

Editorial

Welcome to new editors – development, eco-devo and environmental adaptation

Sonia Sultan, Keith Lindsey and Steve Strauss are three new appointments to the Editorial Board of *New Phytologist*. The scientific theme underlying these appointments is one that we are actively developing in the journal – ecological developmental biology ('eco-devo') and related research areas (e.g. see Dusheck, 2002). As we enter the postgenomics era, we have looked at the scope of the *Function* section with a view to encouraging the best of the emerging new research. Both eco-devo, at the interface between genomics and ecology, and the genetic basis of environmental adaptation are areas in which we see future expansion and are amplified further on our website (<http://www.newphytologist.org/function.htm>, e.g. see Geisler & Sack, 2002; Holroyd *et al.*, 2002; Lerdau & Gray, 2003).

The focus of Sonia's research in evolutionary ecology, at the Department of Biology, Wesleyan University, CT, USA, is on the organism's own capacity to respond to its environment (phenotypic plasticity) and the influence of random microenvironmental factors on individual success. These themes are amplified further on Sonia's website (<http://www.wesleyan.edu/bio/sultan/sultan.html>, e.g. see Ackerly *et al.*, 2000; Sultan, 2000, 2003). Keith Lindsey is at the School of Biological & Biomedical Sciences, University of Durham, UK, where his research aims at a full understanding of the molecular basis of plant development – this work mainly uses *Arabidopsis*, facilitated by the vast array of genetic information already available (<http://www.dur.ac.uk/biological.sciences/Staff/Lindsey/lindsey.html>, e.g. see Casson & Lindsey, 2003; Lindsey *et al.*, 2002; Souter *et al.*, 2002). But many other plants are now being genetically characterized and, among trees, principle among these is *Populus*. Steve Strauss has been at the forefront of these efforts – for example, in 1994, Steve was instrumental in creating the Tree Genetic Engineering Research Cooperative (TGERC; <http://www.cof.orst.edu/coops/tgerc/>). The research in Steve's lab (Forest Science, Oregon State University, OR, USA) focuses on the application of molecular genetics in the analysis of forest trees (<http://www.cgrb.orst.edu/mcb/faculty/strauss/>, e.g. see Strauss, 2002; Busov *et al.*, 2003).

In recognition of these key themes for the future, we will be holding a symposium in 2004 dedicated to the functional genomics of environmental adaptation in *Populus*. Alistair Hetherington has been instrumental in taking

the *Function* section forward to include the research described here, especially in encouraging Tansley reviews that reflect the new directions, and the review featured in this issue (Gutschick & BassiriRad, pp. 21–42; see also the accompanying commentary by David Ackerly, pp. 2–4) highlights pertinent ecological and evolutionary themes. The development of our *Evolution* section (<http://www.newphytologist.org/evolution.htm>), indeed, is complementary here, and on pp. 14–16 Alex Buerkle elaborates on the advances that have been facilitated by modern tools in the study of plant speciation.

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Commentary

Canopy gaps to climate change – extreme events, ecology and evolution

Some years ago, working in the Amazon, I was walking alone through the forest on a perfectly still day. The sun was high in the sky, and not a breath of wind offered relief from the humid, hot air. Without warning, a sound echoed through the forest. In the distance, a large tree cracked and splintered, paused and then crashed to the ground. After a moment, all was quiet again. The death of that tree was inevitable, but the moment of its collapse was highly unpredictable – the culmination of many years of storms and droughts, and the effects of herbivores and detritivores eating away at the dying tree. The sudden opening of the canopy gap would alter the ecological community in that small patch of forest for years to come. For some individuals, it would represent an opportunity – for germination, reproduction, recruitment to the canopy. For others it could signal their demise – overtopped by neighbors, consumed by herbivores, or unable to tolerate photoinhibition, water deficits, and other effects of the changed environment. The memory of that falling tree has stayed with me for many years. It was not only the apparent randomness of its collapse on a perfectly still day. It has also served as a reminder of how seldom we observe the occasional dramatic events that shape ecological communities and drive evolutionary change.

A fresh vision of extreme events

In this issue, Gutschick & BassiRad (pp. 21–42) present a wide-ranging and ambitious review addressing the role of extreme events in ecology and evolution. Viewed from an organismal perspective, they define an extreme event as ‘an episode in which the acclimatory capacities of an organism are substantially exceeded.’ The same event may be extreme

for some individuals but routine for others. Three features of organismal responses are highlighted. First, extreme events may have contingent effects, altering subsequent performance of the organism under more normal conditions. Second, extreme events may cause hysteresis in organismal responses: the acclimation of physiology and development may lag behind changes in driving variables, particularly as the environment returns to normal conditions. Third, Gutschick & BassiRad propose that the costs and benefits of extreme events may accrue primarily during a prolonged recovery phase, rather than during the event itself.

Through the lens of this organism-based definition, the authors offer a fresh vision of the ecological and evolutionary role of extreme events, with particular attention to plant responses and climate change. The novelty lies not in the individual examples, many of which will be familiar, but in providing a conceptual framework that ties them together, that reconfigures a large set of disparate observations as instances of a common phenomenon. Among the many speculations and hypotheses on offer, two areas stand out in terms of their implications for future research and their potential to offer explanations of important observations.

