

Sprouting by plants: the effects of modular organization

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Summary

1. Plant survival following disturbance was modelled simply as the probability that at least one of n stems sprouts, each stem having an independent probability of sprouting, s . This first-order model with any stem on any plant in any species having probability $s = 0.18$ of sprouting after clipping ($s = 0.09$ after burning) explained nearly half of the deviance associated with species' mortality in a field experiment on 43 species from a range of growth forms.

2. Allowing species to take either a low or high per-stem sprouting probability (SSP) improved statistical explanation substantially. Fitting growth form SSP was less effective, showing that much of the apparent among-species variation in SSP was within growth forms.

3. Allowing each species to have a different SSP essentially provided a saturated model. The estimated species-specific probabilities were positively related to the depth from which sprouts could emerge after disturbance. Predicting species' bud depth from some simply measured morphological trait would be a considerable advance. Limited evidence suggested that sprout depth was associated with thick or dense leaves (low specific leaf area and leaf water content).

4. Depicting plants as a collection of independent stems with equal probability of sprouting appears a reasonable first-order model for whole-plant sprouting, despite being morphologically simplified.

Key-words: buds, disturbance response, modular growth, resprouting

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Introduction

Many people have considered the plant as a population of more-or-less independent units or modules (Harper 1977; Watson & Casper 1984; Watkinson & White 1985; Novoplansky *et al.* 1989; Sachs *et al.* 1993; Sachs & Hassidim 1996). Demographic studies of buds and shoots have explicitly invoked this population perspective (Maillette 1987; Lehtila *et al.* 1994; Noble 2001). Sprouting after disturbance (or unfavourable seasons) is a conspicuous link between dynamics at the level of buds or ramets and the level of individual plants or genets (Harper 1977).

Individuals that can sprout can maintain patch occupancy after a disturbance because they have a competitive advantage over seedlings. That competitive advantage comes, at least partly, from a well developed root system. Sprouting after loss of practically all above-ground biomass requires surviving buds or other meristematic tissue, as well as reserves of carbohydrate

and nutrients that can fund expansion of the first leaves of new sprouts (Pate *et al.* 1990; Canadell & López-Soria 1998; Bond & Midgley 2001; Vesk & Westoby 2004a). Individual-based models of sprouting success have focused on carbohydrate storage (Iwasa & Kubo 1997; de Jong & van der Meijden 2000), or on bud banks for sprouting following intense herbivory (van der Meijden 1990; Vail 1992; Tuomi *et al.* 1994; Nilsson *et al.* 1996). Empirical work has shown that the number of stems emerging from ground level (stem number per plant before disturbance) is a good predictor of sprouting success following disturbance, at scales of individuals within species (Malanson & Trabaud 1988; Vesk *et al.* 2004), among species (Vesk *et al.* 2004), and across communities growing on different segments of a productivity gradient (Midgley 1996; Kruger *et al.* 1997).

This paper links the themes of bud banks and modules, and asks how well sprouting success of individual plants following disturbance can be considered as the net result of multiple independent stems (modules) that each have an equal probability of sprouting. Correlations between this sprouting probability and other functional traits, including sprout depth and specific leaf area, are also investigated.

Methods

OVERVIEW

We present a simple, probabilistic model of whole-plant sprouting success being the net result of independent stems sprouting with some unknown probability, followed by a series of refinements. We do not claim that stems actually are independent, nor that sprouts actually emerge from the cut stems. Rather, we ask how well this model predicts whole-plant survival via sprouting. To assess the model we used empirical data on sprouting for 43 semiarid plant species (nine grass, 10 forb, seven chenopod subshrub, 19 woody) from south-eastern Australia. Species selected were those that were common and had individuals less than 1.5 m tall, and so were potentially exposed to browsing by mammalian herbivores, primarily western grey kangaroos *Macropus fuliginosus* and feral goats *Capra hircus*. All growth forms present in this flora were sampled, covering 17 families. Ephemeral species were excluded. The sites would have been fire-free for at least 10 years, judging by the size of fire-sensitive species (P.A.V., personal observation). Experimental plants were subjected to both clipping at base and clipping followed by stump scorching with a blowtorch (Vesik *et al.* 2004). These treatments were intended to inflict equivalent levels of damage across species, mimicking intense herbivory and fire, respectively. Before treatment, the number of stems per plant was recorded on 10 individuals per species per treatment. Stems were shoots that emerged at the base of the plant (<10% of height) and extended >30% of the distance to the canopy and included grass tillers. The numbers of stems per plant were recorded on a categorical scale corresponding to a half-log cycle: 1 (one), 2 (two to three), 3 (four to 10), 4 (11–30), 5 (31–100). Accordingly, some graph axes have been scaled in this manner. We did not assign sprouting to particular individual stems, but only whether the individual or genet survived by sprouting, scored at 4–5 months and 8–9 months following disturbance. The species mean of the maximum depth from which sprouts emerged following clipping or burning was measured on up to 20 plants per species that survived the treatments.

