

## References

- Gurevitch J, Curtis PS, Jones MH. 2001. Meta-analysis in ecology. *Advances in Ecological Research* 32: 199–247.
- Jablonski LM, Wang X, Curtis PS. 2002. Plant reproduction under elevated CO<sub>2</sub> conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* 156: 9–26.
- Körner C. 2003. Nutrients and sink activity drive plant CO<sub>2</sub> responses – caution with literature-based analysis. *New Phytologist* 159: 531–538.
- Lajeunesse MJ, Forbes MR. 2003. Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters* 6: 448–454.

**Key words:** meta-analysis, elevated CO<sub>2</sub>, reproductive responses, environmental stress factors, science policy.

# Drought damage and recovery – a conceptual model

Drought can result in loss of leaves and desiccation of roots and twigs. Whole plants may die in severe drought. Plants may manage losses, for instance by shedding leaves as drought progresses (Orshan, 1954). Drought deciduousness is conspicuous where soil moisture availability is distinctly seasonal, such as in forests and savannas of wet-dry tropics, mediterranean shrublands, annual grasslands, and some temperate deserts (Nilsen & Muller, 1981; Comstock *et al.*, 1988; Borchert, 1994; Williams *et al.*, 1997). This leaf loss occurs to different degrees between species, and covers the range from evergreen to fully deciduous (Williams *et al.*, 1997). In cases where drought is less predictable but still recurrent, how might plants respond to soil moisture deficits that cause significant damage and threaten plant survival? Here we present a conceptual model of drought damage and recovery patterns with observations of leaf loss, stem damage and regrowth after severe drought in a glasshouse for 19 dicotyledonous species from semiarid south-eastern Australia. We then examine evidence and ideas from the literature supporting the processes we propose. Because the observations were not designed to test the model, they should be regarded as illustrating it rather than as rigorously testing it.

## A conceptual model for patterns of drought damage and regrowth

We propose that following severe drought, the observed pattern of loss, damage and regrowth is the outcome of two processes in opposite directions, leaf loss proceeding from base to apex and stem damage from apex to base (Fig. 1). Depending upon the rates of these two processes,

qualitatively different patterns can be observed. In species with high rates of leaf loss compared to stem damage, basal leaf loss is observed. Conversely, in species with low rates of leaf loss and comparatively high stem damage rates, apical stem damage is observed. In species where the two rates are coordinated each of basal leaf loss and apical stem damage may be seen.

We propose that the rates of these two processes (leaf loss proceeding from base to apex and stem damage progressing apex to base) are related to traits reflecting structural investment and expected lifespan of leaves and stems: leaf mass per area (LMA) (Reich *et al.*, 1992; Westoby *et al.*, 2000) and sapwood density (Hacke *et al.*, 2001a). Specifically, low LMA should be associated with high rates of leaf loss and evidence of basal leaf loss. Low sapwood density should be associated with high rates of stem damage and evidence of apical damage. Because these processes are expected to proceed concomitantly, the values of LMA relative to sapwood density may be more closely linked to damage and regrowth patterns than either trait alone. Although we describe mechanisms, we do not wish to claim we have proven these links. Rather we hope that others will be motivated to test and improve the model.