Statistics of extremes and the realized environment

For researchers accustomed to calculating means and standard errors, the statistics of extreme events will be unfamiliar territory. While we are all familiar with the meteorologists admonition of a ‘100-year storm’, how many know how to calculate these return intervals from the raw data of climatic time series? Denny & Gaines (2000) provide an excellent introduction to the statistics of extremes, as this area is known, which merit much greater attention in ecology and evolution. An increase in the frequency and intensity of extreme conditions may represent one of the most potent features of global climate change, in terms of social and biotic impacts, and there is considerable evidence that such changes are under way (Easterling *et al.*, 2000).

Gutschick & BassiRad also focus attention on the very important problem of the cross-correlation structure of environmental variation. The biotic impacts of climate extremes may be critically dependent on the coupling of various factors, rather than the extreme values for any one component. Well-studied examples include the interactive effects of cold and high light on photoinhibition (Ball *et al.*, 1991) and the effects of freezing and drought on xylem embolism (Langan *et al.*, 1997). To understand and predict where such combinations of conditions will occur, we need to know a lot more about the correlation structure of the environment – the patterns of congruence and incongruence of conditions required for growth (Bazzaz, 1996). Recently, Jackson & Overpeck (2000) proposed the term ‘realized environment’ to describe the sets of conditions in a multivariate climate space that are realized in a particular landscape at a particular time. The realized environment intersects the fundamental niche envelope for each species to create a ‘potential niche’ where that species could actually occur.

This approach provides a powerful explanatory framework for interpreting species distributions in today’s communities, and their past and future responses to climate change. One of the most important effects of climate change may be shifts in the realized environment: combinations of conditions that exist today may disappear, and conditions observed in the past may have no contemporary analogs. As species distributions respond to different features of the environment, these ‘no-analog’ climates may produce no-analog communities with combinations of co-occurring species that are not found together in the modern landscape (Williams *et al.*, 2001). Relatively small changes in climate may result in substantial shifts in the realized environment, and the novel conditions experienced across the landscape could promote episodes of adaptive evolution for entire communities (Ackerly, 2003). One of the critical challenges presented by these multivariate problems is that observational studies of species physiology and distribution provide little information about how they will respond to new combinations of conditions that lie outside the current realized environment. In other words, we know very little about the shape of the fundamental niche in regions of climate space that are not currently observed (Jackson & Overpeck, 2000).

Evolution in routine and extreme environments

The second topic of particular interest is the evolutionary consequences of extreme events. What happens when environmental conditions substantially exceed individual acclimation capacities? Presumably, this results in significant negative impacts on individual performance, and Gutschick & BassiRad suggest that extreme events may generate intense episodes of natural selection. Of equal interest is the

converse speculation that most genotypic and phenotypic variation is functionally neutral during ‘normal times’. This neutrality may emerge from truly neutral molecular variation, from optimizing selection on intermediate trait values, from antagonistic effects on different fitness components, or from temporal and spatial variability in the direction of selection in heterogeneous environments. The neutrality of standing variation in a population is not a new idea, as it follows directly from Fisher’s fundamental theorem of the loss of additive variation. The genetic variants that are maintained in a population should have equal fitness under prevailing conditions. Many empirical studies have also grappled with this phenomenon, as traits that are fundamentally important to individual performance may have no detectable effects on fitness in natural populations (e.g. photosynthetic rate, see Ackerly *et al.*, 2000). But what happens in novel environments, or during extreme events? Schmaulhausen (1949) approached this question in terms of the evolution of reaction norms, theorizing that mutations with positive or negative influences on fitness in novel environments may accumulate in a population as long as they are selectively neutral in the current environment. Encounters with novel environments will expose this accumulated variation, and may promote transient or persistent episodes of natural selection (Hoffman & Parson, 1991).

Perspectives

An understanding of the role of extreme events takes on renewed urgency in the face of climate change, anthropogenic land use change, and the global epidemic of biotic invasions. This view of evolutionary responses to novel environments may provide a clue to one of the enigmas of global change research. Despite an enormous research effort from physiology to ecosystem ecology, it remains remarkably difficult to explain the variation in species responses to elevated CO₂ and associated global change factors. The basic biology and life history correlates underlying tolerance of shade, drought and low nutrients are fairly well understood. But species responses to elevated CO₂, alone and in interaction with other factors, are highly variable and few predictive correlates of these responses have been uncovered. Observed trends, such as greater responsiveness in faster-growing species, seem to be more indicative of basic physiological processes than specific evolutionary responses to past selective environments. As CO₂ rises to levels last seen in the Miocene, we may be moving into a portion of the realized environmental space where invisible mutations of unpredictable effect have been accumulating for thousands of generations.

The test of a conceptual advance is its success in provoking new questions and interpreting old results in a fresh light. Gutschick & BassiRad have gathered together a broad array of physiological, ecological and evolutionary phenomena as

facets of the biotic response to extreme events, and provide a timely call for increased study of this challenging topic.

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Key words: global change, climate extremes, realized environment, acclimation, genetic variation.

