

concept of stratification thermal time allowed the dormancy loss kinetics at different chilling temperatures to be conveniently described on a single thermal time scale. By further characterizing the change in light sensitivity with a second threshold distribution that can shift in response to accumulated stratification thermal time (Fig. 2), the response of the entire seed population to any light level after any stratification temperature and duration might be readily modeled using only a few parameters (Figs 1 and 3). Further, as has been argued previously (Bradford, 1995, 2002; Allen & Meyer, 1998), the ability of these models to closely match actual seed behavior suggests that they have biological significance, rather than merely empirical utility. Understanding seed dormancy and its alleviation by environmental signals is equivalent to understanding the physiological, biochemical and molecular bases of sensitivity distributions and how these are shifted in response to both external and internal signals. By combining quantitative mathematical models that can characterize seed dormancy states with modern genetic and molecular techniques such as quantitative trait locus identification (Alonso-Blanco *et al.*, 2003) and microarray analyses of gene expression responses to environmental signals (Yamauchi *et al.*, 2004), we can envision a path to deciphering how seed populations make life and death decisions about when or whether to germinate.

Kent J. Bradford

Department of Vegetable Crops, One Shields Avenue,
University of California, Davis, CA 95616, USA
(tel +1 530 752 6087; fax +1 530 754 7222;
email kjbradford@ucdavis.edu)

References

- Allen PS. 2003. When and how many? Hydrothermal models and prediction of seed germination. *New Phytologist* 158: 1–9.
- Allen PS, Meyer SE. 1998. Ecological aspects of seed dormancy loss. *Seed Science Research* 8: 183–191.
- Alonso-Blanco C, Bentsink L, Hanhart CJ, Blankestijn-de Vries H, Koornneef M. 2003. Analysis of natural allelic variation at seed dormancy loci of *Arabidopsis thaliana*. *Genetics* 164: 711–729.
- Alvarado V, Bradford KJ. 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant, Cell and Environment* 25: 1061–1069.
- Alvarado V, Bradford KJ. 2005. Hydrothermal time analysis of seed dormancy in true (botanical) potato seeds. *Seed Science Research*. (In press).
- Batla D, Benech-Arnold RL. 2004. A predictive model for dormancy loss in *Polygonum aviculare* L. seeds based on changes in population hydrotime parameters. *Seed Science Research* 14: 277–286.
- Batla D, Benech-Arnold RL. 2005. Changes in the light sensitivity of *Polygonum aviculare* buried seeds in relation to cold-induced dormancy loss: development of a predictive model. *New Phytologist* 165: 445–452.
- Benech-Arnold RL, Sánchez RA, Forcella F, Kruk BC, Ghersa CM. 2000. Environmental control of dormancy in weed seed banks in soil. *Field Crops Research* 67: 105–122.
- Bradford KJ. 1995. Water relations in seed germination. In: Kigel, J; Galili, G, eds. *Seed Development and Germination*. New York, USA: Marcel Dekker, 351–396.
- Bradford KJ. 1996. Population-based models describing seed dormancy behaviour: implications for experimental design and interpretation. In: Lang, GA, ed. *Plant Dormancy: Physiology, Biochemistry, and Molecular Biology*. Wallingford, UK: CABI Publishing, 313–339.
- Bradford KJ. 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science* 50: 248–260.
- Christensen M, Meyer SE, Allen P. 1996. A hydrothermal time model of seed after-ripening in *Bromus tectorum* L. *Seed Science Research* 6: 155–163.
- Finch-Savage WE. 2004. The use of population-based threshold models to describe and predict the effects of seedbed environment on germination and seedling emergence of crops. In: Benech-Arnold, RL, Sánchez, RA, eds. *Handbook of Seed Physiology: Applications to Agriculture*. New York, USA: Haworth Press, 51–96.
- Rowse HR, Finch-Savage WE. 2003. Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub- and supra-optimal temperatures. *New Phytologist* 158: 101–108.
- Steadman KJ, Pritchard HW. 2004. Germination of *Aesculus hippocastanum* seeds following cold-induced dormancy loss can be described in relation to a temperature-dependent reduction in base temperature (T_b) and thermal time. *New Phytologist* 161: 415–425.
- VanDerWoude WJ. 1985. A dimeric mechanism for the action of phytochrome: evidence from photochemical interactions in lettuce seed germination. *Photochemistry and Photobiology* 42: 655–661.
- Yamauchi Y, Ogawa M, Kuwahara S, Hanada A, Kamiya Y, Yamaguchi S. 2004. Activation of gibberellin biosynthesis and response pathways by low temperature during imbibition of *Arabidopsis thaliana* seeds. *Plant Cell* 16: 367–378.