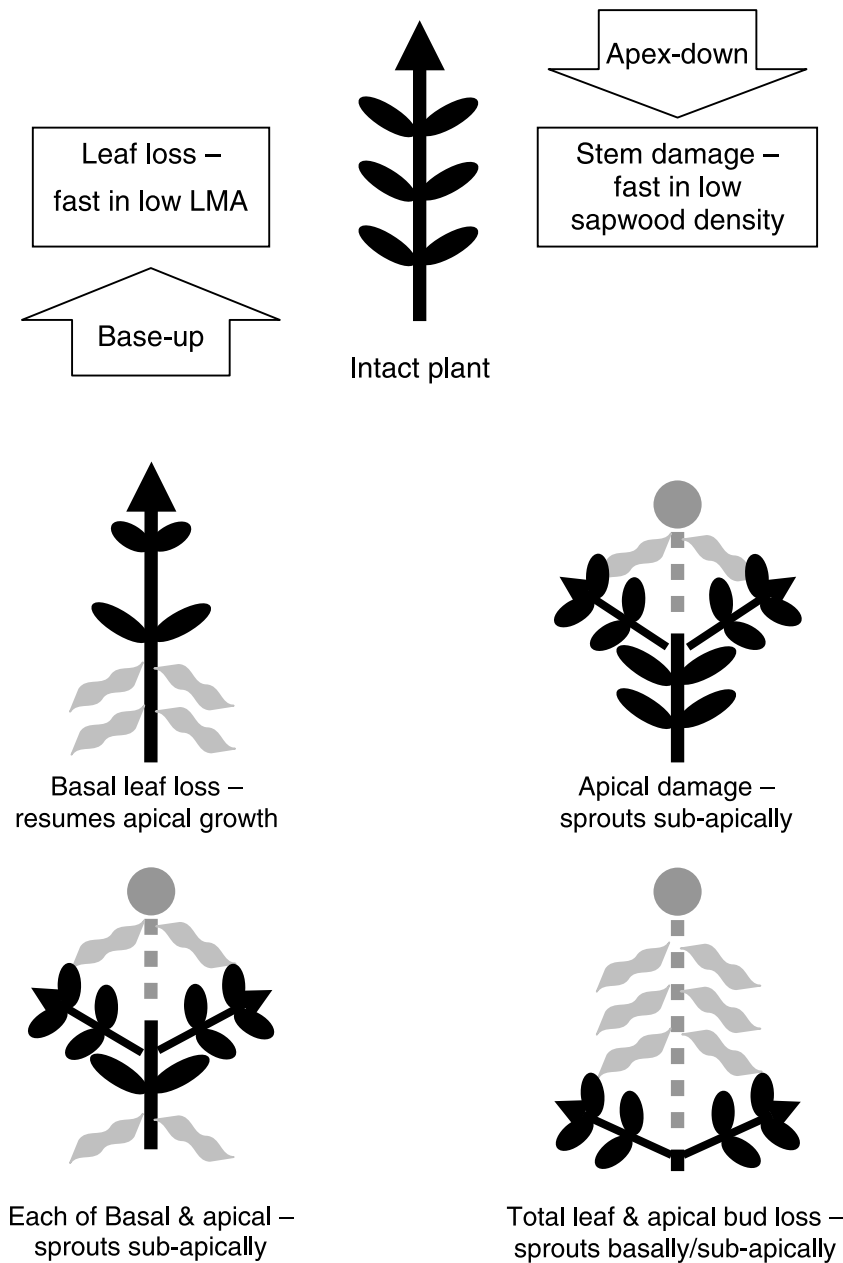
## Experimental drought

Plants from 19 perennial dicotyledonous species from semiarid south-eastern Australia were raised from seed and grown in potting mix in 13 cm diameter pots (soil volume ~1.3 l), watered daily and supplied ample nutrients. At the time of drought treatment, plants ranged in age from a couple of months to approx. 1 yr. The difference in age was partly a function of varied germination time and the age of plants was roughly proportional to expected lifespan, so the youngest plants were short-lived perennial Asteraceae.

Soil drought was imposed by weighing pots each day and adding water to *c.* half the mass that had been lost in the previous day. Plants were closely observed for signs of drought stress (combinations of colour change, wilting and leaf drop depending upon the species). When damage was incurred, plants were transferred to a different glasshouse for re-watering so as not to raise the humidity of the drought treatment glasshouse. Sample sizes for surviving plants were small and varied among species (surviving plants mean 4.7 per species, range 2–11, from total plants mean 8.7 per species, range 5–12; Table 1). Several species were likely to die by the time they started to show signs of drought stress, for example, *Eutaxia microphylla*, hence it was difficult to obtain drought-recovering plants.

## Damage and regrowth responses

For plants that recovered, repeat observations were available of locations of leaf loss and leaves remaining, apical bud loss



**Fig. 1** Conceptual model of drought damage and regrowth patterns. Leaf loss progresses from base to apex, faster in low leaf mass per area (LMA) species. Stem damage progresses from apex to base, faster in low sapwood density species. Depending on species' combination of these traits different patterns of damage and regrowth can occur. When rate of leaf loss is high relative to stem damage, basal leaf loss is seen. When rate of stem damage is high relative to leaf loss, apical damage is seen. Live tissues heavily shaded, dead tissues lightly shaded. Triangle is live apical bud, circle indicates dead apical bud. New leaves are smaller ellipses.

and position of new leaf growth. This was restricted to observations of primary stems. Where no single stem was clearly the main axis, a lineage from base to most distal stems was considered. Individual plants were classified into four groups, based on observations made during this study (see also Fig. 1).

**Apical group (A):** plants that had clearly lost the apical bud and apical leaves, but had leaves remaining at the base. These plants had to sprout from basal or axillary buds below the location of damage to the stem as revealed by loss of colour, turgor and resilience to bending.

**Basal group (B):** plants that had clearly lost leaves at the base of the stem, but either had not lost the apical bud or

had not lost all apical leaves. These plants could recommence growth from the apical bud upon re-watering.

**Each End group (E):** plants that had lost leaves at base and apex of the stem, but had some leaves remaining subapically. These plants sprouted subapically, below the dead portion of the stem, revealed by loss of colour, turgor and resilience to bending.