A reduced data set was used for later questions about a species model, comprising 35 species for which stems were counted on the treated plants; eight grass species were excluded as stem counts were carried out on a representative sample for estimation of species means, but not on the treated plants. Sample size also varied between analyses because not all variables were measured on all species from the full data set, e.g. sprout depth could not be recorded for seven species that failed to sprout.

MODEL DESCRIPTION

Let s be the probability of an individual stem sprouting following a clip. Then, $(1 - s)$ is the probability that the

stem fails to sprout. Suppose this probability is independent of other stems sprouting. If a plant has n stems, then the probability that zero stems sprout will be $M = (1 - s)^n$. This is the probability of mortality (M) for an individual plant. For estimated mortality of the i th species, with j plants per species, we write:

$$\hat{M}_i = \frac{1}{p} \sum_{j=1}^p (1 - s_i)^{n_{ij}}$$

We fit a series of similar models increasing in complexity against two models: a null model, that all species have mortality equal to the average across all species, $\hat{M} = M_i$; and a species mortality model which represents the upper limit for prediction using species traits. First we assume that there is a universal per stem sprouting probability (SSP, $s = \bar{s}_i$), but species differ in the mean number of stems per plant. Second, individual species were allowed either a low or high SSP, following quantitative confirmation that sprouting responses at the whole-plant level are well characterized by a dichotomy following intense disturbances (Vesik *et al.* 2004; Vesik & Westoby 2004b), $s = s_{\text{group}}$. Third, different growth forms (grass, forb, subshrub, woody) were allowed characteristic SSP, $s = s_{\text{growthform}}$. Fourth, each species was allowed a characteristic SSP, $s = s_i$, and individuals differed only in stems per plant. This last model was almost saturated, but served to indicate what traits might be related to among-species variation in SSP. Solutions for s that minimized the deviance due to discrepancies between predicted mortality, $\hat{M}_i = (1 - \bar{s})^n$ and observed mortality for each species, M_i , were found using maximum likelihood estimation. We focus on clipping results, but highlight cases where burning results differed.

Traits examined focused on depth of sprout emergence, indicating allocation to recovery from intense disturbance. Where possible, at least three (range 1–20) sprouting plants per treatment per species were dug up after marking the level of the soil surface with a pen. We then determined the number and depth of sprouting buds. Species mean maximum depth of sprout emergence was estimated as the mean of the maximum depth on each surviving individual that was dug up. For log transformation, 2 mm were added to all sprout depths. We examined species' potential height, estimated from the tallest individuals encountered in the area, as sprouting species are often shorter than non-sprouting species (Midgley 1996). We examined the leaf allocation traits specific leaf area (SLA) and leaf water content (LWC), as these are central to the carbon economy of the plant between disturbances (Reich *et al.* 2003; Wright *et al.* 2004) and may be related to storage strategies (Kobe 1997). From each of five plants we collected approximately five, fully expanded sun leaves (range two to 10 depending on size). All leaves from a plant were optically scanned for total single-sided area, then rehydrated overnight between damp paper towels. Fresh mass (FM) was measured for the set of leaves for a plant after gently blotting excess water away. Dry mass (DM) was

Table 1. Model statistics for stem sprouting probability (SSP) models fitted to observed data on sprouting by semiarid plants

