
Leaf Litter Flammability in Some Semi-Arid Australian Woodlands

Author(s): F. R. Scarff and M. Westoby

Source: *Functional Ecology*, Vol. 20, No. 5 (Oct., 2006), pp. 745-752

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/3806581>

Accessed: 05-12-2015 13:31 UTC

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.org/stable/3806581?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Wiley and British Ecological Society are collaborating with JSTOR to digitize, preserve and extend access to *Functional Ecology*.

<http://www.jstor.org>

Leaf litter flammability in some semi-arid Australian woodlands

F. R. SCARFF† and M. WESTOBY

Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

Summary

1. Wildfires strongly influence the biotic composition and carbon cycle of many ecosystems. Plant species provide the fuel for wildfires, but vary widely in their flammability. This study aimed to determine what plant characteristics control leaf litter flammability and to clarify how they are related to other functional traits.
2. Litter flammability varied across 14 tree species occurring in a mosaic of five floristic associations.
3. Differences in heat-release rate between species were driven by leaf size, from small-leaved conifers, casuarinas and acacias to large-leaved eucalypts and *Brachychiton*.
4. Large leaves created an open litter-bed structure that burned more rapidly because it was better ventilated. The results on heat-release rate were partitioned according to fundamental principles for the transport of oxygen through a packed fuel bed, showing that heat-release rate scaled linearly with estimated gas-flow rates, as expected in ventilation-controlled fires.
5. Species that were able to resprout after fire had litter that burned more intensely and was more likely to sustain a spreading fire than litter from obligate seeders, and were correspondingly larger-leaved.
6. Many fire-prone wooded ecosystems in the region consist of large-leaved resprouting tree species co-occurring with small-leaved obligate seeders.

Key-words: flammability, leaf size, wildfire

Functional Ecology (2006) **20**, 745–752
doi: 10.1111/j.1365-2435.2006.01174.x

Introduction

A major aim of plant ecology is to understand how the characteristics of species affect their distribution and their influence on ecosystem-level properties. A range of functional traits have been identified that determine species' environmental tolerances and effects on ecosystem processes. These include leaf construction and nitrogen content influencing decomposition rates (Pérez-Harguindeguy *et al.* 2000) and carbon fixation rates (Shipley *et al.* 2005); wood anatomy influencing tolerance to drought and freeze–thaw cycles (Hacke & Sperry 2001); and regeneration and seed dispersal traits influencing sensitivity to different fire regimes (Noble & Gitay 1996).

In many ecosystems, wildfires shape plant and animal species composition, as well as processes such as carbon and nitrogen cycling (Bond & Midgely 1995; De Bano, Neary & Ffolliot 1998; Bradstock, Williams & Gill 2002). Plant species provide the fuel for wildfires, and they vary considerably in flammability (Philpot 1970;

van Wilgen, Higgins & Bellstedt 1990; Hughes, Vitousek & Tunison 1991; Fonda 2001). Identifying the functional traits that determine flammability would (1) improve our understanding of why some plants burn better than others, and (2) clarify how flammability is related to other functional traits that influence where species occur and how they affect ecosystem properties.

Species differ not only in flammability, but also in their contribution to fuel continuity and to total fuel load (Hill 1982; Bradstock *et al.* 1992). So fire regimes are substantially modified by the floristic composition of vegetation (D'Antonio & Vitousek 1992; Brooks *et al.* 2004). If the fire regime promoted by a species differs from the regime that most favours the species, then a negative feedback process may be expected, which would reduce the population's contribution to total fuels and hence its influence on local fire regimes. Conversely, where the flammability of a species coincides with its optimum disturbance regime, a positive feedback between population growth and fire regime can be anticipated (Bond & Midgely 1995; Schwillk & Kerr 2002).

Working in semi-arid woodlands in south-eastern Australia, this study aimed to identify the plant traits that affect flammability, and how they covary with other traits that influence species' impacts and occurrence. It

Functional Ecology

ISSN 0269-8463

Volume 20 Number 5

October 2006

Editors:
C. Fox
K. Thompson
J. Cresswell
F. Messina



British Ecological Society

focused on surface fuels because of their importance for fire transmission in this vegetation (Bradstock & Cohn 2002a; Hogkinson 2002). The canopies of adjacent trees tend to be separated so that, even though the tree crowns may be enveloped in flame, fire must travel along the ground if it is to spread. The surface fuels consist of islands of litter beneath tree canopies, with grasses or shrubs in between. Grass and shrub cover is thus a determining factor in fire spread through these landscapes (Bradstock & Cohn 2002a; Hogkinson 2002). But wildfires are often patchy, so the fate of individual plants depends not only on landscape-scale fire transmission, but also on how a spreading fire behaves in the fuels in the immediate vicinity of the plant. Under the general heading of flammability, it is useful to distinguish between the intensity with which these fuels burn (affecting the degree of tissue damage to the live plant) and the capacity of the fuels to propagate a spreading flame (affecting the fire frequency encountered in the immediate vicinity of the individual). Measures were chosen to capture these different aspects of leaf litter flammability.