**Total group (T):** plants that survived total leaf loss, through basal and/or subapical sprouting.

Species were then classified according to the responses of individual plants. A broad definition (species were classified to either of Basal or Apical if any individual was observed displaying that response), and a narrow definition (a species

**Table 1** Responses to severe glasshouse drought and plant traits for 19 species from semiarid south-east Australia. Nomenclature follows Harden (1990). Clipped plants did not experience drought

Species	Family	B: Base-up leaf loss*	E: Each of basal & apical loss*	T: Total leaf lost*	A: Apex- down loss*	Drought mortality* (n)	Sapwood density (D, mg mm <sup>-3</sup> )	Leaf mass per area (LMA, mg mm <sup>-2</sup> )	LMA-D#	Proportion sprouting after clipping (n)
<i>Rhagodia spinescens</i>	Chenopodiaceae	4				3 (7)	0.87	0.069	-0.80	0.0 (8)
<i>Maireana pyramidata</i>	Chenopodiaceae	5				4 (9)	0.84	0.093	-0.13	0.0 (10)
<i>Enchylaena tomentosa</i>	Chenopodiaceae	5				3 (8)	0.95	0.060	-1.64	0.5 (10)
<i>Dodonaea viscosa cuneata</i>	Sapindaceae	1		1		4 (6)	0.79	0.071	-0.06	0.2 (10)
<i>Olearia pimelfoides</i>	Asteraceae	1		2		2 (5)	0.91	0.053	-1.48	0.5 (10)
<i>Eutaxia microcephala</i>	Fabaceae	1	2			8 (11)	0.85	0.063	-0.76	0.0 (10)
<i>Vittadinia triloba</i>	Asteraceae	1	4			2 (7)	0.77	0.024	-1.41	0.5 (10)
<i>Dodonaea viscosa spatulata</i>	Sapindaceae	2	1	1		4 (8)	0.86	0.100	-0.19	0.4 (10)
<i>Atriplex semibaccata</i>	Chenopodiaceae	3	1	1		3 (8)	0.84	0.072	-0.46	0.3 (10)
<i>Minuria leptophylla</i>	Asteraceae	4	1	6		1 (12)	0.83	0.044	-1.10	1.0 (10)
<i>Calotis cuneifolia</i>	Asteraceae	1	3	3		1 (8)	0.72	0.043	-0.09	0.5 (10)
<i>Senna artemisioides</i>	Fabaceae	1	4	2		4 (11)	0.92	0.150	-0.10	0.6 (10)
<i>Vittadinia cuneata</i>	Asteraceae		2	2		4 (8)	0.61	0.042	1.04	0.3 (11)
<i>Eucalyptus populinea</i>	Myrtaceae		7	7		1 (8)	0.72	0.140	1.59	0.9 (10)
<i>Einadia nutans</i>	Chenopodiaceae		4	4	1	7 (12)		0.039		0.4 (11)
<i>Brachyscome ciliaris</i>	Asteraceae		4	4	1	2 (7)	0.59	0.040	1.22	0.9 (10)
<i>Hakea tephrosperma</i>	Proteaceae			2	2	9 (11)	0.83	0.430	2.15	1.0 (10)
<i>Casuarina cristata</i>	Casuarinaceae			3	3	9 (12)	0.65	0.240	3.10	0.5 (10)
<i>Bossiaea walkeri</i>	Fabaceae			3	3	5 (8)	0.86	0.120	0.07	0.7 (10)

\*Numbers of plants. # LMA relative to sapwood density as difference between standardised, log-transformed LMA and sapwood density, see text.

was classified as Basal or Apical if it exhibited only that response) of response were used. Species that had plants with only Each End or Total loss could not be assigned to either Basal or Apical loss.

In six of 19 species, plants recovered either with only basal leaf loss (three species) or with only apical damage (three species) (Table 1). No species that included plants showing only basal leaf loss also included other plants that showed only apical damage. Similarly, no species that included plants recovering with only apical damage had other plants recovering with only basal leaf loss (Table 1). Several species that included plants with only basal leaf loss also had other plants recovering from damage at both ends (on the same plant) or from total leaf loss (Table 1).

So, in response to severe drought, species displayed consistent patterns of damage and regrowth after drought ranging from basal leaf loss and continued apical growth to apical stem damage and subapical or basal sprouting. Next we turn to the question of whether traits are related to these patterns.