Key words: seed germination, threshold models, *Polygonum aviculare*, dormancy, germination ecology.

Understanding a flammable planet – climate, fire and global vegetation patterns

The extraordinary intellectual achievement of the 19th century German botanist Andreas Schimper was his book *Plant-Geography upon a Physiological Basis* (Schimper, 1903). Through sheer force of imagination and by drawing on numerous written observations from around the world, he described the correspondence between global climate and vegetation zones. Such 19th century global ecological syntheses were superseded in the 20th century because attention was directed to specific questions using the hypothetico-deductive approach. However, growing concern over global environmental change and the advent of powerful space-age and computer technologies has seen the pendulum swing away from narrowly focused analyses back towards global synthesis.

'A world without fire has fundamentally different forest zones than occur on our real, highly flammable planet'

Rather than being based on observation and induction, the 21st century syntheses are powered by models that enable the mechanistic integration of data collected across spatial scales and disciplinary boundaries. The predictions possible are sufficiently accurate to be testable against independent observations and meta-analyses of existing datasets. The paper in this issue by Bond *et al.* (pp. 525–538) is an exemplar of this intellectual moment. They have provided the first evidence that global vegetation patterns are shaped by landscape fire. Their study is based on the disciplined marshalling of relevant field and satellite observations and strategic application of existing mechanistic Dynamic Global Vegetation models (DGVMs) based upon physiological processes. Their approach demonstrates a new way of ecological thinking that provides profound insights into global ecological processes and the evolution of the biosphere.

What would a world without fire be like?

Despite the fact that satellite sensors were not originally designed to map landscape fire, an unexpected spin-off of global remote sensing was the demonstration of the ubiquity of landscape fire on every vegetated continent (Cochrane, 2003; Justice *et al.*, 2003). The effect of landscape fire on global vegetation patterns is implicit in several DGVMs because they include 'fire modules' that introduced frequent disturbances to modelled vegetation patterns and processes. Bond *et al.* (2005) asked a beguilingly simple question – what happens if these fire modules are switched off? They found that a world without fire has fundamentally different forest zones than occur on our real, highly flammable planet. Without fire, the extent of forests with >80% tree cover doubled from 26.9% to 56.4% of the vegetated surface of the Earth. Further, more than half (52.3%) of the current global distribution of C_4 grasslands was transformed to angiosperm-dominated forest. Of the 41% of C_3 grassland that was replaced by forests, 53% were dominated by gymnosperms, 34% by angiosperms and 13% by a mixture of both these taxa. The analysis of Bond *et al.* (2005) was unable to capture postfire secondary successional sequences within their broad vegetation formations. If they had done so, there is no doubt they would have provided even more startling evidence of landscape fire upsetting the vegetation–

climate equilibrium. This would be particularly so for pyrophytic forests such as those dominated by *Eucalyptus* in Australia and *Pinus* in the northern hemisphere.

Producing a global perspective

Landscape fire has not been a central concern in ecology. Indeed, only in the past decade have books been published outlining the general principles of fire ecology (Whelan, 1995; Bond & van Wilgen, 1996); most knowledge has been regionally focused. Fire ecologists working in specific flammable biotas, such as tropical savannas, mediterranean shrublands and pyrophytic forests, have long appreciated that landscape fire decouples the tight interrelationship between vegetation and climate: the achievement of Bond *et al.* (2005) has been to unite these disparate findings into a single global perspective.