One possible cause of differences in combustion rate is that some litter types form beds that are better ventilated, allowing a faster supply of oxygen to the fire. In poorly ventilated fuel beds, the burning rate increases linearly with the rate of delivery of oxygen (Drysdale 1998, pp. 325–32). Conversely, in well ventilated fires other factors become limiting, such as the surface area available for combustion and the burning properties of the material (Drysdale 1998). The effect of bed ventilation on the burning rate of leaf litter was investigated based on a fluid mechanical model of the movement of gases through a packed bed of particles. Overall, the aims were to discover (1) which leaf traits determine litter flammability in this system; (2) the physical mechanism underlying these effects; (3) whether cross-species differences in flammability occur mainly within or between floristic associations; and (4) whether flammability traits and fire-response traits covary.

Materials and methods

SAMPLE COLLECTION AND LEAF TRAIT MEASUREMENTS

Fallen leaves were collected from 14 tree species in fire-prone semi-arid woodlands at Yathong Nature Reserve, south-eastern Australia (32°35' S, 145°24' E). At Yathong there is a mosaic of floristic associations, each consisting of a mixture of obligate seeders and facultative resprouters. Trees in these associations are mainly *Acacia*, *Callitris* and *Eucalyptus*, including a multistemmed eucalypt form known as mallee. Litter was collected from five floristic associations: mallee woodland (*Brachychiton populneus* (Schott & Endl.) R.Br., *Callitris verrucosa* (A.Cunn. ex Endl.) F.Muell., *Eucalyptus dumosa* A.Cunn. ex J.Oxley, *Eucalyptus gracilis* F.Muell., *Eucalyptus socialis* F.Muell. ex Miq.); eucalypt woodland (*Eucalyptus intertexta* R.T.Baker, *Eucalyptus populnea* F.Muell.);

rocky hillsides (*Acacia aneura* F.Muell. ex Benth., *Acacia doratoxylon* A.Cunn., *Callitris glaucophylla* Joy Thomps. & L.A.S. Johnson); belah woodland [*Alectryon oleifolius* (Desf.) S.T.Reynolds, *Casuarina cristata* Miq., *Geijera parviflora* Lindl.]; and yarran flats (*Acacia homalophylla* A.Cunn. ex Benth.). The species selected for study represent the structural dominants in each of these floristic associations, and contribute most of the leaf litter. The vegetation was last burned 10 years previously, except for the mallee woodland (20 years previously) and the *C. verrucosa* collection site, also within mallee woodland (>47 years previously).

To ensure purity of the samples, leaves were collected from litter islands beneath isolated trees or monotypic stands, well separated from trees of any other species with similar leaf appearance. Collections were then sorted one leaf at a time to remove litter from other species, twigs and animal matter. Leaves in all stages of decomposition were included, neglecting only small fragments for which positive species identification was impossible. Leaf litter was collected from at least four individuals of each species and stored at 40 °C and 20–40% RH. Fresh leaves were also collected and stored in sealed plastic bags before leaf-area measurements (six leaves from 10 individuals). The mean size of the partly decomposed leaf litter particles was measured as one-sided surface area using a 2400 dpi scanner and image analysis software ($n > 70$). For terete tissues such as cladodes, one-sided area was calculated as scanned area $\times \pi/2$. In the conifer *Callitris*, 'leaf' area was taken as half the surface area of stem internodes covered with leaf scales. Particle thickness (or diameter in terete tissues) was measured with a micrometer (± 0.01 mm, $n = 10$). Following oven-drying at 60 °C, leaves were weighed to calculate tissue density and specific leaf area (± 0.001 g, $n = 10$). The packing ratio of the litter beds (defined as the proportion of bed volume occupied by leaves) was determined from the height of litter samples in containers of known volume.

FLAMMABILITY MEASUREMENTS

The intensity with which fuels burn determines the damage to nearby live tissues. To measure rates of heat release from the burning litter, 4.0-g samples were placed in a basket of expanded steel mesh (base, 150 \times 60 mm; mesh holes, 0.4 \times 0.15 mm). The samples were ignited from below by a stream of hot convected air from a bunsen burner, which also provided the pilot flame for ignition. On ignition, the burner was removed and transfer of gas through the basket floor was blocked with a sheet of fibre-cement. A device for measuring heat flux from the flame was placed 20 mm from the burning litter sample at the centre of the long basket edge. This device consisted of an 8-cm² sheet of copper plate of known mass, with a chromel–alumel thermocouple connected to the rear face. The face directed towards the fire was coated in blackboard paint to maximize absorption of incident radiation (after King

1961). Temperature changes in the copper plate were logged every 3 s and subsequently used to calculate rates of heat flux into the plate. These calculations were adjusted for simultaneous heat loss from the plate to the ambient environment, quantified by heating the plate, removing the heat source and measuring the rate of temperature drop. This cooling rate was a linear function of the elevation of the plate temperature above ambient. The experiment finished when the entire sample was consumed or the fire self-extinguished. For each sample, the maximum heat flux sustained over a 15-s interval and the extent of sample consumption were recorded. The order of experimental burns followed a semi-randomized block design to minimize confounding with ambient temperature and humidity.

