

# Sprouting ability across diverse disturbances and vegetation types worldwide

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## Summary

**1** A widely used classification of plant response to fire divides species into two groups, sprouters and non-sprouters. In contrast, regeneration responses to catastrophic wind throw and small gap disturbance are more often considered a continuum.

**2** We determined general patterns in the distribution of sprouting ability across species with respect to disturbance type and intensity, vegetation type and phylogeny and assessed the adequacy of a dichotomy for describing species' sprouting responses. These are important steps if sprouting is to be adopted widely and consistently as a functional trait.

**3** Quantitative data were compiled from the literature and differences in species' sprouting proportions between disturbance classes were assessed using simple sprouting categorizations, visually using histograms and with mixture models.

**4** The sprouter/non-sprouter dichotomy effectively characterized intense disturbances, such as fires resulting in stem-kill (peaks at 13%, 79% probability of sprouting). But there was a continuum of responses following less intense disturbances. Where substantial above-ground tissue was retained, as for wind throw, localized gap disturbances and low intensity fires, there were fewer non-sprouters and more intermediate sprouters.

**5** Comparisons across diverse vegetation types and disturbances require quantitative records of sprouting, although the simple sprouter/non-sprouter dichotomy was sufficient for comparisons within fire. Patterns appeared consistent across broad vegetation types. Sprouting ability showed little phylogenetic conservatism.

*Key-words:* disturbance response, plant functional types, resprouting, vegetation dynamics

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## Introduction

Sprouting allows a species to persist in a site after a wide range of disturbances (Bellingham & Sparrow 2000; Bond & Midgley 2001, 2003). Sprouting is especially important where opportunities for seedling establishment are limited or only occur in harsh conditions. Sprouting facilitates coexistence in a patch- or sessile-dynamics framework (Bond *et al.* 1992; Fagerström & Westoby 1997; Bond & Midgley 2001). Broader study of sprouting has been recommended as a means of extending our understanding of plant functional types and traits (Weiher *et al.* 1999; Bond & Midgley 2003; Cornelissen *et al.* 2003). Agreement on the definition, measurement and systematic study of sprouting has been difficult, partly because sprouting behaviour is complex.

It may differ with ontogeny and can involve organs of different anatomical origin (see Del Tredici 2001; Bond & Midgley 2003). Bond & Midgley (2001) suggested focusing on sprouting by mature plants to assess the contribution of sprouting to persistence. Sprouting by seedlings would be regarded as part of the regeneration niche (Grubb 1977).

In different vegetation types and research on a range of topics, different emphases have been placed on sprouting, and thus, sprouting ability has been characterized in different ways. In the fire literature, the most widely used classification divides species into sprouters vs. non-sprouters (Keeley & Zedler 1978; Gill 1981; Bond & van Wilgen 1996). This dichotomy is used in addressing many pure and applied questions in vegetation dynamics (Bradstock *et al.* 1998; Franklin *et al.* 2001) and biogeography (Groom & Lamont 1996; Ojeda 1998; Valiente-Banuet *et al.* 1998; Clarke 2002).

In contrast, studies of wind throw in tropical and temperate forests have emphasized a continuum of sprouting responses (Glitzenstein & Harcombe 1988; Zimmerman *et al.* 1994; Bellingham *et al.* 1996).

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Disturbance events are compared in terms of intensity and damage to the vegetation as a whole, rather than in terms of sprouting. Tree size effects on sprouting are emphasized more than component species responses (Putz & Sharitz 1991; Yih *et al.* 1991; Everham & Brokaw 1996; but see Glitzenstein & Harcombe 1988; Bellingham *et al.* 1994, 1996; Zimmerman *et al.* 1994; Bellingham *et al.* 1996).

Local events, such as falls of single trees or branches and animal disturbances can also induce sprouting (Paciorek *et al.* 2000; Ickes *et al.* 2003), but intact neighbours reduce the importance of sprouting due to reduced light levels and infilling (Everham & Brokaw 1996). For both gap and extensive disturbances, the consensus seems to be that all species have some sprouting ability, but that variation in intrinsic sprouting ability has little influence compared with the circumstances of individual disturbances.

Considerable research on sprouting comes from range management, which is concerned with woody plant control and forage plant survival (Stoddart *et al.* 1975; Harrington *et al.* 1984; Noble 1997). Emphasis has been on within-species responses in relation to disturbance type, intensity and timing, while recognizing quantitative variation between species. Here, we examine sprouting ability across species, and within species, in relation to broad scale differences in disturbance type, intensity and vegetation types by analysing a data base of previous publications. We focus on different disturbance classes, but also examine whether the patterns found in proportions of plants sprouting could be a result of differences in vegetation types, which are often the focus of biogeographical studies.

Discrete characterizations or groups have dominated the plant functional type literature (Gitay & Noble 1997; other contributions in Smith *et al.* 1997). Much recent work on particular aspects of functional strategies, e.g. leaf carbon-gain economics, has emphasized quantitative variation between species (Westoby *et al.* 2002;

Reich *et al.* 2003). The extent to which sprouting ability is a dichotomy or a continuum has generally been deferred in the interests of simplicity (Bond & Midgley 2001; but see Vesk 2002). Although an *individual plant* either sprouts and survives, or it dies, as a species trait, sprouting can be represented as a continuous probability between zero and one. We present an approach for assessing the ability of a dichotomy to characterize sprouting distributions between species using simple rules for categorizing species (Gill & Bradstock 1992) and mixture models (McLachlan & Peel 2000).