Model	Clipping			Burning		
	Deviance	Deviance explained (%)		Deviance	Deviance explained (%)	
		Total	Species		Total	Species
Full data set ($n = 43$ species)						
Universal SSP	437.2	22	43	498.1	13	21
Two-group SSP	373.9	34	65	350.9	39	62
Growth form SSP	410.2	27	53	449.0	21	35
Null model (total)	563.0			571.7		
Species mortality*	272.2			217.4		
Reduced data set ($n = 35$ species)						
Universal SSP	420.1	12	27	392.1	7	12
Two-group SSP	360.5	24	55	282.1	33	57
Growth form SSP	393.8	18	39	332.5	21	36
Species SSP	249.7	48		180.1	57	
Null model (total)	477.4	–	–	420.6	–	–
Species mortality*	265.7	–	100	177.4	–	–

*Species mortality is the deviance associated with knowing the species' identity and thus represents the maximum prediction for simplified trait- or functional type-based models.

measured after 1 week drying in a 65 °C oven. LWC was calculated as $(FM - DM)/FM$ and SLA as leaf area/DM. We then used the species mean of the five values for SLA and LWC.

Results

A FIRST-ORDER MODEL – ALL STEMS ARE EQUAL

If each stem, irrespective of species, had an equal and independent probability of sprouting following clipping

of $s = \bar{s}_i = 0.18$, then this first-order model explained 43% of deviance (Table 1) and 45% of variance in observed whole-plant mortality rates among species (slope = 0.87, 95% CI; 0.57 – 1.17, $F_{1,41} = 34.96$, $P < 0.0001$; Fig. 1a, filled symbols, line not shown). Prediction of mortality following burning was poorer (Table 1). A similar model, having independent SSP of $\bar{s}_i = 0.063$, explained 32% of variance (Fig. 1b, filled symbols, $F_{1,41} = 20.36$, $P < 0.0001$). Weaker prediction for burning compared with clipping makes sense, as the role of subsoil bud depth is more important under burning than clipping.

The first-order independent stem-sprouting model has no term to modify the slope of the relationship. Comparison with the best-fit logistic curve and examination of residuals suggested that many-stemmed species sprout less well than expected from the independent stem-sprouting model: there was a negative correlation between stems and residuals after fitting the first-order model (Table 2). This decline in SSP was countered by the fact that many-stemmed plants tended to have deeper sprouts (Table 2). So, for a given stem number, deeper sprouts resulted in more sprouting than predicted (clip, $r = 0.45$, $P = 0.009$, $df = 33$; burn, $r = 0.67$, $P < 0.001$, $df = 33$). For a given sprout depth, though, more stems per plant was associated with less sprouting than predicted (clip, $r = -0.53$, $P = 0.001$, $df = 33$; burn, $r = -0.58$, $P < 0.001$, $df = 33$). This suggests that stems are not entirely independent, and we return to this later. In summary, a universal SSP across all plants and species, although a major simplification, could explain the broad pattern of responses.

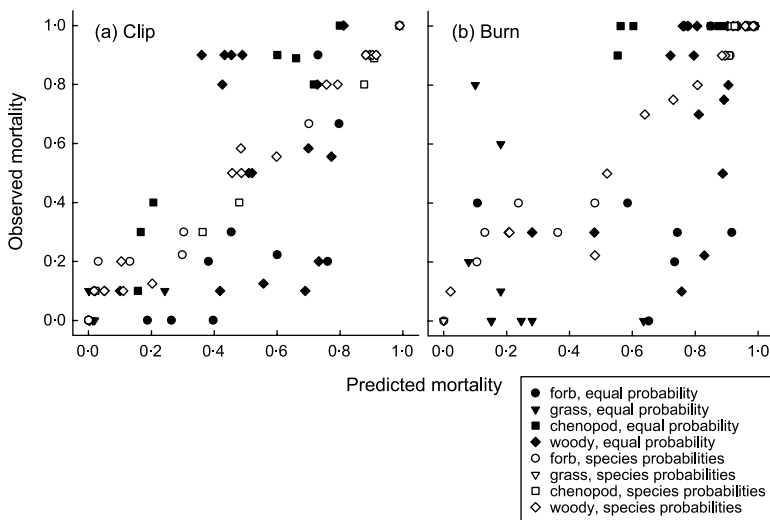


Fig. 1. Comparison of observed and predicted mortality following (a) clipping or (b) clipping and burning for plant species from semiarid south-eastern Australia. Each symbol represents a species. Observed mortality is the proportion of 10 treated plants per species. Prediction of mortality as a failure of all stems on plant to sprout, where they are assumed independent, and may sprout either with equal probability across all species (filled symbols, $n = 43$ species), or with species-specific probabilities (open symbols, $n = 35$ species).