The capacity of a species to sustain the experimental fires through to complete combustion was correlated with its rate of heat release (see Fig. 2), so results are reported mainly by reference to heat release. *Callitris* litter always self-extinguished. Subsequent attempts to establish a self-sustaining fire in *Callitris* litter all failed, even at ambient temperatures as high as 130 °C and using a gas torch and accelerants to assist ignition.

DATA ANALYSIS

The effect of bed ventilation on fire intensity was investigated based on the following theoretical treatment. When a gas diffuses through a barrier, the flow rate depends on the pressure gradient and on how easily the barrier permits gaseous diffusion. This ease of transmission per unit distance is described here as the conductivity, following the convention used in CO₂ transmission through stomata, and water movement through xylem (Farquhar & Sharkey 1982; Reid *et al.* 2005).

$$Q/A = k\Delta p/l \quad (\text{eqn } 1)$$

where Q = volumetric flow rate through a cross-sectional area A , k = conductivity, and Δp = pressure drop across a diffusion distance, l .

In the case of oxygen permeating a fuel bed, the pressure drop reflects the difference between the ambient concentration of oxygen in air and the low concentration maintained at the burning surface. Differences in the rate of oxygen flow through fuel beds then depend on their conductivity and the length of the diffusion path. The conductivity of a bed of solid particles to a viscous fluid can be estimated using the Carman–Kozeny equation (Kay & Nedderman 1974). The version used here is for a packed bed of particles of uniform size and shape:

$$k = [D_s^2(1 - \beta)^3]/(180\mu\lambda^2\beta^2) \quad (\text{eqn } 2)$$

where k = conductivity, D = particle size expressed as diameter of an equivalent-volume sphere, β = packing ratio, μ = viscosity of oxygen (assumed constant at 4.43×10^{-4} Pa m s⁻¹), and λ = ratio of particle surface area to that of an equivalent-volume sphere.

In well ventilated fires, the burning rate is independent of the rate of gas delivery, hence also the conductivity. However, in ventilation-controlled fires, the burning rate increases linearly with the rate of gas flow (Drysdales 1998, pp. 325–32). To determine whether litter fires were ventilation-controlled, the observed rate of heat release was regressed against the estimated conductivity of the fuel beds.

In equation 2 the term D_s^2/λ^2 , representing the size and shape of the particles in the bed, is proportional to (leaf thickness)² for both laminar and terete leaves. Therefore it was expected that the conductivity would respond to (leaf thickness)² and to the packing ratio as $\beta^2/(1 - \beta)^3$. Leaf thickness and packing data were transformed based on this expected relationship, to explore how conductivity responds to observed variation in these traits.

SUPPLEMENTARY STUDIES

Packing, leaf size, specific leaf area and leaf thickness were all correlated. To explore the direct effect on packing ratio, leaf size was manipulated in a *E. intertexta* bed. Leaves were cut in half and the packing ratio remeasured through a 16-fold range in leaf size. These data were used to construct a regression line predicting packing on the basis of leaf size. Predicted packing ratios for the 14 study species were compared with observed values using linear regression, to determine whether packing ratios varied mainly in response to leaf size or some other trait.

Preliminary trials indicated that leaf size was a strong predictor of flammability, and tended to covary with regeneration strategy. To determine how general this correlation might be, data on leaf size and regeneration strategy were collated for dominant trees in semi-arid and dry sclerophyll woodlands in New South Wales, Australia (New South Wales National Parks & Wildlife Service 2004; National Herbarium of New South Wales 2005). Tree species were collated from 37 woodland types described by Keith (2004). Species were categorized as resprouters or as obligate seeders after fire (Buist, Yates & Ladd 2000; New South Wales National Parks & Wildlife Service 2004).

Results

The highest rates of heat release were observed in fuel beds composed of large leaves with open packing (Fig. 1). Specific leaf area, leaf tissue density and surface area-to-volume ratio were not strongly correlated with the rate of heat release (Fig. 1). Ventilation of the fuel beds, estimated as conductivity from the Carman–Kozeny equation (see Data analysis), was an excellent predictor of fire intensity. Fuel beds that were highly conductive to permeating gases had the highest rates of heat output (Fig. 2a, $r^2 = 0.726$, zero slope rejected at $P = 0.0001$). Burning rate was expected to increase linearly with oxygen flow rate in poorly ventilated situations, saturating to a maximum value in well ventilated beds. Our results supported this expectation, showing strong linearity in