Sprouting is widespread among extant species and is thought to be an ancient trait in many angiosperm clades (Wells 1969; Lloret *et al.* 1999; Bond & Midgley 2003). Sprouting has been studied within selected families or lower taxonomic levels (Pate *et al.* 1991; Keeley & Zedler 1998; Bell & Ojeda 1999; Bond & Midgley 2003). We use the data base assembled to assess the broad phylogenetic distribution of sprouting.

## Methods

### DATA SOURCES AND POTENTIAL BIASES

Studies reporting quantitative data on the proportion of plants sprouting after disturbance were located using the bibliographic database BIOSIS (1973–2001) and reference lists of other papers. We considered only the initial ability to sprout, not the vigour or long-term survival of sprouts. No doubt we did not find every paper that has reported sprouting quantitatively. Studies included here covered a range of disturbance classes and vegetation types globally. The majority came from Australia and North America, and from moist warm woodlands (Table 1, Appendix S1). Possibly these regions might be unrepresentative of sprouting in other parts of the world, but we do not see any obvious reason to expect this. Perhaps the most serious bias would come from choice of study species. In studies of single or few species,

**Table 1** Distribution of response lists from 83 studies reporting sprouting by mature plants, classified by vegetation type according to Walter (1984) and broad disturbance class. Some studies reported response lists for more than one disturbance class or vegetation type

Vegetation type	Disturbance class							Total
	Fire, stem killed	Fire, crown killed	Fire, other	Clip at base	Slash < 1 m	Wind throw	Undefined damage	
Glasshouse				5				5
1. Evergreen rain forests	1	2		1	2	5	2	13
2. Semi-evergreen and deciduous forests	3		3					6
2a. Dry woodlands, savannas and grasslands	4	2	5	3	2			16
4. Sclerophyll woodlands, winter rain	8	5	4	3				20
5. Moist warm temperature woodlands	8	5	7	5		3	1	29
6. Temperate deciduous forests	2			1		3		6
7. Temperate steppes				3				3
7a. Semi-deserts, deserts with cold winters	3	4	6	4				17
8. Boreal coniferous forests						1		1
Total	29	18	25	25	4	12	3	116

researchers are unlikely to choose species they believe have no chance of recovery. For example, few researchers perform clipping experiments on palms that have a single, elevated meristem. By contrast, there are many single-species studies of sprouting in species targeted as undesirable, e.g. woody plants in rangelands.

The main database resulting from this search consisted of 83 studies reporting 1160 records of sprouting proportions for juvenile or mature plants (> 1 years) from 864 species (Appendix S1). Species could occur more than once in a study if different treatments were applied, or if different size stages were studied (not considered here). Species could also occur in more than one study. Where species occurred more than once for a disturbance class, samples were summed for analysis. Studies may report more than one disturbance class or vegetation type. The data sets analysed for goodness-of-fit for a dichotomy (sprouter or non-sprouter, see below, How to assess the utility of the dichotomous classification?) contained 819 species sprouting records for mature and juvenile plants. Some records were not analysed for the fitting of a dichotomous model because sample sizes were not supplied and it was not possible to estimate them. Histograms were limited to species with  $n \geq 4$ , as proportions are severely constrained with small sample sizes. Some records without sample sizes were included where we expected  $n \gg 4$ .

Nomenclature was checked in the International Plant Name Index (IPNI; <http://www.ipni.org>). Phylogenetic relationships between major clades followed Soltis *et al.* (2000). Clades were split or aggregated where possible to provide at least 15 species in each clade, except for some clades of special interest. We examined how sprouting ability was distributed within and between major clades of the seed plants. In particular, we asked whether any clade was associated with intermediate sprouting ability and thus might explain poor fitting of a dichotomy. For consistency, this analysis was restricted to two disturbance types (fires and clipping at base).

#### DISTURBANCE SOURCES AND RANKING THEIR INTENSITY

Disturbances were categorized by source and intensity of damage to the plant. Intensity for sources of disturbance (fires, clipping, wind throw) was ranked by the height of undamaged biomass; more undamaged biomass was less intense. Our general ranking was as follows, in decreasing order of intensity with typical descriptors. (i) Fires resulting in stem-kill: burnt to ground level; burns preceded by clipping or 'extreme' fire. (ii) Crown-kill: parts burnt, charred, stem damage, snap, burnt, uprooted, or crown consumed in fire. (iii) Other fire: low and variable intensity, no charring. (iv) Clip: plants cut at base, below 20 cm. For early seedlings, clipping was at the cotyledonary node; for late seedlings clipping was below 5 cm height. (v) Slash: plants cut below 1 m. (vi) Catastrophic wind throw resulting in snapped stems or uprooting in spatially

extensive, high energy storms. (vii) Undefined damage: spatially localized events, unrecorded stem damage to plants variously attributed to wind breakage or uprooting, knockdown by other trees, pathogen attack, other adverse physiological condition and stream bank undercutting.

However, there could be large overlap of intensity of different disturbances. For example, clipping at base could be more intense than some fires and both undefined damage and wind throw could be as intense as clipping. Undefined damage was ranked after catastrophic wind throw because of the relative energy of the events, though this was not ideal. Undefined damage was distinct from catastrophic wind throw in leaving neighbours intact.