### Plant traits

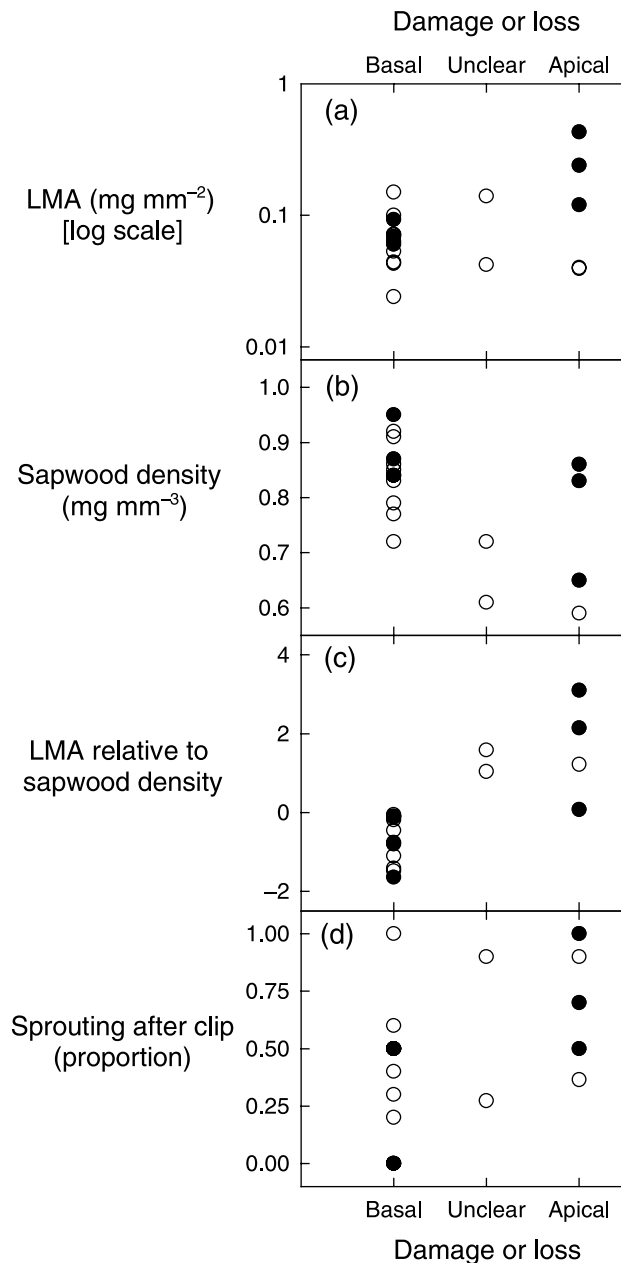
Two to five fully expanded leaves from upper parts of each of five individual plants that had not experienced drought were collected from each species for measurement of LMA. Leaves were scanned with an optical scanner and areas calculated using Delta-T Scan (Kirchhof & Pendar, 1993). After drying for at least 24 h at ~65°C, dry masses were measured and LMA calculated as mass over area. For sapwood density of current season twigs, specific gravity was measured by displacement volume after removing periderm according to the protocol of Hacke *et al.* (2000). Because patterns of damage might be expected to result from the interaction of leaves and stems, we assessed the relative difference between LMA and sapwood density. For this, both variables were first  $\log_{10}$  transformed and then standardised to distributions with mean zero and standard

deviation one,  $X_{\text{stand}} = \frac{X - \bar{X}}{s}$  (eqn 1) (Sokal & Rohlf, 1995: p105). The LMA relative to density was then calculated as  $\text{LMA}_{\text{stand}} - \text{D}_{\text{stand}}$  (eqn 2).

Figures presented here are based upon the broad definition of response groups, but with the narrowly defined groups highlighted (Fig. 2). Statistics are only presented for the narrowly defined groups, as these were considered most representative of the drought response patterns of interest. Trait values for the basal and apical groups were compared in preplanned contrasts (Sokal & Rohlf, 1995).

### LMA and sapwood density in relation to drought damage and regrowth patterns

Sapwood density (D) ranged roughly 1.5-fold and LMA ranged 20-fold among species (Table 1). Species that showed



**Fig. 2** Trait values and their relation to location of damage or leaf loss due to experimental glasshouse drought for 19 semiarid south-eastern Australian species. Filled symbols are species that only had plants displaying that pattern of loss and regrowth, open symbols are species for which at least one plant showed that pattern.

only apical damage tended to have higher LMA than species that had only basal leaf loss ( $t_{(16)} = 2.724$ ,  $P = 0.015$ , Fig. 2(a)). Sapwood density values for the apical damage group extended to lower values than the basal loss group although the two groups did not differ significantly ( $t_{(15)} = 1.271$ ,  $P = 0.223$ , Fig. 2(b)). LMA and sapwood density were uncorrelated ( $r = 0.15$ ,  $P = 0.56$ ,  $n = 18$ ). The apical damage group had higher LMA leaves relative to sapwood density

than did the basal loss group ( $t_{(15)} = 3.024$ ,  $P = 0.009$ ; Fig. 2(c)). Moreover, for all species that displayed any evidence of apical loss, the LMA relative to sapwood density was positive, and for all species with any evidence of basal loss, LMA relative to sapwood density was negative (Table 1).