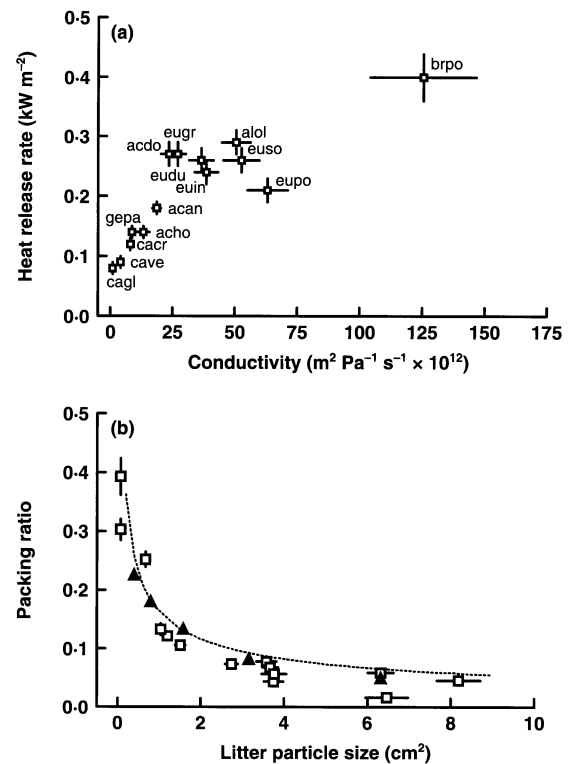
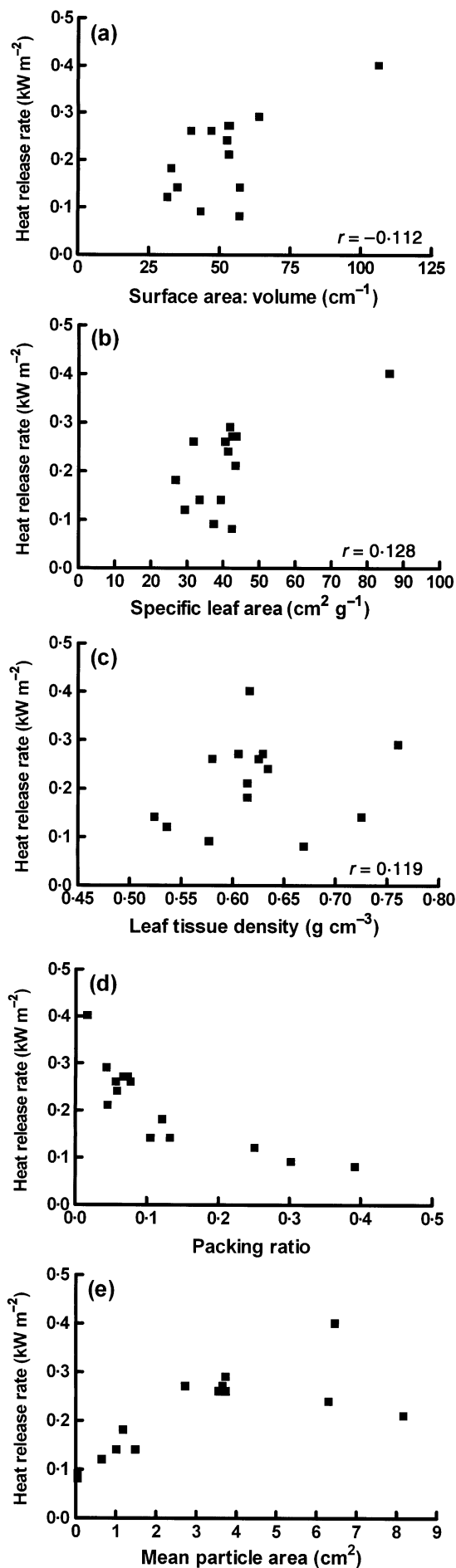


Fig. 2. (a) Relationship between heat flux from fire and estimated conductivity of fuel bed. Points are means \pm SE. acan, *Acacia aneura*; acdo, *Acacia doratoxylon*; acro, *Acacia homalophylla*; alol, *Alectryon oleifolius*; brpo, *Brachychiton populneus*; cagl, *Callitris glaucophylla*; cave, *Callitris verrucosa*; cacr, *Casuarina cristata*; eudu, *Eucalyptus dumosa*; eugr, *Eucalyptus gracilis*; euin, *Eucalyptus intertexta*; eupo, *Eucalyptus populnea*; euso, *Eucalyptus socialis*; gepa, *Geijera parviflora*. (b) Relationship between packing ratio and leaf size. \square , Observed variation in study species; \blacktriangle , manipulated *E. intertexta* litter, the line is a power-curve fit to the *E. intertexta* data.

the least conductive beds, with some slight evidence of saturation towards the right of the graph (Fig. 2a).