Studies were assigned to broad vegetation types according to Walter (1984) (Table 1). We asked: (i) For a given disturbance, were sprouting distributions consistent between vegetation types? (ii) For a given vegetation type, were sprouting distributions consistent between disturbances?

#### FITTING DICHOTOMOUS DISTRIBUTIONS TO THE DATA

For each disturbance class, we asked: (i) If there were only two groups of plants (sprouters and non-sprouters), what would be the distribution of samples (species) between those two groups? (ii) What would be the sprouting probabilities for those two groups of plants? We used the mixture model technique (McLachlan & Peel 2000), which models the data as samples from a mixture of a number of distributions. Each distribution in this case was binomial. Using likelihood maximization, we determined the best fitting model, estimated parameters (probability of being in either of groups one or two, probability of sprouting for each of group one and two), and measured the goodness-of-fit as the sum of the values for  $-2$  times the log-likelihoods (or deviance) for each species. This procedure can also be performed for three or more groups. Full details are elsewhere (Vesik *et al.* 2004). These binomial mixture models explicitly model individuals, so were restricted to species for which sample sizes were supplied or could reasonably be estimated.

#### HOW TO ASSESS THE UTILITY OF THE DICHOTOMOUS CLASSIFICATION?

The utility of a categorization is not an issue of statistical significance alone. Rather, it is an issue of balancing simplicity or parsimony against biological realism. Akaike's Information criterion (AIC) and Bayes' Information Criterion (BIC) are approaches that penalize the model for the number of parameters in it. However, they require regularity assumptions (as do likelihood ratio tests), which are not met in mixture models (McLachlan & Peel 2000).

To assess dichotomous categorizing of species as sprouters or non-sprouters, we applied five criteria.

1. Explanation: what percentage of the deviance between species (species model) does the fitted model explain (e.g. considering only two groups of plants, sprouters and non-sprouters)?
2. Separation: substantial overlap of two groups that are centred on sprouting probabilities ( $P_S$ ) for low (L) and high (H) groups of  $P_S(L) = 25\%$  and  $P_S(H) = 75\%$  suggests an even distribution, not a dichotomy (see below, Deviation from uniformity). If there is clustering at either end of sprouting proportions, then we expect a separation ( $P_S(H) - P_S(L) > 0.5$ ). Separation  $< 0.25$  suggests a mid-range hump.
3. Sufficiency: Does a three-group model improve substantially over the two-group model?
4. Inclusiveness. What proportion of species would belong to the high and low groups of a three-group model? If 95% of species belonged to the high and low groups and only 5% to the intermediate group in a three-group model, then this intermediate group may not be significant or substantial. Thus we would infer that the two-group model is inclusive.
5. Deviation from uniformity. As a further check of the utility of the dichotomous classification, we compared disturbance classes with a null model, to assess the performance of a dichotomous classification in the case where there is a true continuum of sprouting probability from 0 to 1. We used a synthetic data set of random sprouting probabilities, uniformly distributed 0–1. These were coupled with the observed sample sizes for 975 species, which were the majority of the primary data set. There were 10 simulations, although figures show results from a single simulation.

#### WITHIN SPECIES SPROUTING SHIFTS

The observed sprouting proportion can be thought of as a result of a species' intrinsic sprouting ability combined with the specific circumstances of disturbance. Within species, the proportion of plants sprouting declines with increasing disturbance intensity (e.g. Leigh & Holgate 1979; Lloret & López-Soria 1993; Morrison & Renwick 2000) and therefore we examined the effects of different disturbances upon the same species for species recorded in more than one disturbance class. For these comparisons, we plotted sprouting proportions for pairwise contrasts of disturbance classes, for species with  $n \geq 4$ . Ninety-five per cent confidence intervals were calculated from the binomial formula for variance =  $p(1-p)/n$ , assuming normally distributed proportions. These intervals are indicative and unlikely to be accurate with small samples and proportions close to 0 or to 1 (Steel & Torrie 1981).

Specific hypotheses addressed within species were based on cross-species patterns and intensity rankings outlined above (Assigning disturbance classes and ranking their intensity). (i) Did increased fire intensity reduce sprouting? (ii) Was sprouting after fire reduced compared with that following wind throw? (iii) Was sprouting after fire reduced compared with clipping?

- (iv) Was sprouting after undefined damage reduced compared with wind throw?

## Results

### SIMPLE CATEGORIZATIONS OF SPROUTING

The proportion of plants that sprouted after damage varied widely between species. In nearly all disturbance classes, it spanned all deciles from 0 to 100%. The distribution of observed sprouting proportions across species differed between disturbance classes (Fig. 1, black bars, likelihood ratio (LR) = 137.1, d.f. = 12,  $P < 0.0001$ ,  $n = 876$  species). Fires resulting in stem kill showed the clearest separation of species into infrequent and strong sprouters, with 0–10% (52 species) and 90–100% (47 species) being the commonest sprouting proportions (Fig. 1a, black bars). Nevertheless, 86 of the 185 species did not fall into either of these extremes and thus a dichotomy between *c.* 0% and *c.* 100% sprouting was therefore clearly inappropriate, even for this disturbance class. If we consider 30% and 70% as cut-offs for non-sprouters and sprouters (Gill & Bradstock 1992), then about one-sixth of species ( $n = 30$ ) still had intermediate sprouting percentages (Fig. 1a). A dichotomy is even less appropriate for the other damage classes (Fig. 1).