A common inference from regional landscape-scale studies has been that the juxtaposition of patches of forests within a highly flammable matrix is the work of recurrent fires (Fig. 1). Bond *et al.* (2005) argue that such patterns reflect the evolutionary divergence of fire-adapted and fire-tolerant taxa, a process that has occurred independently on all vegetated continents. Evidence for this evolutionary dichotomisation is largely circumstantial, based mainly on field correlation and fire exclusion. The recent study by Fensham *et al.* (2003) is a notable exception. They demonstrated that recurrent fires caused the differential survival of evergreen tree species characteristic of fire-prone savannas compared with evergreen tree species from 'rainforests' on fire-protected sites (Fig. 2). However, the underlying mechanism that causes this differential response remains unexplained.

Surviving fire

There are very few examples that demonstrate the evolution of specific features that enable plants to survive fire. Burrows (2002) showed that epicormic buds were situated on the inside rather than the outside of the cambium in some south-east Australian eucalypts and related taxa. Burrows (2002) interpreted this unique anatomical arrangement as an adaptation to recover vegetatively following fire damage. Research by Prior *et al.* (2003, 2004) has pointed to whole-plant differences between fire-tolerant and fire-sensitive taxa. Eucalypts that dominate vast tracts of fire-prone savanna were found to have photosynthetically less efficient leaves and slower stem growth rates than rainforest tree species that are restricted to small fire-protected sites (Fig. 1). Such whole-plant differences associated with fire tolerance may account for some of the variation between climate parameters and leaf functional attributes documented by Wright *et al.* (2004). The physiological basis for fire tolerance, particularly whole-tree carbon allocation, is a fertile area for research.

Whereas some recent studies have provided some micro-evolutionary insights into plant strategies to survive fire (e.g.



Fig. 1 Savanna fire burning around a topographically fire-protected patch of rainforest. Such a pattern of 'islands' of fire-sensitive vegetation in a 'sea' of fire-tolerant vegetation is evidence that landscape burning disturbs the tight interrelationship between vegetation type and climate. The juxtaposition of floras with contrasting fire tolerances is also interpreted as representing the evolutionary dichotomisation driven by landscape burning. However, there are few hard data about physiological and morphological bases of fire tolerance or how these traits evolved. (Photographer: David Hancock).

Schwilk & Ackerly, 2001), the deeper question of the convergent evolution of fire tolerance between continental floras remains open. Interrogation of the fossil record to determine when flammable vegetation evolved is stymied by the absence of unambiguous morphological features to survive fire. An alternative approach to advance the question of the evolution of flammable floras may be sought by using molecular phylogenies to trace the evolution of unambiguously fire-adaptive traits such as transposed epicormic bud strands (Burrows, 2002).

Past climates and the impact of people

Palaeoecology has proved that landscape fire occurred for millions of years before the advent of fire-wielding hominids. Bond *et al.* (2005) suggest falling CO₂ levels may have stimulated the development of fire-prone C₄ grassland that, in turn, greatly increased the frequency of landscape fire. Keeley and Rundel (2003) argue that the development of monsoon climates may be as an important driver as low atmospheric concentrations of CO₂. This is because the dry

seasons characteristic of monsoon climates are concluded by intense convective storm activity that produce high densities of lightning strikes. The integration of global lightning activity (Fig. 3) in DGVMs would provide far more realistic probability distributions of ignitions than the unrealistic assumption that ignition is not limiting. It would also be instructive to discover the degree of congruence between predicted 'hot spots' of natural fire activity and the diversity of fire adapted biotas. Such an analysis may help advance the timing of the evolution of flammable biotas on Earth and to gauge the evolutionary effect of anthropogenic burning.