Taxonomic misidentification in public DNA databases

There is a growing problem of taxonomic misidentification in public DNA databases, and this issue is highlighted by

Bridge *et al.* (pp. 43–48). DNA sequences are becoming the primary currency by which we measure and study microbial biodiversity (Tautz *et al.*, 2003). The sheer volume of sequence data places enormous pressure on public sequence databases (such as GenBank and EMBL), which must curate and annotate an ever-growing catalogue of genomic and environmental sequences. Like a library in which books are sometimes mistakenly assigned a wrong call number, sequence errors inevitably end up in public databases. A significant portion of the data in public databases is known to contain random as well as systematic sequencing errors (Clark & Whittam, 1992; Harris, 2003). The exponential proliferation of environmental sequences (e.g. directly from soil and other environmental clone banks) has also resulted in the proliferation of an important class of data for which voucher specimens are not available. While environmental sequences can provide useful information about microbial diversity (Vandenkoornhuys *et al.*, 2002), their relevance in DNA databases depends on comparison with reference material from voucher-based taxonomic studies.

‘Upwards of 20% of the named sequences in public databases may be misidentified’

Bridge *et al.* retrieved multiple sequences for ribosomal DNA sequences from the EMBL server for three relatively well-studied groups of fungi (*Phoma*, *Amanita* and the *Helotiales*). Using a combination of standard bioinformatics search tools (FASTA, BLAST) as well as phylogenetic analyses of aligned sequences, they identified numerous cases of obvious or apparent mistaken identity in each group of fungi. The problems in each data set are different. In the case of *Amanita*, most problems are attributable to the use of misidentified cultures (presumably from well reputed culture collections). In the case of *Helotiales*, the problem stems from the diversity of investigators who work with these groups, and might also reflect differences in taxonomy between specialists. The most common causes of errors they cite include misidentification or mislabeling of original materials, contamination by other fungi during culture, or other PCR-based errors including chimaeric sequences. Although their study primarily addresses ribosomal DNA sequences (the most common type of data used for molecular systematics), it applies to any genes for which comparative sequence data may be collected. By their estimate, upwards of 20% of the named sequences in public databases may be misidentified in some fungi. This is a

serious problem, which threatens the utility of public sequence databases as archives of biodiversity.

By their inclusivity, public databases sometimes become a home for junk data (like the rest of the internet). Unless curated and annotated, mistakes can proliferate and reduce the ability of correct entries to serve as references for new data. For this reason, Bridge *et al.* recommend that protocols be adopted by public databases similar to those used by taxonomic and culture collections. Like forensic biologists who must adhere to fixed standards for handling of DNA evidence, natural historians who study DNA must also apply appropriate controls to guarantee the identity of strains, collections, and even DNA samples. One solution they propose is the annotation of questionable database sequences by taxonomic experts who work with the public databases.

How serious is the threat of misidentified sequences? As DNA databases grow, the most blatant taxonomic misidentifications are often sorted out by nonspecialists (e.g. a basidiomycete sequence that erroneously groups with ascomycete sequences). The inclusivity of public databases may also be their greatest asset. The prospects for better taxonomic accuracy of databases may not be so bad. In most instances, it is still too hard to tell if a sequence has been misidentified with certainty. For most fungi, taxonomic coverage in public databases is still relatively poor (< 1% of the estimated 1.5 million fungal species are represented in public databases). Although a complete taxonomic scaffolding is not yet in place, programs have recently been established to populate the fungal 'tree of life' with useful sequences (e.g. the Deep Hypha research coordination network supported by the U.S. National Science Foundation, <http://ocid.NACSE.ORG/research/deephyphae/>). By working together, the greater community of systematists can help plug the larger gaping holes that exist in our taxonomic coverage of known fungi, and also help in the discovery of unknown groups (Vandenkoornhuysen *et al.*, 2002). Another solution is for the systematics community to develop special-purpose databases for taxonomic identification, such as the Ribosomal Database Project (<http://rdp.cme.msu.edu>), with tools necessary for accurate sequence identification and analysis. New sequences will always need to be compared against standard reference data sets as well as special aligned sequence data sets for ribosomal DNA-based identification in mycorrhizal fungi (Bruns *et al.*, 1998), yeasts (Kurtzman & Robnett, 1997; Scorzetti *et al.*, 2002), and agarics (Moncalvo *et al.*, 2002).

It will always be the responsibility of users to check the identity of specimens and the integrity of their sequence data. As with all systematics research, responsible vouchering is also essential (Agerer *et al.*, 2000).

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- Key words:** DNA sequences, public sequence databases, GenBank, EMBL, voucher-based taxonomic studies.

Letters

Assessing elevated CO₂ responses using meta-analysis

Körner (Körner, 2003) recently provided a critique of meta-analysis in ecological CO₂ research, specifically focussing on our work (Jablonski *et al.*, 2002). This meta-analysis was the first attempt in many years to provide summary statistics from a large body of literature covering both domesticated (crop) and nondomesticated (wild) plant species' reproductive responses to elevated atmospheric CO₂. Our goal was to calculate the mean CO₂ treatment effect on several measures of reproductive quantity and quality and to explore possible causes for variation in CO₂ effect size across studies. Another result of our work was to document gaps in the literature as related to specific research areas or study species. However, meta-analysis is not an appropriate tool for establishing firm causal relationships among variables – rather, it provides a statistically defensible means for evaluating the degree to which published data obtained from independent sources support specific hypotheses (Gurevitch *et al.*, 2001). As the scientific domain in which meta-analytic tools are applied continues to expand, the statistical basis for these new applications must keep pace (Lajeunesse & Forbes, 2003) and be understood both by meta-analysts and their critics.