These data indicate that the drought damage and regrowth patterns were related to LMA and sapwood density in the manner proposed in our conceptual model. However, it is not so much the absolute values of LMA and sapwood density that are important but rather their relative values. We now examine each of the processes and supporting evidence and ideas from the literature in greater detail.

### Leaf turnover and leaf lifespan

What is the significance of the spatial pattern of leaf loss, and why should LMA be related to the rate of leaf loss? New leaves are added at the distal end of the new shoot, and under drought stress old leaves are shed from the base of the stem (Pook, 1985; Comstock & Ehleringer, 1986; Davidson & Reid, 1989). In terms of economics of investment, younger leaves have higher expected future value than older leaves (Westoby *et al.*, 2000). Younger leaves might also occupy superior positions to older leaves for photosynthesis, being further toward the surface of the canopy. Hence, older basal leaves should be shed preferentially to younger apical leaves.

Slow leaf turnover (long leaf lifespan) is associated with high structural investment measured as LMA (Reich *et al.*, 1992; Westoby *et al.*, 2000; Wright & Cannon, 2001). Hence, in species of higher LMA and longer leaf lifespan, loss of leaves from base to apex would be expected to progress more slowly. This means, all else being equal, a decreased probability of basal leaf loss for higher LMA species, as observed in this study.

### Hydraulic failure

Why should stem damage progress from apex to base? Water potentials become more negative with distance from the stem base and drop sharply at branching points (Zimmermann, 1978, 1983; Hacke & Sperry, 2001). As embolisms accumulate with progressive drought, the number of embolisms should increase with distance from the stem base (Comstock & Sperry, 2000). Thus distal regions of stems would be expected to exhibit total loss of conductance first and this should progress from apex to base, although hydraulic failure at roots could also occur (Comstock & Sperry, 2000; Hacke *et al.*, 2000; Hacke & Sperry, 2001; Davis *et al.*, 2002). Cavitation in short-lived 'cheap' tissues such as twigs may protect main stems and roots by 'segmentation' (Zimmermann, 1978, 1983; Sperry, 1995; Pockman & Sperry, 2000; Rood *et al.*, 2000). Indeed, hydraulic failure in petioles may well be the mechanism of leaf shedding under drought proceeding up the stem (Zimmermann,

1978, 1983; Sperry, 1986; Tyree *et al.*, 1993). Exactly why it proceeds up the stem is unclear; perhaps the accumulated minor cavitation events over time cause older petioles to be more vulnerable (Hacke *et al.*, 2001b).

### Determinate twigs and flowering

Although progressive leaf loss from base to apex is the norm in most species, determinate shoots are also common, where whole leaf sequences or distal twigs may be lost (Gray & Schlesinger, 1981; Nilsen & Muller, 1981; Gill & Mahall, 1986; Comstock *et al.*, 1988). Determinate and sympodial growth is often associated with irreversible switching of apical meristem function from growth to flowering (Bell, 1991). However, flowering is not the mechanism that leads to stem death. Six species had flowered by the time of treatment (*Brachyscome ciliaris*, *Vittadinia triloba*, *V. cuneata*, *Calotis cuneifolia*, *Atriplex semibaccata*, *Einadia nutans*). In *Atriplex semibaccata* and *Einadia nutans*, flowering was restricted to the short lateral branches. In the remaining species, all from the Asteraceae, the apex had sometimes switched to reproduction. Hence, flowering was conflated with drought for these plants. This may have led to increased representation of species in the each end group for *Vittadinia triloba*, *V. cuneata* and *Calotis cuneifolia* (Table 1), and of the single *Brachyscome ciliaris* in the apical loss group, but did not alter the substance of these results. It is not clear to what extent hydraulic failure and other mechanisms can be disentangled as explanations for the majority of species with determinate shoots. However, dieback of shoots similar to the apical stem damage seen here has been convincingly attributed to hydraulic failure of stems for some species (Rood *et al.*, 2000; Davis *et al.*, 2002). We suspect that the apical stem damage observed in this experiment is a function of stem hydraulic failure, though we have no data to prove this.