Although it is accepted that indigenous people have moulded landscapes through the use of fire, understanding the extent of this impact is difficult given uncertainty about the background rate of fire activity from lightning. For example, in North American forests it is widely regarded that the impact of Native American burning was negligible because stand-replacing fires are under the control of long-term drought cycles (e.g. Grissino-Mayer *et al.*, 2004). Conversely, it is widely assumed that Aboriginal landscape burning caused a continental-wide transformation of the Australian

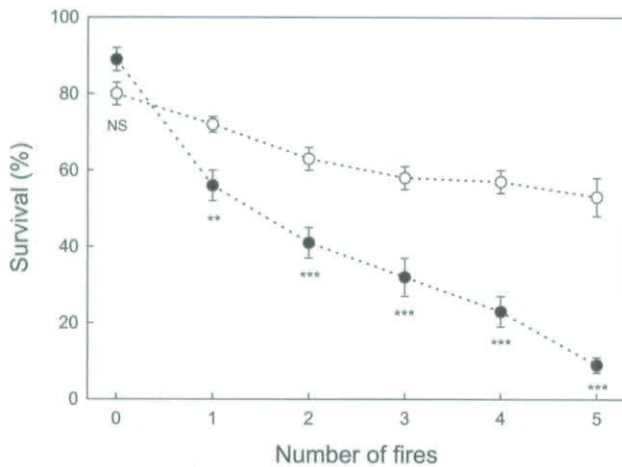


Fig. 2 Declining mean percentage (\pm SE) of the survival of resprouting species in response to five successive fires in a previously fire-protected savanna fragment in north-east Queensland. Closed circles: rainforest species; open circles: savanna species. The physiological and morphological base of the differential survival between rain forest and savanna species to recurrent fire remains to be elucidated. Significance of Mann–Whitney u -tests are where: NS, $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$. (Modified from Fensham *et al.* (2003) with additional data from R. J. Fensham, unpublished).

flora and fauna (Bowman, 1998; Miller *et al.*, 1999). Following the same logic as Bond *et al.* (2005), a comparison of actual global vegetation patterns with those produced under lightning ignitions alone would help resolve the effect of

anthropogenic ignitions, both historically and prehistorically, on changing global vegetation patterns (Fig. 3). The positive feedback between smoke plumes and cloud-to-ground lightning strikes (Lyons *et al.*, 1998), however, may confound a simple causal relationship between the apparent concordance of the spatial distribution of current observations of high lightning activity and fire-tolerant floras.

There can be no escaping the increasing global impact of contemporary anthropogenic landscape burning. The increased spatial scale of landscape burning in fire-prone environments reflects failed attempts to totally suppress fires (e.g. Grissino-Mayer *et al.*, 2004) or the breakdown of skilful indigenous fire management (e.g. Bowman *et al.*, 2004). Fire is being used indiscriminately to clear tropical rain forests. An ensemble of positive feedbacks greatly increases the risk of subsequent fires above the extremely low background rate (Cochrane *et al.*, 1999; Cochrane, 2003). Recurrent burning can therefore trigger a landscape-level transformation of tropical rainforests into flammable scrub and savanna. The transformation of tropical rain forest by fire provides insights into the evolution and spread of flammable floras worldwide.

Perspectives

Clearly, much remains to be done to bring fire to the same footing as climate variables as a factor driving biogeographic patterns and biogeochemical processes. Discovering the