One of the surprising results in Jablonski *et al.* (2002) was the relative insensitivity of CO₂ effects on reproduction to interacting environmental stress factors (see Table 1 in Jablonski *et al.* (2002)). The most common stress factors present in our dataset and hence examined closely were high temperature, low nutrients, high ozone, and drought. Of the eight response variables we reported on, only one, fruit number, showed a significant effect attributable to low nutrient stress, and this result was based on only four studies, all conducted with crop plants. More typical was the CO₂ effect on total seed number, in which plants grown with some stress factor in combination with elevated CO₂ were no different in their reproductive output than unstressed plants grown at high CO₂. Whether this insensitivity was a result of real underlying biological causes or was an artifact either of the nature of the published data, or our sampling of it, was not resolvable. However, given this result and that taxonomic and functional group identity had

highly significant effects on the magnitude of the CO₂ response, we had no statistical justification for first stratifying the data based on plant nutritional status. Put another way, our data did not support the hypothesis that interacting stress factors (many of which could affect plant resource status) were important drivers of plant reproductive responses to elevated CO₂. The same was true for annual vs perennial life history (sink strength?) or duration of CO₂ exposure (plant age?).

We share Körner's assessment of the database on plant reproduction under elevated CO₂ as being heavily biased towards crop plants or to annual wild plants grown like crops (i.e. not in their native habitat). Relevant experiments with perennial species (crop or wild) remain both very rare and highly idiosyncratic, rendering them of questionable value in a meta-analysis. The first condition could be corrected with greater levels of funding for long-term elevated CO₂ experiments in natural ecosystems. The second condition unfortunately is a fact of life for those integrating ecological data and is likely to compromise many quantitative research syntheses. Meta-analysts desire replication at the level of the publication. The more similar two independent experiments are to each other in design and execution, the better. Meta-analysis has proven invaluable in the biomedical sciences where many-fold replication of experimental findings are required (and supported) before clinical decisions based on treatment effect size can be made. Ecologists are rewarded for proposing experiments that are different from any previously done, and novelty of results is a prime factor for manuscript acceptance in front-line journals (including this one). This framework for conducting ecological science may need to be rethought as ecologists become increasingly involved in providing policy-relevant data, such as quantitative assessments of the biological consequences of global change, to problems of substantial societal concern.

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Key words: meta-analysis, elevated CO₂, 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