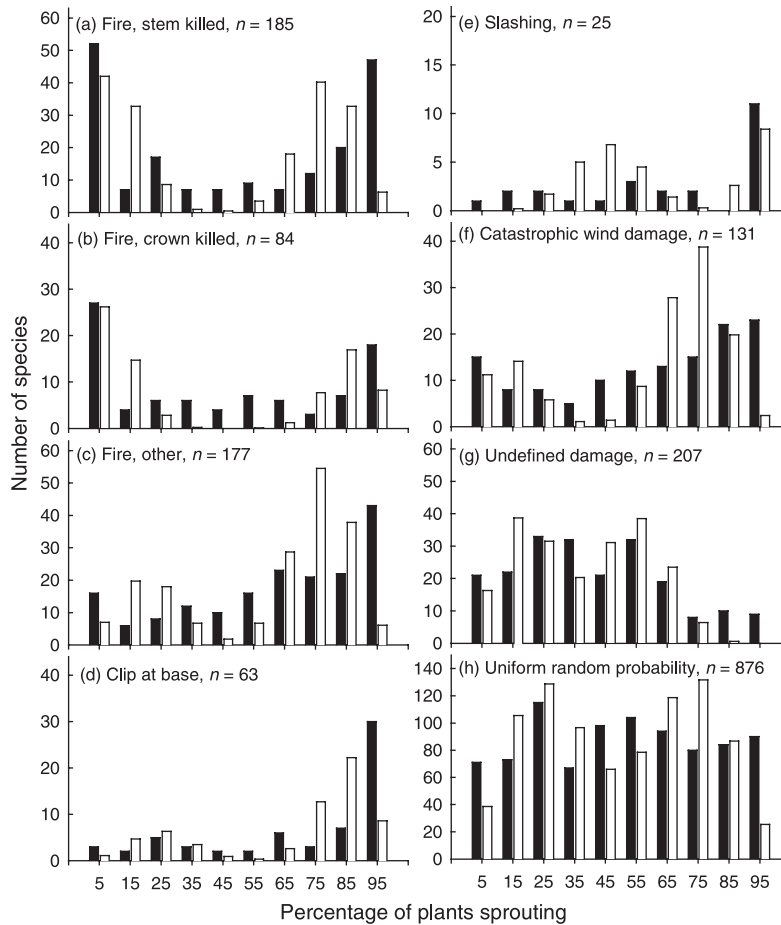
### SPROUTING SHIFTS ACROSS DISTURBANCE CLASSES

Considering fire and clipping, more species sprouted as disturbance intensity decreased (from Fig. 1a to Fig. 1e, black bars). Infrequent sprouters were common after stem-killing and crown-killing fires (Fig. 1a,b, Pearson residuals (PR) = 2.7, 2.0, respectively), but were rare after low intensity fires and clipping (Fig. 1c, d, PR = -3.2, -2.1, respectively). Conversely, strong sprouters were most frequent after low intensity fires and clipping (Fig. 1c,d, PR = 2.2, 3.4, respectively) and intermediate levels of sprouting were rare after stem-kill (Fig. 1a, PR = -3.7).

Wind throw resulted in a more even distribution of sprouting proportions among species than did fire or clipping (Fig. 1f). Of 131 wind-thrown species, 93 had sprouting proportions between 10 and 90%, and 40 between 30 and 70%. Intermediates were most frequent after undefined damage, for which 41% of species had sprouting proportions of 30–70% (Fig. 1g, PR = 4.7).

### ASSESSING MIXTURE MODEL DISTRIBUTIONS FITTED TO THE DATA

Best-fit dichotomous distributions consistently underestimated the number of species in the extreme deciles (0–10% and 90–100%; Fig. 1, white bars), because there were substantial numbers of species with intermediate sprouting proportions, which the mixture models tried to accommodate.



**Fig. 1** Frequency histograms of sprouting proportions for mature plants from different species in various disturbance classes from previous studies. Black bars are observed data; white bars are predictions from best-fit two-group model of sprouting probabilities. See Table 2 for sprouting probabilities for modelled groups and proportions of species belonging to each group. See Methods for full description of disturbance classes.

**Table 2** Criteria for assessing utility of a dichotomous (two-group) model of species' sprouting proportions in different disturbance classes. Further information on model fitting and the criteria (explanation, separation, inclusiveness and sufficiency) is supplied in Methods.  $P_S$  is probability of sprouting for a particular group.  $P_M$  is probability of membership of that particular group. Results for uniform random data are means (and standard deviations) from 10 simulations