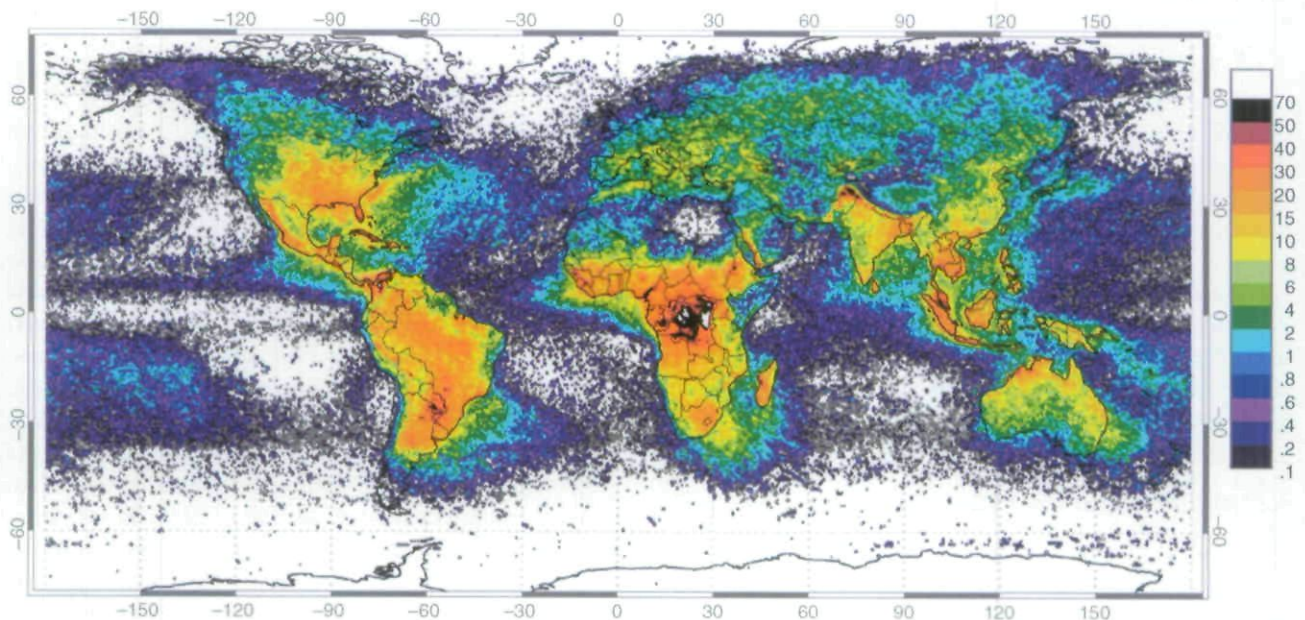


Fig. 3 Global lightning activity (number of flashes per km² per year). These data include both cloud-to-cloud and cloud-to-ground strikes. There is a general concordance between high lightning activity in seasonally dry climates and those areas identified by Bond *et al.* (2005) as susceptible to vegetation change when fire is 'switched off' in Dynamic Global Vegetation Models. Further, there appears to be association between high lightning activity and regions with fire-adapted floras such as the Florida Peninsula, California coast, southern Africa and northern Australia. The v1.0 gridded satellite lightning data were produced by the NASA LIS/OTD Science Team (Principal Investigator, Dr H. J. Christian, NASA/Marshall Space Flight Center) and are available from the Global Hydrology Resource Center (<http://ghrc.msfc.nasa.gov>).

causes of the evolution of flammable vegetation is of great importance in understanding and managing landscape fire, particularly given the accelerating rate of global environmental change. Of prime interest are the effects of climatic variation, atmospheric CO₂ concentrations and prehistoric anthropogenic fire use relative to the background rate of lightning ignitions. Bond *et al.* (2005) provide a vital jolt in developing such global perspective and evolutionary thinking about landscape fire.

David Bowman

Key Centre for Tropical Wildlife Management,
Charles Darwin University, Darwin NT 0909, Australia
(tel +61 8 89467762; fax +61 8 89467088;
email david.bowman@cdu.edu.au)