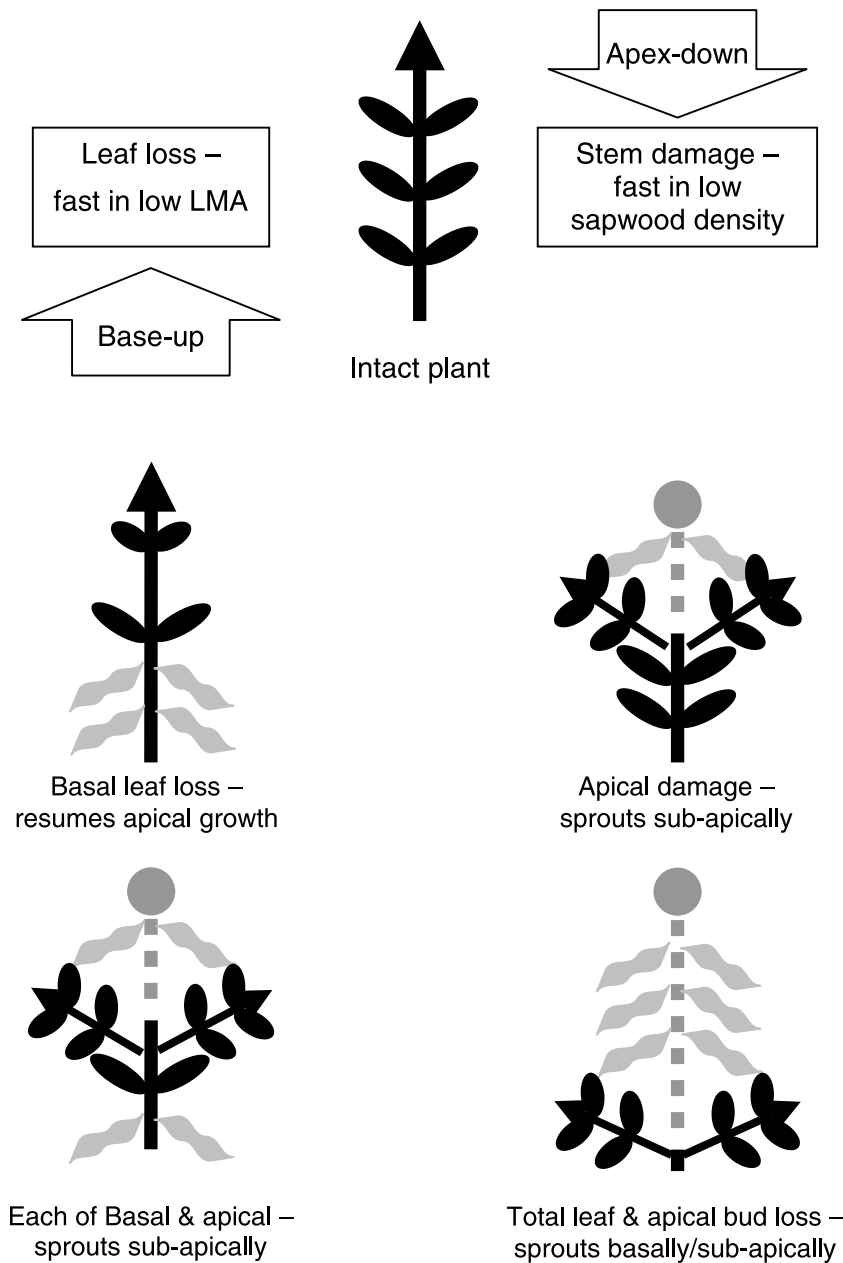


Fig. 1 Conceptual model of drought damage and regrowth patterns. Leaf loss progresses from base to apex, faster in low leaf mass per area (LMA) species. Stem damage progresses from apex to base, faster in low sapwood density species. Depending on species' combination of these traits different patterns 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 ⁻³)	Leaf mass per area (LMA, mg mm ⁻²)	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		1 (8)	0.72	0.140	1.59	0.9 (10)
<i>Einadia nutans</i>	Chenopodiaceae			4	1	7 (12)		0.039		0.4 (11)
<i>Brachyscome ciliaris</i>	Asteraceae			4	1	2 (7)	0.59	0.040	1.22	0.9 (10)
<i>Hakea tephrosperma</i>	Proteaceae				2	9 (11)	0.83	0.430	2.15	1.0 (10)
<i>Casuarina cristata</i>	Casuarinaceae				3	9 (12)	0.65	0.240	3.10	0.5 (10)
<i>Bossiaea walkeri</i>	Fabaceae				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 $\sim 65^{\circ}\text{C}$, 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

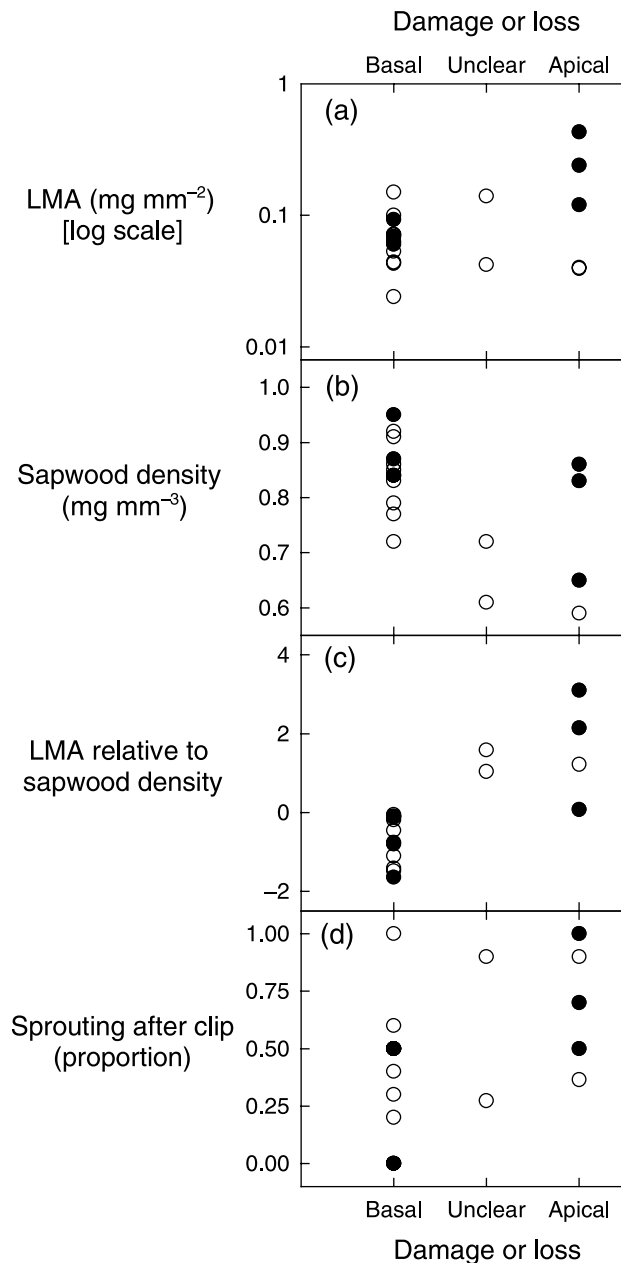


Fig. 2 Trait values and their relation to location of damage or leaf loss due to experimental glasshouse drought for 19 semiarid south-eastern Australian species. Filled symbols are species that only had plants displaying that pattern of loss and regrowth, open symbols are species for which at least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

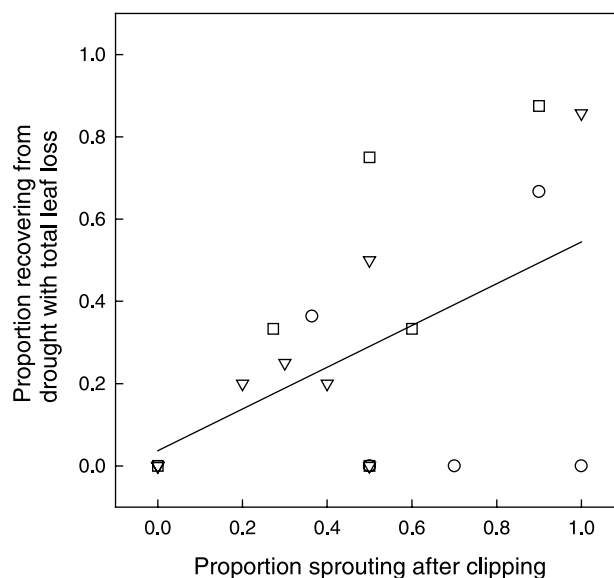


Fig. 3 Proportion of plants that recovered after total leaf loss due to drought compared to proportion sprouting after clipping. Calculated as number displaying recovery with Total leaf loss, divided by the sum of plants recovering with Total leaf loss and dead plants [$T/(T + D)$]. Circles represent 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.

