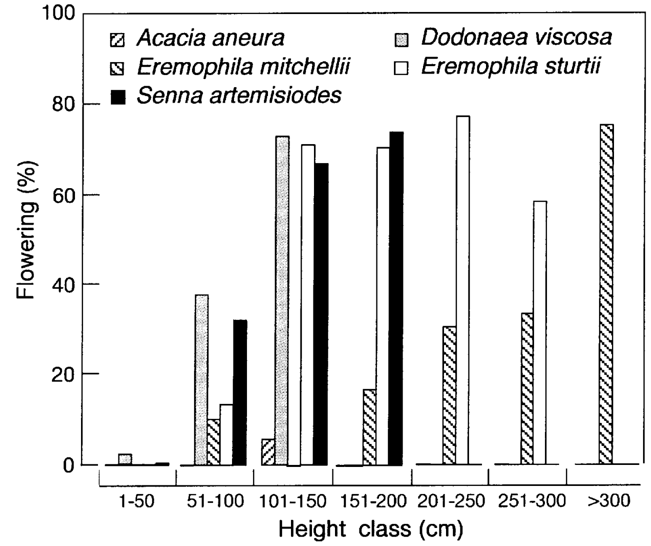

Fig. 2 Percentage of shrubs which flowered in spring within 50-cm height classes for five shrub species. The sample size of each group was as small as 10 and as large as 437

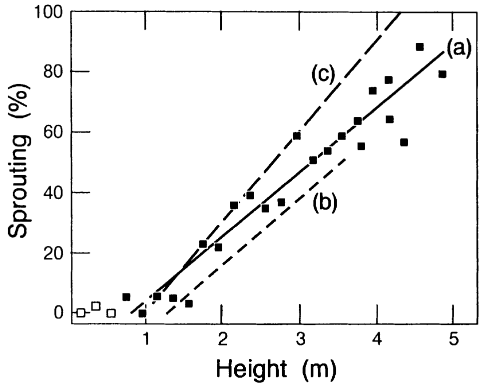

Fig. 3 Percentage of surviving shrubs which sprouted from epicormic buds along stems in relation to median values for each of the 10-cm height classes. Data came from 64 burned plots but only shrubs with total leaf scorch and minor fire damage to fine branches were included. Data points shown are for *Eremophila mitchellii. Closed squares* were used in the regression analysis. Fitted linear regression (a) *E. mitchellii*, % sprouting = −17.8 + 21.6 height, r^2 = 0.92; (b) *E. sturtii*, % sprouting = −28.2 + 22.2 height, r^2 = 0.68; (c) *Geijera parviflora*, % sprouting = −29.8 + 30.3 height, r^2 = 0.86

Table 4 Relationship between bark thickness (mm) measured at ground level and plant height (m) for five species. Basal bark thickness for 1- and 2-m-high shrubs is derived from the fitted regressions

Species	Sample size (n)	Regression coefficients			Bark thickness (mm)	
		Intercept (mm)	Slope	r^2	1 m	2 m
Acacia aneura	25	1.399	0.772	0.45	2.17	2.94
Dodonaea viscosa	20	0.252	0.847	0.76	1.10	1.95
Eremophila mitchellii	24	1.356	2.477	0.78	3.83	6.31
E. sturtii	23	1.454	0.900	0.66	2.35	3.25
Senna artemisiodes	30	0.266	0.903	0.68	1.17	2.07