WHAT IF THERE WERE LOW AND HIGH PROBABILITIES OF STEM SPROUTING?

Allowing SSP to take either high or low values, the best-fit dichotomous solution for clipping explained

Table 2. Correlation matrix for stem sprouting probabilities (SSP), measured traits and Pearson residuals after fitting SSP

	Stems	Sprout depth	Clip residual	Burn residual	Clip SSP	Burn SSP	Height	SLA	LWC
Sprout depth	<i>r</i>	0.35*							
	<i>n</i>	36							
Clip residual	<i>r</i>	-0.29	0.23						
	<i>n</i>	43	36						
Burn residual	<i>r</i>	-0.22	0.49**	0.71***					
	<i>n</i>	43	36	43					
Clip SSP	<i>r</i>	0.23	0.65***	0.76***	0.56***				
	<i>n</i>	35	28	35	35				
Burn SSP	<i>r</i>	0.14	0.66***	0.47**	0.78***	0.57***			
	<i>n</i>	35	28	35	35	35			
Height	<i>r</i>	-0.44**	0.06	0.03	0.06	-0.21	-0.13		
	<i>n</i>	43	38	43	43	35	35		
SLA	<i>r</i>	0.19	-0.36*	-0.05	-0.19	0.13	-0.14	-0.54***	
	<i>n</i>	41	36	41	41	35	35	43	
LWC	<i>r</i>	-0.02	-0.48**	0.08	-0.22	0.17	-0.22	-0.50***	0.64***
	<i>n</i>	41	36	41	41	35	35	43	43

See Methods for details of scaling particular measurements. Significant at *, $P = 0.05$, **, $P = 0.01$, ***, $P = 0.001$.

65% of the species mortality deviance (Table 1). In the best fit, 49% of the species had a low SSP of $s = 0.09$, and 51% had a high SSP of $s = 0.39$. For burning, explanation improved even more (Table 1). In the burn model, 70% of species had a low SSP of $s = 0.03$, and 30% had a high SSP of $s = 0.34$.

GROWTH FORMS

Interestingly, when we fitted a growth form-specific model, where grasses all share one SSP and forbs another, etc., less deviance was explained than by a simple dichotomy (clipping: 53% of species mortality explained, Table 1; forb $s = 0.32$; grass $s = 0.17$; chenopod $s = 0.12$; woody $s = 0.17$). This indicates that variation in SSP was greater within than among growth forms.

SPECIES-SPECIFIC PROBABILITIES

We then explored relaxing further the assumption of equal SSP to allow each species to have a characteristic SSP. Similar models were constructed for each species, the aggregate of which we refer to as the 'species model'. This model could not be constructed for species for which stem numbers were not recorded on treated plants, but which were estimated for the species mean from a separate sample of plants. So all graminoids (with many tillers or stems and high sprouting success) except *Lomandra robusta* were excluded, leaving 35 species. The first-order models explained less deviance in this reduced data set than in the full data set (clipping, $s = 0.19$; burning, $s = 0.07$; Table 1).