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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

occurring (Turelli *et al.*, 2001) – what we lack is an understanding of the number and types of genetic changes that are required for populations to set off on independent evolutionary trajectories. Similarly, we are only beginning to describe the genetic basis of trait evolution and adaptation through natural selection (Via, 2002). In fact, the genetics of reproductive isolation and of adaptation are overlapping fields of inquiry (Orr, 2001). In many cases reproductive isolation is associated with adaptive phenotypic differences between species (e.g. niche differences), and comparisons of closely related species are often particularly interesting and tractable (e.g. outcrossing vs selfing species, and species with different pollinator syndromes).

Aided by genetic maps, researchers are estimating the genomic distribution, number, and effects of quantitative trait loci (i.e. the genetic architecture) contributing to reproductive isolation in plants (Bradshaw *et al.*, 1998; Kim & Rieseberg, 1999; Fishman *et al.*, 2002; Hodges *et al.*, 2002; Lexer *et al.*, 2003). It is probably premature to make general statements about the genetic architecture of species' boundaries based on these empirical studies, except to note that a small number of quantitative trait loci explain a majority of the phenotypic variation between some species (Bradshaw *et al.*, 1998). This observation is consistent with loci of large effect underlying phenotypic differences between domesticated and artificially selected species, but contrary to the classical view of adaptation proceeding by many genes of small effect (Orr, 1998a).

Further study of the genetic architecture of reproductive isolation and of species' differences in general will yield a greater understanding of the roles of adaptation and genetic drift in shaping long-term evolutionary trajectories. For instance, the accumulation of data on quantitative trait loci has spurred the development of new theories to assess the contribution of selection and genetic drift to macroevolutionary patterns (Orr, 1998b). Using this theory and associated statistical tests, a recent review of empirical studies of plants and animals found that divergent selection is very frequently responsible for phenotypic differences between species (Rieseberg *et al.*, 2002).

Localization of quantitative trait loci is also leading to studies of candidate genes and molecular mechanisms involved in reproductive isolation. Experiments could involve transgenes to validate the role of specific loci in functions that contribute to isolation, as has been performed in animals (Presgraves *et al.*, 2003). Analysis at the level of single genes and molecular mechanisms will more precisely and conclusively describe the genetic architectures of phenotypic traits.

Compared to estimates of the number and size of effect of loci, less attention has been given to the genomic distribution of loci contributing to reproductive isolation. The distribution of loci is of particular relevance to naturally hybridizing taxa, for which the genomic location of factors subject to selection in hybrids will dictate what regions of the genome

will be protected from or will experience introgression (i.e. maintenance of linkage disequilibria). Relevant data from sympatric European oak species were presented during the symposium (Caroline Saintagne, INRA, France). Loci responsible for quantitative differences in leaf morphology between pedunculate and sessile oak (*Quercus robur* and *Q. petraea*) lie within genomic regions that experience the lowest levels of interspecific gene flow at neutral genetic markers.

Beyond their importance to the genetics of speciation, these various approaches to studying genetic architectures complement efforts to describe the genetics of domestication and studies of gene exchange between domesticated or non-native plants and their wild, native relatives (Abbott *et al.*, 2003).

Ecology and natural selection

Participants in the symposium repeatedly drew attention to the importance of ecological traits in speciation and the isolation that ecological divergence may bring about (Schemske, 2000; Schluter, 2001; Via, 2002). While this intuitive perspective is not new, the emphasis is required in part because disproportionate attention has been given to intrinsic, postzygotic isolating mechanisms and, in particular, to the genetic basis of hybrid male sterility in *Drosophila*. There are good reasons to believe that ecological and spatial barriers constitute the bulk of reproductive isolation for many species, with intrinsic postzygotic isolation playing a secondary role (Schemske, 2000; Turelli *et al.*, 2001).

Two studies of the salt tolerance of plants in extreme edaphic conditions are good examples of current research that incorporates ecology into studies of speciation. The history and genetics of ecological differentiation are being studied in *Helianthus paradoxus*, a homoploid hybrid species that may have escaped gene flow from parental species by colonizing an extreme habitat, salt marshes (Lexer *et al.*, 2003). Recombinant hybrid plants (BC2) from an initial cross of the parental species (*H. annuus* and *H. petiolaris*) were transplanted into a salt marsh and quantitative trait loci for ion uptake traits and survivorship were identified. Selection intensities on the survivorship loci were estimated to be of a magnitude sufficient to contribute to the isolation of a hybrid neospecies. Similarly, tolerance of extreme ionic stress plays a role in differentiation between two races of plants that have arisen in parallel within two closely related species of *Lasthenia* (Rajakaruna *et al.*, 2003a). One race is associated with habitats with high soil ion concentrations and the second is restricted to more benign habitats. Differences in habitat preferences are matched by differences in ion uptake rates and tolerances under laboratory conditions, suggesting that races have diverged genetically for critical ecophysiological traits (Rajakaruna *et al.*, 2003b). Because salt tolerant races have apparently arisen in parallel within two very closely related species, this system presents an opportunity

to examine whether repeated evolutionary transitions are achieved in a consistent and possibly predictable manner.