Conductivity to gases, as defined in the Carman–Kozeny equation, depends on two fuel properties. These are packing ratio, transformed as $(1 - \beta^3)/\beta^2$ and (leaf thickness)². In practice, bed conductivity varied mainly in response to transformed fuel packing ($r^2 = 0.793$, $P < 0.001$), as particle thickness was not highly variable. Transformed thickness ranged 30-fold, whereas transformed packing ranged 920-fold.

It was difficult to distinguish which leaf traits determined how tightly fuel beds were packed, as packing, leaf size, specific leaf area and leaf thickness all covaried. By manipulating leaf size within *E. intertexta*, the effect on packing was determined independently from variation in the other traits (Fig. 2b), and fitted to a power curve (packing = $-0.163 \text{ size}^{-0.4949}$, $r^2 = 0.98$). This relationship was then used to predict packing ratio in the 14 study

Fig. 1. Relationship between heat-release rate and leaf functional traits, with partial correlation coefficients. Correlation coefficients not shown for (d,e) because the relationship is nonlinear; see text.

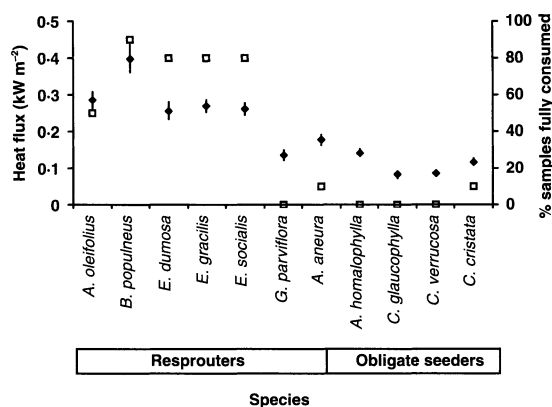


Fig. 3. Relationship between litter flammability and species-regeneration strategy. Closed symbols, heat flux from fire (mean \pm SE); open symbols, number of replicates in which the sample was fully consumed by flame before self-extinguishing ($n = 10$). Species are classified as obligate seeders or resprouters; *Acacia aneura* exhibits a varied regeneration strategy.

species, based on the observed size of litter particles. Correlation of predicted packing ratios with observed packing indicated a close fit ($r^2 = 0.93$, $P < 0.001$).

Thus leaf size largely controlled the rate of heat release from burning fuel beds, by creating an open-bed structure with a high conductivity to permeating gases. The effect of bed ventilation overwhelmed any effects of chemical composition on fire intensity. The sample included leaves of three eucalypt species which, when fresh, contain $\approx 1\%$ oil by fresh weight (*E. dumosa*, *E. gracilis* and *E. populnea*) (Boland, Brophy & House 1991), but these were not obvious outliers in the conductivity–heat output relationship (Fig. 1a). Similarly, high-lignin species (*A. doratoxylon*, *B. populneus*, *C. glaucophylla*) and low-lignin types (*E. dumosa*, *E. socialis* and *G. parviflora*) fell broadly on the same line (lignin contents from W. Cornwell, Stanford University, unpublished data).

Information on regeneration strategy was available for 11 of the 14 study species. Resprouters tended to be more flammable than obligate seeders (Fig. 3), and correspondingly larger-leaved. The tendency for resprouting species to have larger leaves (and hypothetically more flammable litter) appears widespread across many of the fire-prone wooded ecosystems of New South Wales. Data for comparing leaf size by regeneration strategy were available for 20 of the 37 semi-arid and dry sclerophyllous woodlands identified by Keith (2004). In 14 of these, all resprouting species had larger leaves than all co-occurring obligate seeders. The reverse situation, where obligate seeders had consistently larger leaves than co-occurring resprouters, was not observed. This tendency of larger-leaved species to be resprouters was strongly connected to phylogeny. Eucalypts were larger-leaved and usually resprouters, while among smaller-leaved genera *Callitris* and *Casuarina* were always obligate seeders, and *Acacia* and *Allocasuarina* were often obligate seeders (Fig. 4). It remains to be seen, therefore, whether the tendency of larger-leaved species to be resprouters generalizes to other floras.