Disturbance class	Explanation 2-group fit (%)	Separation $P_S$ (Low)– $P_S$ (High)	Sufficiency 100–(3-group fit–2-group fit (%))	Inclusiveness $1 - P_M$ (Mid) in 3-group model	Parameters of best 2-group model			3-group fit (%)	Species ( <i>n</i> )
					$P_S$ (Low)	$P_S$ (High)	$P_M$ (High)		
Fire, stem killed	70.1	0.66	88.0	0.83	0.13	0.79	0.55	82.1	196
Fire, crown killed	68.9	0.76	79.8	0.67	0.11	0.87	0.44	89.2	78
Slashed	66.8	0.48	82.7	0.70	0.47	0.95	0.36	84.2	31
Clip at base	65.7	0.58	91.6	0.74	0.27	0.85	0.74	74.1	63
Fire, other	64.3	0.55	84.8	0.60	0.23	0.78	0.72	79.5	202
Uniform random	63.9	0.50	84.6	0.62	0.24	0.74	0.52	76.7	975
SD	(1.9)	(0.02)	(1.3)	(0.02)	(0.02)	(0.01)	(0.03)	(1.0)	
Wind throw	61.9	0.59	88.8	0.67	0.16	0.75	0.75	73.1	181
Undefined damage	53.3	0.35	83.1	0.56	0.21	0.56	0.54	70.2	222

*Explanation*

The disturbance class best fitted by a two-group model was stem-killing fire (Table 2, Fig. 1a), where 70% of the between-species deviance was explained. Generally, explanation decreased as disturbance intensity decreased. However, a two-group model explained *c.* 64% of the sim-

ulated data generated from random sprouting proportions uniformly distributed 0–1, more than was explained for the undefined damage class (Table 2, Fig. 1g,h).

*Separation*

Under a null model, expected separation between

weak sprouters (sprouting probability 0.25) and strong sprouters (0.75) is 0.5 (Table 2, Fig. 1h). Crown-killing fires most strongly separated weak and strong sprouters ( $P_S(H) - P_S(L) = 0.76$ ; Table 2, Fig. 1b). For the undefined damage class, the separation of the groups was smaller than for random probabilities, reflecting the presence of a mid-range hump (Table 2, Fig. 1g).

### Sufficiency

A three-group model improved the fit substantially for crown-kill fire (Table 2), where a distinct mid-range hump can be seen (Fig. 1b), but had least impact for clipping (Table 2, Fig. 1d).

### Inclusiveness

Across the different damage classes, the probability of species falling into the middle group of a three-group model was greatest for undefined damage, where 44% of species were in this category (Table 2, Fig. 1g).

### WERE THESE CRITERIA FOR ASSESSING ADEQUACY OF FUNCTIONAL TYPES CORRELATED?

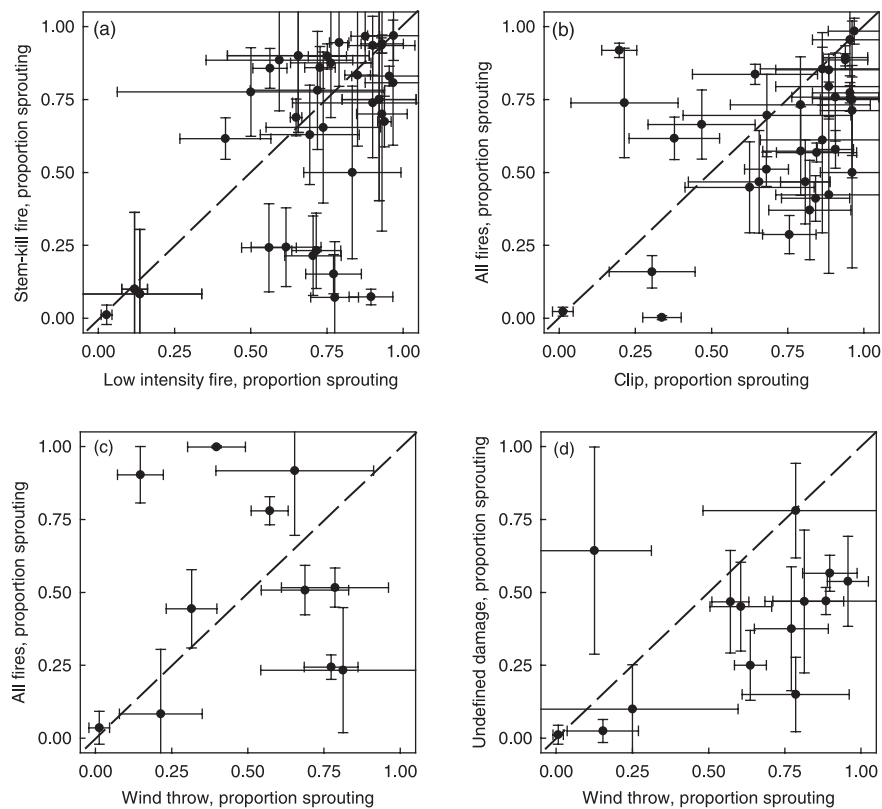
Explanation by the two-group model was positively correlated with separation between the peaks ( $r = 0.76$ ,

$P = 0.003$ ,  $n = 11$ ). These criteria captured the tendency of species to cluster at the extremes of sprouting ability. Inclusiveness was weakly, positively correlated with both sufficiency ( $r = 0.48$ ,  $P = 0.07$ ,  $n = 11$ ) and separation ( $r = 0.44$ ,  $P = 0.09$ ,  $n = 11$ ). These criteria were indicators of the absence of a large group of intermediate species.