### Stem construction

Why should stem hydraulic failure be related to sapwood density? The mechanism of drought-induced loss of conductance has been widely attributed to air seeding resulting in transfer of embolisms from air-filled to water-filled vessels mediated by interconduit pits (Sperry, 1995; Hacke & Sperry, 2001). But how do pits relate to sapwood density? The segmentation hypothesis and explicit use of the word 'cheap' by Zimmermann (1983), hint at an argument on the grounds of construction costs (Hacke *et al.*, 2000). The vulnerability of xylem to conductance loss was well correlated with the strength of vessel walls to resist implosion due to large negative pressures within the vessels, across a wide range of North American woody species (Hacke *et al.*, 2001a). Wall strength is, in turn, directly related to sapwood density (Hacke *et al.*, 2001a). The

check-valve function of interconduit pits (that mediate air-seeding) should be coordinated with wall strength such that resistance to implosion is greater in species that do not embolise extensively until water potentials are very negative.

Because low sapwood density stems are less resistant to total conductance loss, all else being equal, they would be expected to show evidence of more extensive apical stem damage and a consequent failure to regrow from that region of dead stem. Further, the rate with which stem conductance loss progresses from apex to base should be faster in species with lower sapwood density.

Positive correlation of LMA and stem density might be expected. To maintain long-lived leaves through dry seasons, xylem conductivity must be maintained, requiring safe stem construction reflected in high stem density (Sobrado, 1993; Kolb & Davis, 1994; Ackerly, 2003). Ackerly (2003) found a positive relationship between LMA and stem density across 20 species of chaparral shrubs, and Sobrado (1993) found higher stem density in two evergreen compared to four deciduous tropical trees. Both these authors used whole wood, which includes non-conductive tissue, but whole wood density and sapwood density are likely correlated (here  $r^2 = 0.36$ ,  $n = 18$  species).

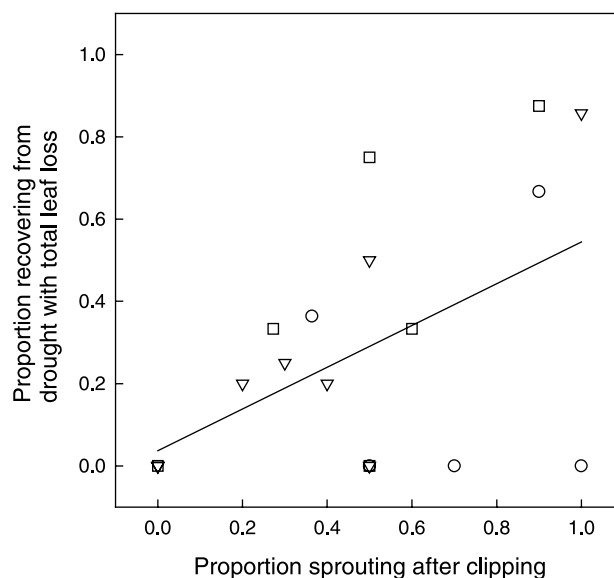
### Was regrowth after drought related to sprouting after clipping?

Sprouting after clipping (not exposed to drought) was assessed on a separate sample of plants by clipping above the cotyledonary node. The maximum number of plants that sprouted (i.e. ignoring subsequent mortality of sprouted plants) was expressed as a proportion of treated plants. Species that suffered apical damage tended to have higher sprouting ability following clipping ( $t_{(16)} = 2.404$ ,  $P = 0.029$ ; Fig. 2(d)), meaning that species that respond to drought with apical loss need to have at least moderate (basal) sprouting ability.

The ability to recover from total leaf loss induced by drought was common (11 of the 19 species), and was related to species' sprouting ability following clipping (Fig. 3). As a measure of species' ability to recover following total leaf loss due to drought, the number of plants recovering with total leaf loss was divided by the sum of the number of plants with total leaf loss and the number of dead plants [ $T/(T + D)$ ]. Across all species there was a triangular relationship, such that species that were poor sprouters after clipping did not recover well from drought-induced total leaf loss (Fig. 3). Species that were good sprouters after clipping ranged widely in how well they recovered from total leaf loss due to drought.

### Apical bud maintenance and sprouting

Maintaining the apical bud should benefit further growth once the drought has passed, especially if height growth is



**Fig. 3** Proportion of plants that recovered after total leaf loss due to drought compared to proportion sprouting after clipping. Calculated as number displaying recovery with Total leaf loss, divided by the sum of plants recovering with Total leaf loss and dead plants [ $T/(T + D)$ ]. Circles represent species that mostly recovered with Apical damage, upside-down triangles are species that mostly recovered with Basal leaf loss, squares are species that mostly recovered with damage at Each end. Solid line is linear regression for all species (recovery =  $0.043 + 0.503 \times$  clip sprouting,  $r^2 = 0.26$ ,  $P = 0.026$ ,  $n = 19$ ).

an important aspect of the plant's strategy. So why would a species consistently show apical loss? Presumably it has to do with the cost of maintaining a water column to apical meristems through drought (Westoby, 1980). This cost may be incurred through resistant stems as outlined above, or through deep root systems (Davis *et al.*, 1999; Davis *et al.*, 2002).