The species model, using species-specific SSP, was almost saturated and had a far tighter fit to the observed species mortalities than the first-order model, which assumed equal SSP (Fig. 1a open vs filled symbols). The species model explained 98% of variance in mortality of individuals between species, with a slope of

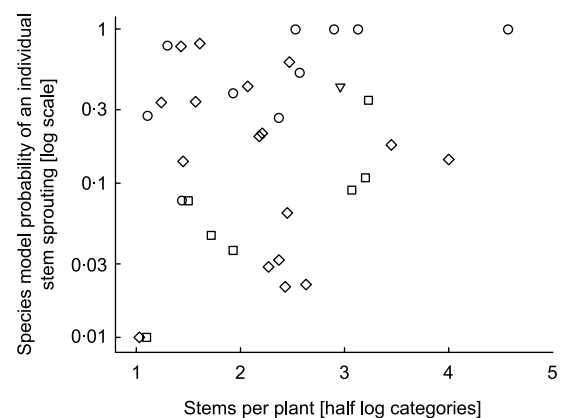


Fig. 2. Probabilities of individual stems sprouting (SSP) fitted to each species according to a model predicting plant survival after clipping as a function of at least one stem sprouting, given an equal independent probability of sprouting. Stems per plant scale is a half-log cycle (1, one stem; 2, two to three stems; 3, four to 10 stems; 4, 11–30 stems; 5, 31–100 stems). Symbols as in Fig. 1 represent species ($n = 35$); species mean stems per plant are based on 30 plants.

0.95 (95% CI: 0.90–1.00, line not shown, $F_{1,33} = 1502$, $P < 0.0001$). Similar fitting applied for burning ($F_{1,33} = 811.8$, $P < 0.0001$, $r^2 = 0.96$, slope = 0.97 (95% CI: 0.90–1.04)). These models explained less than 100% of the variance, presumably because of variability in stem number and sprouting within species.

The species' SSP covered the full range 0.01–0.99 (0 and 1 were defined as not possible). There was a wide range within each growth form. Forb species tended to have higher SSP, woody species covered the range, and chenopods ranged from low to middling probability (Fig. 2). Overall, this confirmed the earlier conclusion that variation in SSP is greater within than among growth forms. The cross-species relationship between SSP and stems per plant (Fig. 2) is discussed in the following section.

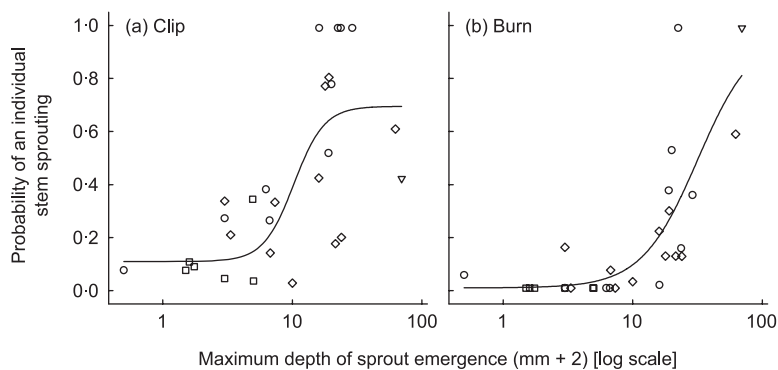


Fig. 3. Probabilities of individual stems sprouting (SSP) fitted to each species for (a) clipping and (b) burning as related to maximum depth of sprout emergence. Sprouts were measured on one to 10 surviving individuals following clipping or burning for 28 species; symbols as in Fig. 1. For log transformation, 2 mm was added to all depths. Logistic functions fitted – clipping: $y = 0.11 + 0.59/[1 + (x/10.27)^{-3.7}]$, $R^2 = 0.51$, $F_{(3,24)} = 8.42$, $P = 0.0005$; burning $y = 0.01 + 0.97/[1 + (x/31.71)^{-2.0}]$, $R^2 = 0.62$, $F_{(3,24)} = 13.11$, $P = 0.0001$.

WHAT DO THE SPECIES MODEL PROBABILITIES REPRESENT?

The probability of a stem sprouting can be thought of as the probability that at least one bud manages to sprout from below the level of stem damage. Species capable of sprout emergence from deeper in the soil have higher probabilities of plants sprouting (Vesk *et al.* 2004). Sprout depth explained most of the variation between species' SSP in simple untransformed correlations (Table 2) or with logistic functions fitted (clipping, $r^2 = 0.51$, $F_{3,24} = 8.42$, $P = 0.0005$; burning, $r^2 = 0.62$, $F_{3,24} = 13.11$, $P < 0.0001$; details in Fig. 3. No other measured traits (stems per plant, plant height, SLA and LWC) were related to the species' SSP (Table 2).