Phylogenetics, hybridization and parallel evolution

Robust phylogenies form a basis for the study of speciation. Along with biogeographic information, they may provide tests for hypotheses about the roles of geography, ecology, and hybridization in the origin of species (Schemske, 2000). Phylogenies also provide a means to estimate diversification rates among different clades (Magallón & Sanderson, 2001) and test hypotheses about the rate of speciation within clades (Hodges, 1997; Wendel & Cronn, 2003).

Some recent phylogenies are challenging our understanding of species boundaries and limits to gene transfer. Allopolyploid cottons are thought to have arisen within the last million years as a result of polyploidization and intercontinental genomic transfer between *Gossypium* species (Old World to New World, Wendel & Cronn, 2003). While this finding is puzzling, it is perhaps less so than recent evidence of transfer of genes between monocot and dicot species (Bergthorsson *et al.*, 2003).

For studies of speciation, one of the particularly significant outcomes of phylogenetic analysis is the discovery of taxa that have originated repeatedly and independently (Soltis & Soltis, 1993; Schwarzbach & Rieseberg, 2002; Rajakaruna *et al.*, 2003a). As noted above, the parallel evolution of independent lineages provides evolutionary biologists with replicated natural experiments for tests of hypotheses about the origin of species (Schluter, 2001).

Conclusions

Given the amount of attention given to species concepts in the literature, some might be surprised to learn that none of the symposium presentations dealt with species concepts, except perhaps to lament their proliferation. Various reasons might exist for this omission, but it is clear that plant speciation will continue to progress significantly without a universally accepted species concept, and that students of plant speciation are content with the 'biological species concept' for many applications.

In recent years novel applications of various research methodologies and tools have produced long-sought empirical data to test hypotheses about the origin of species. For instance, the increasing resolution and broad applicability of genetic tools allow the construction of comparative genomic maps, and studies of genome and molecular evolution within the context of speciation; we can now search for molecular evidence that a species had a single or multiple origins; and we can use genetic data to study the basis of species-specific ecological traits. We will continue to accumulate information about speciation within individual taxonomic groups and

certain ecological settings, but generalizations and a comprehensive understanding of speciation will require complementary studies of a wide diversity of plant taxa. Current empirical studies of the genetics, ecology, physiology and evolutionary history of plants hold great promise for the future.

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Key words: speciation, hybridization, natural selection, polyploidy, introgression.

Books

Attraction, predation and marriages of convenience

Plant–animal interactions: An evolutionary approach

Ed. by C. M. Herrera & O. Pellmyr. 313 pages. Oxford UK: Blackwell Science Publishing, 2002. £35.00 s/b. ISBN 0-632-05267-8

Plant–animal interactions: an evolutionary approach is remarkable in that it successfully encompasses the effects of plant–animal interactions on both individuals and the wider ecosystem, and how such interactions were moulded by evolution. In exploring this, a comprehensive range of subject matter is used to explore the ancient, modern and usually complex relationships between plants and animals. The high degree of specialisation involved in these associations is demonstrated by examples of biological control methodologies, some of which have been unsuccessful because of an unexpected third party interaction.

The book opens with a diagrammatic representation of the major events in evolution, which is both detailed and

clear. This effectively places palaeobiology in context. We are shown that plant characteristics are central to many aspects of natural history, especially trophic levels and food webs. Plants determine which herbivores are present, and this in turn determines which carnivores can survive in that habitat. The concepts of phylogeny and coevolution are introduced and clearly illustrated with examples from around the world. Floral biology and pollination strategies are possibly the easiest systems to accept as models for coevolution and speciation – or is it just luck that some orchids produce both a floral mimic and the exact chemical used as a sexual attractant by its pollinator wasps? We are shown how the smell, colour and axis of symmetry of flowers interact to attract the desired pollinator – and here at least size really does matter! Particularly intriguing is the idea that flowers could even be involved in sound transmission by acting as acoustic guides for bats. Although much of floral biology is descriptive, the book looks to the future with a description of the potential of molecular genetics both to dissect out interactions (which may involve multiple species) and to test hypotheses relating to the basis of attraction.

Plant–animal interactions usually fall into one of three categories, protection, shelter or food, and it is the latter which is covered in most depth. Examinations of the fossil record and dinosaur stomach contents have revealed the origins of invertebrate and vertebrate herbivory. Fossil information

indicates that food is the main reason for evolutionary change and that adaptations can be beneficial for considerable periods of evolutionary time. The origin of vertebrate herbivory is believed to be due largely to the evolution of specialised mouthparts which could dictate and drive what or how to eat. This is elegantly demonstrated by the variation in bat mouthparts according to food source. The importance of mouthpart evolution is corroborated by the statistics (just under one fifth of all terrestrial plant biomass is removed by herbivores) but it is explained that herbivore type is just as important in determining the final habitat makeup. Vertebrate herbivores have the potential to remove plant parts whole and so could have a greater impact on plant populations than invertebrate herbivores. In fact, grasslands can be considered to be an extreme example of this type of plant–animal interaction, as they are believed to have originated as a result of vertebrate herbivores developing specialised grinding teeth.