Having to sprout subapically after apical loss and then continue upward has three disadvantages: structural discontinuities in the stem due to growing past dead tissue (Midgley, 1996); a time cost in gaining leaf area and height (Davidson & Reid, 1989); possible entry of pathogens through the dead branches (Davis *et al.*, 2002). On the other hand, if lateral expansion or space filling is more important than height growth, then dying back at the tips and sprouting subapically is no disadvantage and actually improves filling of space. This may be the case for semiarid species, such as those studied here. Plants that are prone to losing their apices to drought may require good sprouting ability (see Davidson & Reid, 1989). Sprouting is useful for recovery from a variety of hazards that result in major loss of above-ground biomass (Bond & Midgley, 2001), but is not commonly associated with drought. In locations subject both to recurrent drought and to recurrent fire however, ongoing selection might lead to tandem solutions to these hazards.

## Caveats to results and their generality

The difference in ages of plants would definitely affect the rate of soil drying. Though this should not affect the pattern of damage. The size of plants may affect the ability to detect pattern. In small plants with short hydraulic pathways, the whole plant may desiccate more-or-less simultaneously. In large plants, the patterns of damage may be clearer as there is more space and time for the progress of damage to be noted. Finally the age of leaves relative to their potential lifespan may have a large effect. In species with long leaf lifespan leaves (approx. 2 yr), a 1-yr-old plant has no 'old' leaves to shed. For these reasons it would be good to see whether these patterns hold in adult plants in the field.

When response groups were defined narrowly, statistically significant patterns were detected. However, when defining the groups more broadly such that more species were included in the Basal and Apical groups, the trends persisted, giving confidence in the generality of the patterns for the species set. Species that only showed partial basal leaf loss were exclusively in the Chenopodiaceae. This family of leaf-succulent plants are known to be poor sprouters and biogeographically tend to be associated with conditions of summer drought and clayey, often saline, soils. The structural support of these leaves is due largely to water, and the implications for leaf lifespan, particularly with respect to drought, are unclear (Vendramini *et al.*, 2002). In the apical group, *Bossiaea walkeri* has photosynthetic stems and bears leaves only as a juvenile and on recovery from damage. *Casuarina cristata* has very small leaves closely appressed to the stem. Whole needles (distal stems ensheathed by scale-like leaves) may be abscised or may grow into stems and the leaves simply lose photosynthetic capacity and become part of the periderm. These two species serve to suggest that responding to drought solely through apical stem damage is an unusual strategy. This reinforces our earlier expectation that basal leaf loss and apical maintenance should be the norm. However, solely basal leaf loss and solely apical stem damage are the extremes, between which lie a range of possibilities that we expect to be related to strategies of growth, architecture and coping with disturbances. We propose that patterns of damage and regrowth are important aspects of plants' ecological strategies in locations subject to periodic drought and that links between carbon gain strategies and disturbance responses may reward further research.

## Acknowledgements

For assistance in the glasshouse we thank A. Downing, J. Grubba & A. Stock. For comments on earlier drafts we thank D. Ackerly, W. Allaway, E. Garnier, A. Nicotra, I. Wright and 3 anonymous referees. PAV was supported by a Land & Water Australia Postgraduate scholarship. This is

publication no. 385 of the Research Unit for Biodiversity and Bioresources, Macquarie University.

**Peter A. Vesk\* and Mark Westoby**

School of Biological Sciences, Macquarie University, North Ryde NSW 2109 Australia  
(\*correspondence and current address: Australian Centre for Biodiversity: Analysis, Policy, Management. School of Biological Sciences, PO Box 18, Monash University, Clayton VIC 3800 Australia. fax +61-3-9905-5613; email peter.vesk@sci.monash.edu.au)

## References

- Ackerly DD. 2003. Functional strategies of chaparral shrubs in relation to seasonal water stress and disturbance. *Ecology* (In press.)
- Bell AD. 1991. *An illustrated guide to flowering plant morphology*. Oxford, UK: Oxford University Press.
- Bond WJ, Midgley JJ. 2001. The persistence niche: ecology of sprouting in woody plants. *Trends in Ecology and Evolution* 16: 45–51.
- Borchert R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437–1449.
- Comstock JP, Cooper TA, Ehleringer JR. 1988. Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species. *Oecologia* 75: 327–335.
- Comstock JP, Ehleringer JR. 1986. Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia* 68: 271–278.
- Comstock JP, Sperry JS. 2000. Theoretical considerations of optimal conduit length for water transport in vascular plants. *New Phytologist* 148: 195–218.
- Davidson NJ, Reid JB. 1989. Response of eucalypt species to drought. *Australian Journal of Ecology* 14: 139–156.
- Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker MC, Adams GC. 2002. Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *American Journal of Botany* 89: 820–828.
- Davis SD, Ewers FW, Wood J, Reeves JJ, Kolb KJ. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of southern California. *Ecoscience* 6: 180–186.
- Gill DS, Mahall BE. 1986. Quantitative phenology and water relations of an evergreen and a deciduous chaparral shrub. *Ecological Monographs* 56: 127–144.
- Gray JT, Schlesinger WH. 1981. Biomass, production, and litterfall in the coastal sage scrub of southern California. *American Journal of Botany* 68: 24–33.
- Hacke UG, Sperry JS. 2001. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics* 4: 97–115.
- Hacke UG, Sperry JS, Pittermann J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology* 1: 31–41.
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA. 2001a. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.