References

- Bond WJ, van Wilgen BW. 1996. *Fire and Plants*. London, UK: Chapman & Hall.
- Bond WJ, Woodward FI, Midgley GF. 2004. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–538.
- Bowman DMJS. 1998. The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* 140: 385–410.
- Bowman DMJS, Walsh A, Prior LD. 2004. Landscape analysis of Aboriginal fire management in Central Arnhem Land, north Australia. *Journal of Biogeography* 31: 207–223.
- Burrows GE. 2002. Epicormic strand structure in *Angophora*, *Eucalyptus*, and *Lophostemon* (Myrtaceae) – implications for fire resistance and recovery. *New Phytologist* 153: 111–131.
- Cochrane MA. 2003. Fire science for rainforests. *Nature* 421: 913–919.
- Cochrane MA, Alencar A, Schulze MD, Souza CM, Nepstad DC, Lefebvre P, Davidson EA. 1999. Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests. *Science* 284: 1832–1835.
- Fensham RJ, Fairfax RJ, Butler DW, Bowman DMJS. 2003. Effects of fire and drought in a tropical eucalypt savanna colonized by rain forests. *Journal of Biogeography* 30: 1405–1414.
- Grissino-Mayer HD, Romme WH, Floyd ML, Hanna DD. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85: 1708–1724.
- Justice CO, Smith R, Gill AM, Csizsar I. 2003. A review of current space-based fire monitoring in Australia and the GOF/GOLD program for international coordination. *International Journal of Wildland Fire* 12: 247–258.
- Keeley JE, Rundel PW. 2003. Evolution of CAM and C₄ carbon-concentrating mechanisms. *International Journal of Plant Sciences* 164: 555–577.
- Lyons WA, Nelson TE, Williams ER, Cramer JA, Turner TR. 1998. Enhanced positive cloud-to-ground lightning in thunderstorms ingesting smoke from fires. *Science* 282: 77–80.
- Miller GH, Magee JW, Johnson BJ, Fogel ML, Spooner NA, McCulloch MT, Ayliffe LK. 1999. Pleistocene extinction of *Genyornis newtoni*: Human impact on the Australian megafauna. *Science* 283: 205–208.
- Prior LD, Eamus D, Bowman DMJS. 2003. Leaf attributes in the seasonally dry tropics – a comparison of four habitats in northern Australia. *Functional Ecology* 17: 504–515.
- Prior LD, Eamus D, Bowman DMJS. 2004. Tree growth rates in north Australian savanna habitats: seasonal patterns and correlations with leaf attributes. *Australian Journal of Botany* 52: 303–314.
- Schimper AFW. 1903. *Plant-Geography Upon a Physiological Basis*. Oxford, UK: Clarendon Press.
- Schwilk DW, Ackerly DD. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94: 326–336.
- Whelan RJ. 1995. *The Ecology of Fire*. Cambridge, UK: Cambridge University Press.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas E, Villar R. 2004. The world-wide leaf economics spectrum. *Nature* 428: 821–827.

Key words: biogeography, fire ecology, fire tolerance, evolution, global ecology, global vegetation patterns.

Are liverworts imitating mycorrhizas?

Among the similarities between the liverworts and vascular plants (Tracheophyta; Fig. 1), the mycorrhizal symbiosis is perhaps the least expected. Vascular plants associate intimately with soil fungi: a limited colonization of roots by the fungus builds a dual organ, the mycorrhiza, that allows nutrient exchanges. The fungus exploits plant photosynthates and provides mineral resources for its host. However, nonvascular plants, such as liverworts, also form various associations with fungi, imitating the mycorrhizas: Russell & Bulman report on new advances in our understanding of this symbiosis on pp. 567–579 in this issue.

Background

Liverworts (6000–8000 species) belong to the (presumably) paraphyletic Bryophyta (Fig. 1) and consist of a reduced sporophyte growing on a free-living gametophyte. Although some debate still exists (Goffinet, 2000; Nishiyama *et al.*, 2004), most phylogenies place liverworts as the most basal extant land plants (Dombrowska & Qiu, 2004; Groth-Malonek *et al.*, 2004). Liverworts are classically divided into two subclades (Fig. 1 and Table 1) whose monophyly is now questioned (He-Nygren *et al.*, 2004). Jungermanniopsida mostly have small shoots with leafy expansions, but some show a simple thalloid organization; Marchantiopsida are thalloid, and some have a complex structure, including a lower storage parenchyma, a green aerenchyma with stomata-like pores and sometimes a hydrophobic cuticle. In addition, some Jungermanniales have subterranean axes bearing rhizoids, with positive gravitropism reminiscent of roots (Duckett *et al.*, 1991). Among the similarities between liverworts and tracheophytes, the mycorrhizal symbiosis is certainly the least expected one.

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.