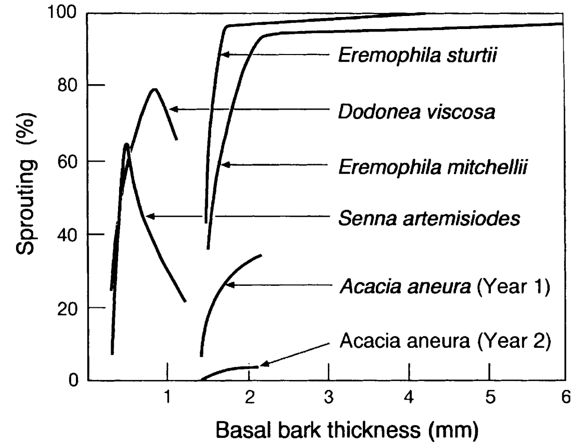

Fig. 4 Relationship between basal bark thickness and the percentage of shrubs sprouting after a low-intensity fire. *Lines* for each species were derived from the regressions presented in Fig. 1 a–e and Table 4

A stem sprouting capability began when individuals of the three species had grown to a height of around 1 m (Fig. 3). Thereafter the percentage of shrubs sprouting from stems increased linearly with height. The rate of increase with height was similar for *E. mitchellii* and *E. sturtii* but higher for *G. parviflora*.

Bark thickness and sprouting success

The thickness of bark at stem bases increased linearly with shrub height in all five species examined (Table 4). Recently established seedlings of *A. aneura*, *E. mitchellii* and *E. sturtii* had a bark thickness of around 1.4 mm whereas *S. artemisiodes* and *D. viscosa* were much thinner, at around 0.26 mm (derived from the intercept on the y-axis). Thereafter, the rate of bark thickness increase in relation to shrub height (slope) differed amongst species, with *E. mitchellii* having the greatest rate of increase.

The relationship between bark thickness and sprouting success for each species (Fig. 4) was derived from the regression relationships given in Fig. 1 and Table 4. The hand-fitted lines indicate that the acquisition of sprouting ability after seedlings established in all species occurred with only a small increase in bark thickness. The sprouting success of two species, *S. artemisiodes* and *D. viscosa*, declined after peaking as their bark thickened with increasing height. Furthermore, for shrubs with similar bark thickness, for example 2 mm, sprouting success varied greatly amongst species.

Discussion

The species of shrub co-occurring in this semi-arid woodland ranged in sprouting success from very low to very high (Table 2). Similar variation amongst co-occurring species has been reported for the shrub floras of other plant communities prone to fire, both within Australia (e.g. Purdie 1977) and elsewhere (e.g. Naveh 1975). The present study revealed that sprouting success is also highly variable within a species. There were large differences in both the rate and direction of change of sprouting success as individuals grew in height. It follows that the proportion of plants surviving the passage of fire will be determined by the height structure of each population of shrub species present.

Recently established individuals of all species were not successful at sprouting (Fig. 1). However, the proposition that this was due to a lack of suitably located meristems was not supported, since juvenile plants of all species when cut down a little above the soil surface formed visible sprouts, except for 20% of the *A. aneura* juveniles (Table 3). Three other explanations for low survival of seedlings are possible. First, that the meristems on juveniles are consumed during the passage of fire. Alternatively, their thinner bark inadequately protects meristems from the heat of passing flames, compared to thicker-barked adults. The lowered survival of similar-sized shrubs after fire compared with that after cutting down (Table 3) supports this view, but whether bark thickness played a crucial role is equivocal because species differences were poorly related to survivorship (Table 4, Fig. 4). Third, sprouting may occur after fire damage but sprouts may not persist in some individuals. Such a failure occurred for 5–25% of the cut-down juveniles in most of the species (Table 3) and for over 50% of *A. aneura*.

The lower ability of juveniles to sprout after fire damage has important implications for prescribed burning of these and other woodlands. In many of the woodlands that have been used for pastoralism, native shrubs have become very abundant, to the detriment of domestic animal management. Prescribed fire is the only economic means of shifting the vegetation towards grass dominance and the aim is to kill as many shrubs as possible (Hodgkinson et al. 1984). With this objective, prescribed fire should occur soon after major shrub germination events. Levels of shrub seed in soil seed stores are very high in these shrub-dominated woodlands (Hodgkinson et al. 1980) and local persistence of plant species is not likely to be threatened by rare opportunistically prescribed fires. In semi-arid areas, germination is episodic (Hodgkinson 1979) and the rainfall events usually induce abundant grass growth, thereby predisposing the plant community to fire (Hodgkinson and Harrington 1985).