Species with deeper sprouts also tended to have more stems per plant (Table 2). However, species mean stems per plant were not related to species model SSP (linear regression with probabilities log transformed: clip $F_{1,33} = 2.25$, $P = 0.14$, Fig. 2; burn $F_{1,33} = 0.81$, $P = 0.37$, not shown; there were also no relationships when untransformed, Table 2). Neither were there partial correlations between stems per plant and species SSP when controlling for sprout depth, which was the strongest correlate of species' SSP (clip, $r = 0.01$, $P = 0.95$, $df = 25$; burn, $r = -0.11$, $P = 0.60$, $df = 25$).

MORE ON SPROUT DEPTH

The fact that the SSP in the species model could be predicted by depth of sprout emergence makes sense. Unfortunately, it is problematic for practical purposes, because measurement of sprout depth requires clipping plants and then digging them up. Hence it would be convenient if we could predict sprout depth with a more easily measured morphological trait. Sprout depth was negatively related to both LWC and SLA (Table 2). Relationships between sprout depth and either

LWC or SLA were little affected by cross-correlations with stems per plant and with height (controlling for both: LWC, $r = -0.45$, $P = 0.011$, $df = 30$; SLA, $r = -0.39$, $P = 0.025$, $df = 30$). LWC could also explain some of the variance in the species model SSP for burning when stems and height were controlled ($r = -0.45$, $P = 0.021$, $df = 24$), although the same relationship for clipping was non-significant ($r = -0.27$, $P = 0.15$, $df = 24$). SLA was unrelated to per stem probabilities of sprouting (Table 2), even after controlling stems and height (clipping, $r = 0.059$, $P = 0.80$, $df = 24$; burning, $r = -0.27$, $P = 0.19$, $df = 24$). Although correlation does not prove causation, this relationship between LWC and sprout depth deserves further study. Kobe (1997) found that under growth limitation, storage is favoured in tree species typified by low SLA and LWC, which have slow potential growth rates because opportunity costs of not investing in growth are smaller relative to fast growth-rate species (high SLA, LWC).

Discussion

A first-order model that considers the probability of whole plants sprouting as a function of the number of stems per plant explained the observed mortality of species remarkably well. However, this model had a systematic bias, which indicated that the SSP was not constant but declined as species-mean stems per plant increased. When we constructed a species model, the species' SSPs were well explained by depth of sprout emergence. We now discuss some assumptions and implications of these models.

STEMS OR SOME OTHER TRAIT?

How do we know that it is the probability of individual stems sprouting that determines survival of the plant? We were unable to assign sprouts to particular treated stems. Often sprouts emerged from a root crown or lignotuber. Perhaps plants with more stems command more resources to fund resprouting, and stems only indicate the resources available. Indeed, within species, stems per plant and other measures of size (basal area, projected canopy area) are related (Vesk *et al.* 2004). However, cross-species relationships between stems per plant and size are likely to be much weaker – consider a single-stemmed pine tree compared with a bunch grass or a creeping saltbush. In the species set covered in this paper, neither canopy area, basal area nor height was a better predictor of sprouting success than stems per plant (Vesk *et al.* 2004). Hence, size does not appear a better basis for this model.

In the same manner as for size, it could be that the number of stems per plant indicates the number of buds available. All else being equal, more stems means more buds, unless there is a negative correlation between stems per plant and buds per stem. While this could conceivably occur, for example if the same

lignotuber volume supported different numbers of stems, it seems unlikely to be generally the case across species. As with size, there seems no good reason to replace stems with buds for this model.

NON-INDEPENDENCE OF STEMS?

When we examined the first-order model closely, we found systematic variation in sprouting success with species mean stems per plant. It appeared that the SSP actually decreased with increasing numbers of stems per plant. Is this evidence of non-independence of stems? It is not possible to tell from these data, as the shift in SSP occurred across, not within species. Moreover, the subsequent species model showed that much of the variation in species' SSP was due to species differences in sprout depth, and was unrelated to stems per plant. To assess the importance of non-independence would require substantial sample sizes within species. For the moment, though, there seems little reason to discard the conclusion that plants are behaving as if stems were independent for resprouting, despite this being morphologically inaccurate.