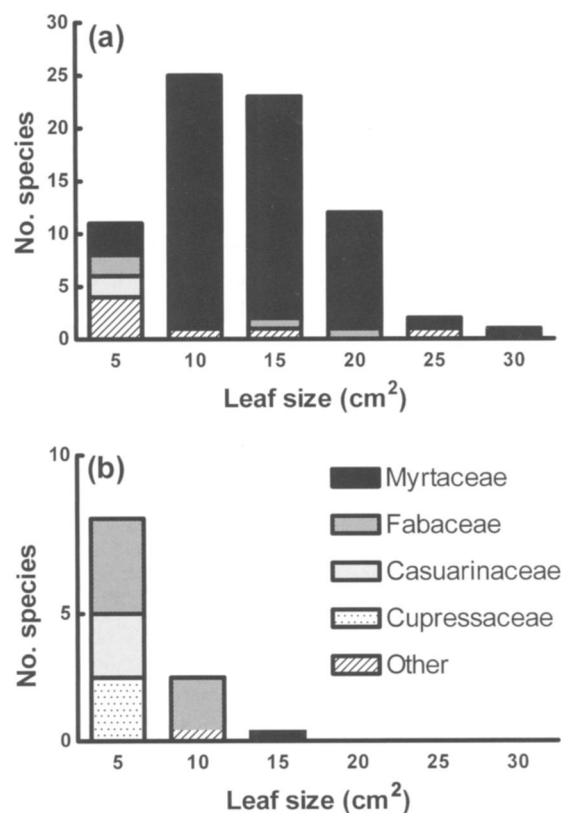


Fig. 4. Leaf-size distribution in dominant tree species of fire-prone communities in New South Wales in (a) resprouters; (b) obligate seeders.

Litter flammability was not a community property. Rather, species with strongly contrasting litter flammability co-occurred within each of mallee (*B. populneus*, *C. verrucosa*), belah woodland (*A. oleifolius*, *C. cristata*) and rocky hillside vegetation (*A. doratoxylon*, *C. glaucophylla*).

Discussion

LEAF SIZE AS A DETERMINANT OF LITTER FLAMMABILITY

Leaf size emerges from the results as the most important trait influencing the intensity and sustainability of litter fires. The importance of fuel packing has long been recognized (Rothermel 1972; Rundel 1978). What is new here is that the effects of leaf size on packing apparently overwhelm chemical factors known to influence flammability, such as oil and lignin content (Vines 1981; Parker & LeVan 1989).

Leaf size affects fire intensity because ventilation is better in more openly packed fuel beds. In well ventilated beds, burning rate is independent of gas-flow rates, and is thought to be limited by the surface area and kinetic properties of the fuel (Drysdale 1998). By contrast, our data fit the pattern expected for ventilation-controlled fires, in which the rate of fuel consumption increases linearly with gas flow. They indicate that ventilation is limiting for dry litter in the leaf size range sampled.

Ventilation may influence fire intensity through two separate mechanisms. When cellulosic fuels burn with a flame, the main heat-releasing reaction is between oxygen and pyrolysates, gases evolved from the solid surface by thermal decomposition. When oxygen delivery is slow, it limits the rate at which pyrolysates can be oxidized (Drysdales 1998). In a parallel reaction pathway, gaseous decomposition products can, instead, react with the solid phase to form char. This competing reaction reduces the supply of pyrolysates for oxidation. The char-forming pathway is promoted by poor ventilation, because gases evolved from the fuel are detained in the vicinity of the solid phase (Antal & Varhegyi 1995). So the observed relationship between bed packing and fire intensity may arise through effects on the supply of both oxygen and pyrolysates to the combustion reaction.

Gill & Moore (1996) also conducted a study of leaf litter flammability, identifying leaf surface area-to-volume ratio, rather than leaf area, as the best predictor for dry material. Our study differed from theirs in how the leaves were presented and in what was measured. They measured time to ignition of a single dry leaf immersed in a furnace heated to 400 °C, across 50 species. This presentation models widely separated canopy leaves suspended above a surface fire. Individually immersed in a hot environment, thin leaves heated through faster and ignited more rapidly (Montgomery & Cheo 1971). Ignition delay time, as measured by Gill & Moore (1996), is an important factor influencing fire spread rates (Atreya 1998). Rate of spread is important for wildfire containment, and models for it attract continuing interest (Dupuy & Larini 1998; Catchpole *et al.* 2002). In the present study we focus instead on the ecological factors bearing on individual plants – whether the flame front reaches an individual (fire sustainability); and the tissue damage caused by exposure to rapidly combusting fuels (fire intensity).

The importance of bed ventilation places litter flammability on a spectrum of plant functional traits correlated with leaf size. Species with small leaves tend to have narrow, frequently branched twigs and dense wood (Westoby & Wright 2003; Pickup, Westoby & Basden 2005). High wood density is associated with strong stems and greater resistance to drought-induced embolism of conducting vessels (Givnish 1995; Hacke *et al.* 2001). Highly branched stems of fine twigs burn more intensely (e.g. chaparral; Rothermel 1972). This structure provides a large reacting surface area per unit volume and efficient heat transfer between closely spaced twigs, without reducing conductivity to the point where ventilation becomes limiting. Hence species with low-flammability litter will tend to have a relatively flammable stem structure.

must affect the behaviour of real wildfires. Some positive field evidence is available for *C. verrucosa*, which produced litter among the least flammable measured in the present study. A wildfire near our study site was patchy enough to leave some *C. verrucosa* individuals undamaged (personal observation). Original foliage was retained, even where the canopies were intermeshed with *Eucalyptus* canopies, which all experienced 100% foliage scorch. This observation is not attributable directly to litter flammability, but indicates the potential effect of flammability differences on the fine-scale behaviour of fires. Regarding the influence of litter, Bradstock & Cohn (2002b) reported limited penetration of a wildfire into a *C. verrucosa* stand, with flame fronts often extinguishing at boundaries between eucalyptus and *Callitris* litter.