With the onset of herbivory comes the need for the plants to protect themselves. As discussed early in the book, the fossil record reveals the ‘arms race’ between plants and animals to be an ancient phenomenon. Secondary metabolites are cru-

cial to this interaction and have multiple roles in defence against pathogens/predators, protection of fruit until the seeds are ready for dispersal and conversely as attractants to pollinators or seed dispersal agents. This raises an interesting conundrum – how much effort should a plant invest in attraction vs defence for a given reward in fitness? The discussion of herbivore load and fitness of host and herbivore is touched on in several places. In the context of biochemical defences it is a pity that wounding responses in plants are not discussed as fully as other topics. A summary table of secondary compounds and potential signalling molecules would be well placed.

Trophic levels are inefficient in transfer of energy and so mutualisms have evolved to maximise efficiency of food use. For example, recruitment of microorganisms in the gut to aid with the digestion of lignin and cellulose is seen both in insects and in larger herbivores such as cattle and sheep with their specialised rumen. A comparison of digestive systems is presented from the simplest (human) to most complex (ruminant). This reflects the physiological limitations of food selection although the basis of choice is far more complex and the effects often surprising. Examples from both leaf and fruit feeders prove that digestive refinements together with habitat-based limitations contrive to push the boundaries of sustainable body size in relation to diet selection.

Considerations of food quality justifiably include nutrients and antinutrients. There is some very good background on the nutritive value of plants but what makes this account novel is that the variability of forage quality is discussed. It is clear that addressing forage quality on the basis of chemical composition alone is inadequate if an understanding of the relationship between those chemicals and the herbivore is lacking. It is pointed out that although, generally, nitrogen is the main determinant of food selection, this does depend on (a) herbivore species and (b) form of nitrogen used as a storage compound in a particular plant species. Seasonal effects make some plants unpalatable or even toxic at certain times, or there may be a reliance on feeding stimuli of which the researcher is unaware. This goes some way to answering the question of why food selection on the basis of apparent quality (chemical composition) may be inconsistent.

Plant–animal interactions can have far reaching consequences for the environment and so any attempts to gain a more complete understanding of such relationships are timely. The way that the size and type of seed determines the interactions with dispersal agents and hence the distribution radius (Janzen-Cornell model) is covered in some detail in more than one place in this book. Herbivory may also involve predation of seeds (granivory). The specialised reward body (elaiosome) attached to the seed in ant-dispersed seeds and the positive selection pressure exerted on seed production by herbivory are just two of the examples given to demonstrate strategies that plants use in either preventing or



Credit: *Sitona lineatus* on *Pisum sativum*. Courtesy of Serge Carré, INRA, France.

accepting seed predation. Perhaps less obvious is the conclusion that granivory can actually promote species diversity via imperfect hoarding practices or disturbance of the seedbank, and this can be effected by classes of animals from rodents to ants. There is also a detailed explanation as to how herbivory can affect nutrient cycling, which then has a direct effect on the timing and availability of nutrients to plants and so affects the succession of colonising plant species. The ensuing species composition will in turn affect animal diversity via availability of housing and the establishment of new food webs. It is argued that in temperate grasslands plant–animal interactions not only maintain species diversity but also help to prevent tree invasion and maintain the traditional look of much of our countryside. These are important clues to best practice while western agriculture is attempting to become more environmentally benign.

This book encourages us all to consider complementary methodology in tackling complex biological problems. At the beginning of the book the case is put for the pivotal role of flight in the colonisation of land by both plants and animals. This should encourage us all to look beyond the boundaries of our own research area. Only through multi-disciplinary biology do the complex relationships involved in species diversity of both plants and animals become unravelled. Maintaining species diversity is important because it promotes interactions which can have unusual follow-on effects. For example, the ability of some plants to accumulate toxic heavy metals may initially have been a defence against herbivores, but is now being exploited by man in reclamation of contaminated soils, which may eventually become diverse habitats. Many valid areas for future research are suggested: interspecific hybridisation, control of poly-

ploidy, the marine ecosystem, the cause of patchiness in herbivory. Intrinsic to these is the recognition of the importance of long-term field ecology. These are challenging questions that need to be answered by careful observation and construction of detailed models. Furthermore, it is acknowledged that microbiology is currently under-represented in research into mutualisms even though bacteria and fungi play a key role in many interdependent systems (e.g. the complex interaction of plants, ants, their fungal gardens and the bacteria of the genus *Streptomyces* which protects against a pathogen of the fungus).

In general the text of this book is lively and generously illustrated. The authors are not afraid to challenge conventional assumptions, which are sometimes found wanting in the light of recent evidence. Possibly the only notable omission is a general glossary section (although there is some explanation of specialist terminology provided in Chapter 2, which would make some parts of the text more accessible to the reader lacking a background in evolutionary biology). The book is intended for use by undergraduates, but the detail of some chapters and relevance of some of the arguments may be more suited to those actively involved in research. In summary, I would recommend this book to anyone with an interest in natural history as well as students and researchers in the ecological and biological sciences.

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