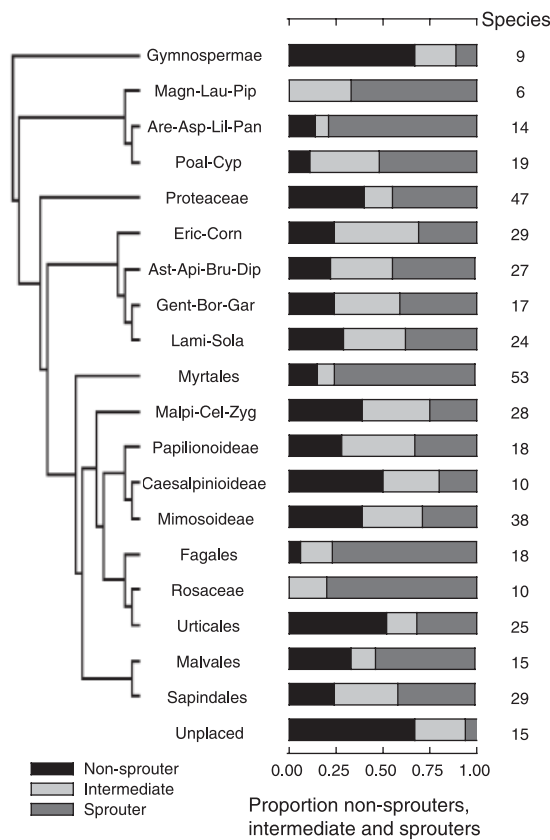
In general, the criteria indicated that stem-killed plants were well characterized by a sprouter/non-sprouter dichotomy (Table 2, Fig. 1a), but the adequacy of such a model decreased as disturbance intensity decreased. None of the criteria succeeded in characterizing undefined damage as a dichotomy (Table 2, Fig. 1g). Crown-kill disturbances were well explained by a dichotomy, but fitting was substantially improved by adding a third, intermediate response group (Table 2, Fig. 1b), as were fits for slashing and ill-defined fires (Table 2, Fig. 1c,e).

### DID WITHIN-SPECIES RESPONSES SUPPORT CROSS-SPECIES PATTERNS?

In general, within-species patterns supported shifts observed between the histograms in Fig. 1. No species that was an infrequent sprouter after low intensity fires was a strong sprouter after stem-killing fires (Fig. 2a). Fires tended to reduce sprouting success compared with clipping treatments (Fig. 2b), but wind throw and



**Fig. 2** Pairwise contrasts of disturbance class effects on sprouting proportions within species. Each symbol represents a species with indicative 95% confidence intervals. Dashed line shows equal sprouting proportions for the two disturbance classes. One-half added to counts of sprouting and dying plants. (a) Low, variable intensity fire compared with stem-killing fire,  $n = 40$ ; (b) clipping compared with any class of fire,  $n = 35$ ; (c) wind throw compared with any class of fire,  $n = 11$ ; (d) wind throw compared with undefined damage,  $n = 14$ .



**Fig. 3** Distribution of sprouting ability within and between clades of a high level phylogenetic tree. Sprouting ability of species was determined as percentage of plants sprouting after any fire or clipping treatment below 4 cm above ground. Species categorized into: non-sprouting,  $\leq 30\%$ ; intermediate,  $30-70\%$ ; sprouting  $\geq 70\%$ . Abbreviations of clades: Magn, Magnoliales; Lau, Laurales; Pip, Piperales; Are, Areaceae; Asp, Asparagales; Lil, Liliales; Pan, Pandanales; Poal, Poales; Cyp, Cyperales; Eric, Ericales; Corn, Cornales; Ast, Asterales; Api, Apiales; Bru, Bruniaceae; Dip, Dipsacales; Gent, Gentianales; Bor, Boraginales; Gar, Garryaceae; Lami, Lamiales; Sol, Solanales; Malpi, Malpighiales; Cel, Celastrales; Zyg, Zygophyllales.

fire did not show consistent differential effects on sprouting success (Fig. 2c). Plants experiencing wind throw were more likely to sprout than were plants suffering undefined damage (Fig. 2d), possibly because the undefined damage class may be associated with localized events that had less effect on surrounding canopy and light availability.

**PHYLOGENETIC PATTERNS OF SPROUTING AFTER CLIPPING OR FIRE**

Clades differed significantly in the proportions of species that were sprouters ( $\geq 70\%$  of plants sprout), intermediate ( $30-70\%$  sprout), or non-sprouters ( $\leq 30\%$  sprout) (Fig. 3, likelihood ratio = 106.73, d.f. = 38,  $P < 0.0001$ ,  $n = 451$  species between 19 clades and one 'unplaced' group). The proportion of species in a clade that were sprouters ranged from 11% for Gymnospermae to 80% for Rosaceae, with a mean of 45% (Fig. 3).

For non-sprouters, proportions ranged from 0% for Rosaceae and Magnoliales-Laurales-Piperales to 67% for Gymnospermae, with a mean of 29% (Fig. 3). The proportions of intermediate species ranged from 7% in the monocots Areaceae-Asparagales-Liliales-Pandanales to 45% in Ericales-Cornales, which was the only clade to appear associated to any extent with intermediate sprouting (PR = 2.0, Fig. 3). This analysis suggests (i) that most clades have a mix of sprouting ability among their component species; (ii) that sprouting is not conserved along phylogenetic lineages; and (iii) that phylogeny does not underlie the occurrence of frequent intermediate sprouters or even sprouting distributions in some disturbances and vegetation.