The effect of litter flammability on the fitness of individual trees will depend on regeneration strategy. Obligate seeders are killed by 100% scorch; they benefit from longer fire intervals enabling time to reach reproductive maturity. Populations of *C. verrucosa*, for example, would probably be reduced to low densities under a regime of frequent fire (Bradstock & Cohn 2002b). Obligate seeders produced litter with low flammability in the present study. Conversely the facultative resprouters, which are better able to persist in the face of more frequent intense fire, had more flammable litter. Given that leaf size was a strong predictor of heat-release rate, this seems to be a general pattern in fire-prone wooded landscapes in New South Wales, where large-leaved resprouters widely co-occur with smaller-leaved obligate seeders.

This correspondence between regeneration strategy and relative leaf size, whether produced by continuing natural selection or by phylogenetic history, generates the potential for positive feedback between fire regime change and floristic change. Shorter intervals between fires favour resprouters which, in turn, could increase local fire probability. Periods of extreme fire weather, associated with high temperatures and drought, are projected to increase under all plausible climate-change scenarios for southern Australia (Pittock 2003; Pitman, Narisma & McAneney, unpublished). In the semi-arid woodlands it seems likely that a shift in the balance of obligate seeders and more flammable resprouters might result from, and reinforce, externally forced shifts in the fire regime.

Acknowledgements

We are grateful to Tony Hodge (Murdoch University) and Barbara Rice (Macquarie University) for help with field work, and to Dylan Schwilk (US Geological Survey) and an anonymous referee for comments on the manuscript. This work was supported by Australian Research Council funds.

References

- Antal, M.J. & Varhegyi, G. (1995) Cellulose pyrolysis kinetics: the current state of knowledge. *Industrial and Engineering Chemistry Research* **34**, 703–717.