- Hacke UG, Stiller V, Sperry JS, Pittermann J, McCulloh KA. 2001b. Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiology* 125: 779–786.
- Harden GJ. 1990. *Flora of New South Wales*. Sydney, Australia: New South Wales University Press.
- Kirchhof G, Pendar K. 1993. *Delta-T Scan Software*. Cambridge, UK: Delta T Devices.
- Kolb KJ, Davis SD. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* 75: 648–659.
- Midgley JJ. 1996. Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than reseeders. *Ecography* 19: 92–95.
- Nilsen ET, Muller WH. 1981. Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. *Ecological Monographs* 51: 323–342.
- Orshan G. 1954. Surface reduction and its significance as a hydrological factor. *Journal of Ecology* 42: 442–444.
- Pockman WT, Sperry JS. 2000. Vulnerability of xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* 87: 1287–1299.
- Pook EW. 1985. Canopy dynamics of *Eucalyptus maculata* Hook. III. Effects of drought. *Australian Journal of Botany* 33: 65–79.
- Reich PB, Walters MB, Ellsworth DS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62: 365–392.
- Rood SB, Patino S, Coombs K, Tyree MT. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* 14: 248–257.
- Sobrado MA. 1993. Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia* 96: 19–23.
- Sokal RR, Rohlf FJ. 1995. *Biometry, 3rd edn*. New York, USA: W.H. Freeman.
- Sperry JS. 1986. Relationship of xylem embolism to xylem pressure potential, stomatal closure and shoot morphology in the palm *Rhapis excelsa*. *Plant Physiology* 80: 110–116.
- Sperry JS. 1995. Limitations on stem water transport and their consequences. In: Gartner BL, ed. *Plant stems: physiological and functional morphology*. London, UK: Academic Press, 105–124.
- Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell & Environment* 16: 879–882.
- Vendramini F, Díaz S, Gurvich DE, Wilson P, Thompson K, Hodgson J. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* 154: 147–157.
- Westoby M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany* 28: 169–194.
- Westoby M, Warton D, Reich PB. 2000. The time value of leaf area. *American Naturalist* 155: 649–656.
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D. 1997. Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* 78: 2542–2558.
- Wright IJ, Cannon K. 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. *Functional Ecology* 15: 351–359.
- Zimmermann MH. 1978. Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany* 56: 2286–2295.
- Zimmermann MH. 1983. *Xylem structure and the ascent of sap*. New York, USA: Springer-Verlag.

**Key words:** leaves, stems, LMA, sapwood density, disturbance response, plant ecological strategies.

---

## Meetings

---

### Speciation – a rebirth

#### Plant speciation – the 11th *New Phytologist* Symposium, St. Francis Xavier University, Nova Scotia, Canada, June 2003

Contemporary studies of speciation span several levels of biological organization and many subdisciplines within biology. For instance, they include identification of single gene changes that are responsible for hybrid inviability (Presgraves *et al.*, 2003), analysis of physiological characters associated with habitat differences between sister taxa (Lexer *et al.*, 2003; Rajakaruna *et al.*, 2003b), phylogenetic reconstruction of character evolution and diversification rates (Hodges, 1997; Magallón & Sanderson, 2001), and study of genomic additivity in polyploids (Liu *et al.*, 2001). The

diversity of empirical approaches reflects the complexity of how species arise and are maintained through time. However, while species and an understanding of speciation play a central role in biology, a comprehensive description of the speciation process remains elusive. The 11th *New Phytologist* Symposium (June 2003) brought together scientists to discuss recent, substantial progress in plant speciation research and to honor Verne Grant for his long-lasting and profound conceptual and empirical contributions – by utilizing a diversity of methods and modern tools, significant progress is now being made and there is also a wealth of novel insights.

#### Genetics of speciation

Speciation is the evolution of reproductive and genetic isolation between populations. We have numerous conceptual models of the circumstances that might lead to this process