The degree of physiological integration between modules of plants has been variously described. Watson emphasized plants as collections of integrated physiological units with little interdependence between them (Watson & Casper 1984; Watson 1986). Sachs, Novoplansky and colleagues have emphasized long-run integration via competition between redundant modules (Novoplansky *et al.* 1989; Sachs *et al.* 1993; Novoplansky 1996; Sachs & Hassidim 1996). Doubtless, there is a range of possibilities explored by different species. Having a large collection of buds with access to a distributable resource may allow a plant to have multiple sprouts emerge, with more in reserve in case of sprout damage, while also being able to redistribute resources among buds to ensure the success of at least one. By contrast, module autonomy and restricted redistribution might be favoured as diversification bet hedging against spatially restricted disturbances and for clonal expansion.

Why do some stems sprout and others not? Possible reasons are: (a) a size hierarchy exists, by which larger sprouts go and others do not; (b) apical dominance is exerted by the first sprouts that emerge, suppressing or pre-empting resources for later sprouts; or (c) there is a non-linear advantage to redistribution of resources. These possibilities are not mutually exclusive. Indeed, it could be because of a non-linear advantage to resource allocation that only the largest sprouts emerge and that apical dominance is established to maintain that advantage.

These results reflect and validate the approach of previous empirical work on sprouting responses of species with rhizomes or buried lignotubers where the extent of the genet could not be identified (Kayll & Gimingham 1965; Mallik & Gimingham 1985; Malanson & Traubad 1988; Matlack *et al.* 1993; Potash & Agee

1998). Those studies are largely from temperate zones and relatively continuous vegetation. It is interesting that this approach also works for the relatively discontinuous, semiarid vegetation studied here.

GROWTH FORM ALONE IS NOT A GOOD PREDICTOR OF SPROUTING

Here and elsewhere (Vesik *et al.* 2004), we have shown that sprouting varies among and within growth forms. In this model, stems are more important than SSP because stems appear in the exponent of the equation. But stem number varies within growth form. In other words, there are different approaches to disturbance response within the same growth form. This suggests that growth forms may often not be useful predictors for a wide range of ecological responses or functions and that plant functional type schemes need to be specific to particular responses and functions (Lavorel *et al.* 1997).

MULTI-STEMMED GROWTH

Is it possible that multi-stemmed growth is simply the result of past resprouting? There are two possibilities. First, within species – when plants sprout, they typically do so with multiple sprouts that are self-thinned over time, but often not back to single stems. As a result, plants with more stems might be those that have sprouted before, either in response to damage or because apical control is weak. Testing this would require waiting several years until sprouting plants recovered to pre-disturbance size to assess whether, for the same size, resprouted plants have more stems. Our data cannot be used to address this point because we scored survival within a year of treatment, but we see no reason to dispute it. However, single-stemmed plants have similar but slightly lower sprouting success than multi-stemmed plants of the same species (Vesik *et al.* 2004). This suggests that there are two components of sprouting success – being multi-stemmed, and having intrinsic sprouting ability, as the results reported here also suggest.

Second, among species, species with more stems might be those that have a higher intrinsic probability of sprouting. If this were true, one would expect that multi-stemmed species should have higher SSP. Our data do not support this. Species with more stems had deeper sprouts, and deeper sprouts were associated with higher SSP. However, species with more stems did not have higher SSP, whether or not sprout depth was controlled.

In this study only three species had the potential to become single-stemmed trees >4 m high (*Eremophila longifolia*, *Hakea tephrosperma*, *Callitris glaucophylla*). It would be useful to investigate this model further in relation to the commonly used distinction between trees and shrubs on multi-stemmed architecture. Including grasses in the SSP model would also advance understanding of the role of stems or growing points.

Identifying an easily measured trait correlated with species' bud depths would be a considerable advance. This may require study of morphological or developmental controls of bud depth distribution. But for now the assumption that all stems have an equal probability of sprouting, irrespective of how they are distributed between plants and species, appears a reasonable first-order model of vegetation response to disturbance.

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