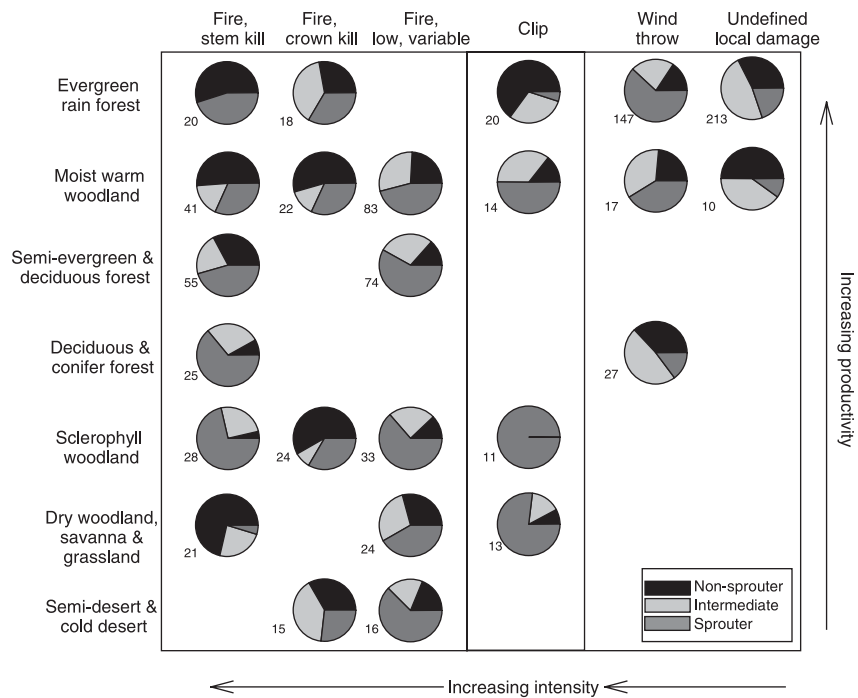
**HOW DO PATTERNS OF SPROUTING SHIFT BETWEEN VEGETATION TYPES AND HOW IS THIS RELATED TO COMPARISONS OF DISTURBANCE CLASSES?**

Disturbance classes were not equally distributed between vegetation types (Table 1, LR = 92.56, d.f. = 36,  $P < 0.0005$ ). Hence, comparisons across disturbance classes were confounded with vegetation type differences. We cross-classified responses by vegetation type and disturbance class and used the three-group classification cut at 30% and 70%, to produce an overview of sprouting responses (Fig. 4). Apart from in sclerophyll woodlands and deserts, sprouters and intermediates increased and non-sprouters decreased as fire intensity decreased (Fig. 4). In all vegetation types, intermediates were frequent after wind throw and especially after undefined, localized damage. These results indicate that the patterns of many examples of both non-sprouters and sprouters in intense disturbances (Fig. 1a,b vs. left-hand side of Fig. 4) and most intermediates after milder disturbances (Fig. 1f,g vs. right-hand side of Fig. 4) are general and little influenced by vegetation type.

How similar was the mix of sprouting responses to a particular disturbance across different vegetation types (i.e. comparing pie charts within columns of Fig. 4)? In low and variable intensity fires (Fig. 4, third column) it was remarkably consistent, but for wind throw, as productivity increased, there was a systematic shift to increase in sprouters and a decrease in intermediate and non-sprouters (LR = 22.89, d.f. = 4,  $P = 0.0002$ ,  $n = 191$ , Fig. 4, fifth column) (Peterson & Pickett 1991; Everham & Brokaw 1996). There were also substantial differences between vegetation types for stem-killing fires (Fig. 4, first column).

**Discussion**

This study has illustrated the shifts in distributions of sprouting across disturbances and vegetation types and assessed the adequacy of a dichotomous classification of sprouting ability. A dichotomy was most useful where intense disturbances remove practically



**Fig. 4** Effect of vegetation type (in rough order of productivity) and disturbance class (in rough order of intensity) on distribution of sprouting ability between species. Species categorized into: non-sprouting,  $\leq 30\%$ ; intermediate,  $30\text{--}70\%$ ; sprouting,  $\geq 70\%$ . Vegetation types based on Walter (1984), see Table 1. Restricted to combinations of disturbance type and vegetation type with  $n \geq 10$  species ( $n$  at lower left of each pie chart).

all above-ground biomass. It was less useful where substantial amounts of stem were retained and where neighbouring vegetation was left intact. Comparison across a wide range of vegetation types and disturbances therefore requires quantitative records of sprouting.

#### ENVIRONMENTAL FACTORS CONTRIBUTING TO SHIFTS IN DISTRIBUTIONS OF SPROUTING ABILITY

At least three circumstances contribute to the sprouting proportion after a single disturbance event: intensity of the event, variation or patchiness in intensity and post-disturbance neighbouring vegetation.

High disturbance intensity reduces options for regrowth. Where disturbances kill the stem, plants must rely upon sprouting from basal buds, buried stems and root buds. Where a substantial portion of the stem remains intact, such as after wind throw or slashing or fires of low intensity, more meristems are available to sprout, including epicormic and axillary buds (Gill 1981; Burrows 2002). More species would be therefore expected to have some individuals survive mild disturbances simply on probabilistic grounds, and so the dichotomy would be less clear (Bellingham & Sparrow 2000).

Variation in disturbance intensity will tend to blur any dichotomy. For infrequent sprouters, variation allows some individuals to survive that ordinarily would be killed, whereas at greater than average intensity even some strong sprouters will die.