- Atreya, A. (1998) Ignition of fires. *Philosophical Transactions of the Royal Society of London A* **356**, 2787–2813.
- Boland, D.J., Brophy, J.J. & House, A.P.N. (1991) *Eucalyptus Leaf Oils: Use, Chemistry, Distillation and Marketing*. Inkata, Melbourne.
- Bond, W.J. & Midgely, J.J. (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* **73**, 79–85.
- Bradstock, R.A. & Cohn, J.S. (2002a) Fire regimes and biodiversity in semi-arid mallee ecosystems. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent* (eds R.A. Bradstock, J.E. Williams & A.M. Gill), pp. 238–258. Cambridge University Press, Cambridge, UK.
- Bradstock, R.A. & Cohn, J.S. (2002b) Demographic characteristics of mallee pine (*Callitris verrucosa*) in fire-prone mallee communities of central New South Wales. *Australian Journal of Botany* **50**, 653–665.
- Bradstock, R.A., Auld, T.D., Ellis, M.E. & Cohn, J.S. (1992) Soil temperatures during bushfires in semi-arid, mallee shrublands. *Australian Journal of Ecology* **17**, 433–440.
- Bradstock, R.A., Williams, J.E. & Gill, A.M., eds. (2002) *Flammable Australia: The Fire Regimes and Biodiversity of a Continent*. Cambridge University Press, Cambridge, UK.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M. *et al.* (2004) Effects of invasive alien plants on fire regimes. *Bioscience* **54**, 677–688.
- Buist, M., Yates, C.J. & Ladd, P.G. (2000) Ecological characteristics of *Brachychiton populneus* (Sterculiaceae) (kurrajong) in relation to the invasion of urban bushland in south-western Australia. *Austral Ecology* **25**, 487–496.
- Catchpole, W.R., Catchpole, E.A., Tate, A.G., Butler, B. & Rothermel, R.C. (2002) A model for the steady spread of fire through a homogeneous fuel bed. *Forest Fire Research and Wildland Fire Safety* (ed. D.X. Viegas), pp. 1–11. Millpress, Rotterdam.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**, 63–87.
- De Bano, L.F., Neary, D.G. & Ffolliot, P.F. (1998) *Fire's Effects on Ecosystems*. John Wiley & Sons, Brisbane.
- Drysdale, D. (1998) *An Introduction to Fire Dynamics*, 2nd edn. John Wiley & Sons, Brisbane.
- Dupuy, J.L. & Larini, M. (1998) Fire spread through a porous forest fuel bed: a radiative and convective model including fire-induced flow effects. *International Journal of Wildland Fire* **9**, 155–172.
- Farquhar, G.D. & Sharkey, T.D. (1982) Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* **33**, 317–345.
- Fonda, R.W. (2001) Burning characteristics of needles from eight pine species. *Forest Science* **47**, 390–396.
- Gill, A.M. & Moore, P.H.R. (1996) *Ignitability of Leaves of Australian Plants*. CSIRO Division of Plant Industry, Canberra.
- Givnish, T.J. (1995) Plant stems: biomechanical adaptation for energy capture and influence on species distributions. *Plant Stems: Physiology and Functional Morphology* (ed. B.L. Gartner), pp. 3–49. Academic Press, New York.
- Hacke, U.G. & Sperry, J. (2001) Functional and ecological wood anatomy. *Perspectives in Plant Ecology, Evolution and Systematics* **4**, 97–115.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**, 457–461.
- Hill, R.S. (1982) Rainforest fire in western Tasmania. *Australian Journal of Botany* **30**, 583–589.
- Hogkinson, K.C. (2002) Fire regimes. *Acacia wooded landscapes: effects on functional processes and biological diversity. Flammable Australia: The Fire Regimes and Biodiversity of a Continent* (eds R.A. Bradstock, J.E. Williams & A. M. Gill), pp. 259–277. Cambridge University Press, Cambridge, UK.
- Hughes, F., Vitousek, P.M. & Tunison, T. (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* **72**, 743–747.
- Kay, J.M. & Nedderman, R.M. (1974) *An Introduction to Fluid Mechanics and Heat Transfer: With Applications in Chemical and Mechanical Process Engineering*. Cambridge University Press, Cambridge, UK.
- Keith, D.A. (2004) *Ocean Shores to Desert Dunes: The Native Vegetation of New South Wales and the ACT*. Department of Environment and Conservation, Sydney.
- King, A.R. (1961) Compensating radiometer. *British Journal of Applied Physics* **12**, 633–634.
- Montgomery, K.R. & Cheo, P.C. (1971) Effect of leaf thickness on ignitability. *Forest Science* **17**, 475–478.
- National Herbarium of New South Wales (2005) Flora of New South Wales. *PlantNET – The Plant Information Network System of the Botanic Gardens Trust, Sydney*. <http://plantnet.rbgsyd.nsw.gov.au/floraonline.htm>
- New South Wales National Parks & Wildlife Service (2004) *New South Wales Flora Fire Response Database. Guidelines for Ecologically Sustainable Management*. Biodiversity Strategy Priority Action 43. New South Wales National Parks and Wildlife Service, Hurstville, New South Wales.
- Noble, I.R. & Gitay, H. (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science* **7**, 329–336.
- Parker, W.J. & LeVan, S.L. (1989) Kinetic properties of the components of Douglas-fir and the heat of combustion of their volatile pyrolysis products. *Wood and Fiber Science* **21**, 289–305.
- Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M. & Castellanos, A. (2000) Chemistry and toughness predict leaf decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil* **218**, 21–30.
- Philpot, C.W. (1970) Influence of mineral content on the pyrolysis of plant materials. *Forest Science* **16**, 461–471.
- Pickup, M., Westoby, M. & Basden, A. (2005) Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology* **19**, 88–97.
- Pittock, B., ed. (2003) *Climate Change: An Australian Guide to the Science and Potential Impacts*. Australian Greenhouse Office, Canberra.
- Reid, D.E.B., Silins, U., Mendoza, C. & Loeffers, V.J. (2005) A unified nomenclature for quantification and description of water conducting properties of xylem sapwood based on Darcy's law. *Tree Physiology* **25**, 993–1000.
- Rothermel, R.C. (1972) *A Mathematical Model for Predicting Fire Spread in Wildland Fuels*. Research Paper INT-115. US Department of Agriculture Forest Service, Washington, DC, USA.
- Rundel, P.W. (1978) Structural and chemical components of flammability. *Fire Regimes and Ecosystem Properties: Proceedings of the Conference, 11–15 December 1978, Honolulu, Hawaii* (eds H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan & W.E. Reiners), pp. 183–207. US Department of Agriculture Forest Service, Washington, DC, USA.
- Schwilk, D.W. & Kerr, B. (2002) Genetic niche-hiking: an alternative explanation for the evolution of flammability. *Oikos* **99**, 431–442.
- Shipley, B., Vile, D., Garnier, E., Wright, I.J. & Poorter, H. (2005) Functional linkages between leaf traits and net photosynthetic rate: reconciling empirical and mechanistic models. *Functional Ecology* **19**, 602–625.
- Vines, R.G. (1981) Physics and chemistry of rural fires. *Fire*

- and the Australian Biota (eds R.M. Gill, R.H. Groves & I.R. Noble), pp. 129–149. Australian Academy of Science, Canberra.
- Westoby, M. & Wright, I.J. (2003) The leaf-size twig-size spectrum and its relationship to other important spectra of variation among species. *Oecologia* **135**, 621–628.
- van Wilgen, B.W., Higgins, K.B. & Bellstedt, D.U. (1990) The

role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* **78**, 210–222.

Received 12 February 2006; revised 14 June 2006; accepted 16 June 2006

Editor: Ken Thompson