Sprouting success increased with shrub height up to a critical height, which appears to be species dependant, beyond which survival either remained the same or declined (Fig. 1). The proposition that this rise (and fall) in sprouting success with growth is associated with reaching reproductive maturity was not supported (Figs. 1 and 2). The linearity of the relationship between the relative change in plant height with absolute change in sprouting success suggests a physiological basis for the rise (and fall). The explanation cannot lie with a steady rise (and fall in some species) in the proportion of individuals with meristems, since meristems do not appear to limit sprouting (Table 3). The characteristics of the relationship between sprouting and shrub height suggest that change in the ability of plants to supply nutrients, carbohydrates and/or water to activated meristems may be involved. As plants grow and age, the size and extent of their root systems expand. The acquisition and loss of sprouting ability may therefore reflect a change in the ability of plants to supply nutrients and water to sprouts from erratic and spatially variable sources (Hodgkinson 1992; Tongway and Hodgkinson 1992).

The proposition that species with a high sprouting success will sprout from positions along stems rather than stem bases was supported and may be explained in adaptive terms. For a species largely relying on sprouting to continue occupying ground already won during the germination and establishment phases, it would be an advantage to quickly regain an efficient leaf surface after fire damage. Sprouting along stems would maximize the number of meristem points on a plant. Furthermore, a new leaf surface generated well above the ground would more efficiently intercept sunlight than leaves on sprouts on or near the soil. In this woodland environment, the combined leaf mass of trees and shrubs is quite high (Harrington 1979) and spatially variable. Shading is prevalent and would limit photosynthesis in areas.

Species relying mostly on sprouting to enable populations to persist after fire damage, the ‘sprouters’, for example *E. mitchellii* and *E. sturtii*, do so by a set of linked characteristics. First, they quickly acquire an ability to initiate and sustain sprouts as juveniles. The period for juveniles to grow to 50 cm would be less than the time required to build up sufficient fuel to carry another fire across the landscape. Second, they maintain the ability to support growth of sprouts when mature, unlike species with a strong recruitment capability after fire (e.g. *S. artemisiodes*). Third, they develop dormant axillary meristems along the length of most stems so the plants quickly regain their pre-fire leaf surface area. Whilst these linked characteristics foster shrub survival after damage from an isolated fire, the combined effect of two fires, a year apart, in the autumn but not in the spring, weakens the resource supply to the second crop of sprouts and leads to high plant mortality (Hodgkinson 1986).

In contrast, species relying mostly on recruitment after fire for population survival, the ‘non-sprouters’, are poorer at sprouting. Whilst some, for example *D. viscosa* and *S. artemisiodes*, quickly acquire an ability to initiate and sustain sprouts and juveniles, they lose this initial sprouting success with maturity. The process involved in this loss is not known; it begins with the onset of reproduction in *D. viscosa* and *S. artemisiodes* but there is no loss in sprouting success for *E. mitchellii* and *E. sturtii* as they mature and gain reproductive capability. Other species, such as *A. aneura* do not sprout very successfully at any stage. Additionally, there is no development of axillary meristems along stems; all sprouting is from the stem base.

The wide range of sprouting success found here in the shrub flora of these semi-arid woodlands is similar to that of other fire-prone floras. This reflects the parallel evolution of the trait under the stress of periodic fire. However, these generalisations hide the considerable variation in sprouting success within individual species. Figure 1 shows that this within-species variation is as large as the within-shrub flora variation. This within-species variation for a population appears to be adequately described by survival percentages at three stages in the life of a shrub: the established seedling stage and height of about 5 cm, the stage of first reaching maximum survival ability (25–60 cm), and at the onset of maturity.

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