Disturbance events in the undefined, localized damage class vary in gap size, disturbance agent and intensity, which would tend to obscure any sprouting dichotomy. Whereas intense disturbances yield more homogeneous post-disturbance conditions. With no canopy overhead and no competition from established neighbours, infrequent sprouters have no refuges and strong sprouters are not hindered by neighbours, enabling a sprouting dichotomy to be maintained. Intact neighbouring vegetation will, in general, decrease sprouting through reduced light and other competition.

#### PLANT TRAITS INFLUENCING DISTRIBUTIONS OF SPROUTING ABILITY

Why might sprouting be a discrete trait, at least in some circumstances? For many functional traits, e.g. seed size, leaf life span and height, species appear to lie continuously along a wide range of points on the trade-off line. Other traits occur as discrete groups, e.g. growth form, dispersal morphology and root symbionts (Westoby *et al.* 2002; Cornelissen *et al.* 2003; Reich *et al.* 2003). Sprouting is part of a complex demographic trade-off and carries allocation costs expressed as delayed maturity and reduction in seedling growth rates, above-ground biomass accumulation, maximum height and annual seed production (Keeley & Zedler 1978; Bond & van Wilgen 1996; Midgley 1996; Bond & Midgley 2003). Perhaps this complex coordination leads to optimization of distinct criteria (Clark 1991), rather than a balance of two components of an allocation

trade-off that can be expressed as a decomposition, e.g. reproductive allocation = seed mass  $\times$  seed number (Henery & Westoby 2001).

Another potential explanation for discrete sprouting/non-sprouting strategies is that there is a non-linear benefit of allocation to sprouting, such that a small allocation has minimal effect on sprouting probability. Analogous models may be those for trade-offs between avoidance and tolerance of herbivory (Loehle 1996; Mauricio *et al.* 1997), and for evolution of dioecy through non-linear benefits of male and female function (Charnov 1982).

#### DISCRETE CLASSES OR A CONTINUUM?

The question of whether functional variation across species should best be represented as a continuum or as categories is of interest for many traits other than sprouting (e.g. Prior *et al.* 2003; Ackerly 2004). The methods developed here might be helpful for other traits, for example the method for assessing whether a three-category model is a substantial improvement over a two-category (dichotomous) model. Unfortunately, our methods cannot provide a general solution to the problem of assessing categorical vs. continuum representations. For example, the binomial mixture models require: (i) that the single binomial parameter defines both the location and the spread of the data; and (ii) that a continuum is defined as a uniform distribution of probabilities 0–1. The issues are discussed further in Appendix S2.

#### PREVALENCE OF SPROUTING

Sprouting ability was broadly distributed across vegetation types. While comparisons between disturbance classes were confounded with vegetation differences, the general patterns described were little influenced by vegetation type (Fig. 4). However, incomplete coverage of combinations of disturbances and vegetation types prevented decisive analysis, and indeed, some of the confounding is natural; vegetation types do differ in the disturbances they experience. The coverage of species is restricted and biased by our use of quantitative data. Having demonstrated that the dichotomy is adequate, at least for fires, some questions may be more broadly investigated using species' sprouting classifications in floras and large fire response data bases (Gill & Bradstock 1992; le Maitre & Midgley 1992). This work validates broad-scale biogeographical comparisons and modelling efforts to parameterize fire responses with a minimum trait set consisting of a sprouting dichotomy and a dichotomy of propagule persistence through the next fire (Bond & van Wilgen 1996; Pausas 1999; J.G. Pausas *et al.*, unpublished data).

Sprouting ability was broadly spread across a high-level phylogenetic tree and mixed within clades, with sprouting least common in gymnosperms (Fig. 3). Recent analyses within clades *Banksia* (Proteaceae),

*Protea* (Proteaceae) and *Cliffortia* (Rosaceae) in fire-prone shrublands have confirmed the present result of a mixture of sprouting responses within clades and the suggestion that sprouting is a highly evolutionarily labile trait (Bond & Midgley 2003).

A possible limitation of this paper has been the need to group growth forms to maximize species coverage. Previous work has found that sprouting ability is mixed within growth forms (Bellingham *et al.* 1994; Hodgkinson 1998; Vesik 2002) although some growth forms are less variable, e.g. grasses tend to be sprouters and subshrubs from the Chenopodiaceae tend to be non-sprouters (Vesik 2002).

Many studies report whether individuals of species sprout. Far fewer report quantitative data. To facilitate effective comparisons across diverse disturbances and vegetation types we urge the collection and reporting of quantitative sprouting data (Cornelissen *et al.* 2003). We hope that the sparse matrix of studies under different disturbances and vegetation types presented here (Fig. 4) will motivate systematic efforts to fill the gaps and promote quantitative study of sprouting within different vegetation and disturbance types with controlled intensities. This paper has increased our depth of understanding of sprouting as a potential strategy dimension, and also clarified the question of how it might best be coded. These efforts contribute to putting sprouting more firmly on a shortlist of useful strategy dimensions (Weiher *et al.* 1999; Westoby *et al.* 2002; Cornelissen *et al.* 2003).

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#### Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC871/JEC871sm.htm>

**Appendix S1** Table of studies contributing data on proportions of plants sprouting after various disturbances from various vegetation types.

**Appendix S2** Issues in choosing discrete or continuous characterizations of functional traits.

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