Editorial

Modelling and theory

Plant science and biology in general is progressing through a new data-rich era. From molecular biology to global-scale ecology, large teams are making observations and databases that describe one or more components of activity at the chosen scale of investigation. In the 19th century, Henri Poincaré made a comment on science that is equally relevant today:

'Science is facts. Just as houses are made of stones, so science is made of facts. But a pile of stones is not a house and a collection of facts is not necessarily science.'

Moving from large data sets to understanding requires theory, and theory often requires models to test understanding. Two papers in this issue (Ainsworth & Long, pp. 351–372; Bond *et al.*, pp. 525–538), dealing with increases in atmospheric CO_2 and world vegetation patterns, complete this full cycle, while the seed serves as a fitting biological contrast in the work of Battla & Benech-Arnold (pp. 445–452), highlighting the extremely diverse application of modelling approaches.

Ainsworth & Long bring together data from 12 large-scale Free-Air CO_2 Enrichment (FACE) experiments, and 120 publications, to identify the most likely impacts of future atmospheric increases in CO_2 on plants in the closest possible artificial creation of the natural environment. This Tansley review sits on top of a mass of research spawned from the general theory that increasing CO_2 concentrations stimulate photosynthesis. A feature of this mass of research is the practicality of enriching CO_2 concentration around the leaf, plant or plants. At its simplest, the question is addressed from squeezing a part of a leaf in a tiny cuvette, then there have been many observations on potted plants in greenhouses to the most expensive but most naturalistic approach of FACE. Read the review to see which plant responses are robust, and those which are not, in spite of the imposed practical constraints.

Bond *et al.* flesh out comments raised in a previous article (Lusk & Bellingham, 2004) that 25% of the Earth's vegetation is fire-maintained. Such a global view results from applying a vegetation model, based on process understanding and not simple correlations, with natural fires turned on and off. The large impact shows the almost invidious way in which the grass super biome is slowly changing world vegetation. Here, theory is tested against observations at the largest scale possible for terrestrial ecology. This approach is elaborated on in detail also in the accompanying commentary by David Bowman on pp. 341–345.

Theory and modelling approaches are integral to the research in diverse areas of plant science published in *New Phytologist*. The Battla & Benech-Arnold paper is one of a series from scientists interested in understanding the process of seed germination, as discussed by Bradford in a commentary on pp. 338–341, and other areas covered span a range from biochemistry (Stal, 2003; Stephens *et al.*, 2003) and physiology (Vesk & Westoby, 2003; Wynn, 2003; Barbour & Whitehead, 2004) through to development (Tooke & Battey, 2003) and back to plant responses to increases in atmospheric CO_2 (Pendall *et al.*, 2004).

The journal's commitment to all major areas of plant science is now further enhanced in the area of theory and modelling by the appointment of our most recent editor, David Ackerly. David's interests lie in identifying functional characteristics of species and then applying theory of ecological and evolutionary processes to understand how these key functional characteristics have emerged (Ackerly, 2003; Knight & Ackerly, 2003; Ackerly, 2004a). One application of this research is that the theory that has been established can then address the potential impacts on vegetation structure and dynamics of future environmental changes. The particular vegetation of focus is the Californian chaparral. The ever likely possibility of fire raises again the question proposed by Bond *et al.* (2005) of what the community would be like in the absence of fire. This question parallels another of David's research interests on historical precedence in this vegetation type. Research suggests that the current chaparral, with its Mediterranean climate, was assembled from floristic elements that already possessed many of the traits that confer contemporary success, even before the advent of the Mediterranean climate (Ackerly, 2004b). In such a situation a previous theory of *in situ* convergent evolution seems unlikely, even though, like many unsuccessful theories, it appears very attractive.

Call for papers

Papers highlighted here are freely available on our website at http://www.newphytologist.org – also, you will now find specific guidelines for the presentation of these types of research in our Author Guidelines.

Ongoing projects serve to highlight the commitment of *New Phytologist* to mathematical modelling and theoretical approaches across the four sections of the journal – such as in the application of modelling to understanding the evolution of phenotypic plasticity (discussed in the 'eco-devo' feature forthcoming in April) and the use of three-dimensional modelling to probe structure–function relationships in plants, using computer simulations (structure–function modelling feature forthcoming in June). Both these issues will be available as free content for three-month periods in 2005.

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Commentary

Threshold models applied to seed germination ecology

Seed dormancy is a complex phenomenon by which seeds schedule their germination to coincide with favorable periods for seedling establishment. Dormant seeds do not complete germination even though environmental conditions (e.g. water, temperature) would normally be conducive to it. Once dormant seeds have received required signals from the environment, which are specific to each species, dormancy is alleviated and germination can proceed. The alleviation of dormancy is often regulated by environmental factors such as temperature and light that can inform the seed about its location in the soil, whether it is shaded by other plants, the season of the year and other information relevant to its 'decision' as to whether to germinate at a given time (Benech-Arnold *et al.*, 2000). The work of Batlla & Benech-Arnold on dormancy of *Polygonum aviculare* seeds (see pp. 445–452 in this issue) illustrates how multiple environmental cues can interact to affect the germination potential of a seed population.

'The concept of a distribution of threshold sensitivities among seeds in a population has resulted in a remarkably robust yet simple mathematical model'

Polygonum aviculare and threshold modelling

Batlla & Benech-Arnold show that dormant seeds of *Polygonum aviculare* are unable to germinate in either light or dark, but when imbibed and held at chilling temperatures, the seeds become responsive to red light through the action of phytochrome. The sensitivity of the seeds to light is increased by exposure to a chilling temperature ('stratification'), as is known to occur in various species (e.g. lettuce; VanDerWoude, 1985). Further, Batlla & Benech-Arnold showed that this change in light sensitivity occurs in proportion to the accumulation of 'stratification thermal time', or the difference between the maximum effective temperature (17°C in this case) and the storage temperature (< 17°C) multiplied by the duration of chilling; the lower the temperature below the threshold, the more rapid the increase in light sensitivity (i.e. loss of dormancy). In related work, Batlla & Benech-Arnold (2004) showed that chilling also resulted in a decrease in the threshold water potential at which seeds of the same species could complete germination, and that this decrease also occurred in proportion to the accumulation of stratification thermal time.

These studies contribute to a growing body of evidence that threshold models are useful for describing and quantifying the responses of seeds to diverse conditions, including temperature, water, light, afterripening, chilling and other dormancy-breaking factors (reviewed in Bradford, 1995, 2002; Allen, 2003; Finch-Savage, 2004). Threshold models are based on the concept that the magnitude or speed of a biological response is proportional to the difference between the level of a signal input and the threshold sensitivity for that input. Thus, the response of a given seed in terms of when and whether it completes germination is determined by its sensitivity threshold in relation to the current signal input from the environment – the greater the signal level above the threshold, the more rapid the response. In addition, populations of seeds, particularly those of weedy or native plants, tend to vary widely in the depth of dormancy or the extent of dormancy-breaking conditions that are required to allow germination. Such population variation extends the viable duration of seed banks in soil and spreads the risk that germination will occur in an unfavorable environment with subsequent death of the seedlings. The concept of a distribution of threshold sensitivities among

seeds in a population has resulted in a remarkably robust yet simple mathematical model that can account for many aspects of seed dormancy and germination behavior (Bradford, 1996, 2002; Rowse & Finch-Savage, 2003; Finch-Savage, 2004).

Quantifying changing sensitivity

An underappreciated aspect of this threshold model concept is that rather than identifying static parameters of a seed population, the model can quantify the changes in sensitivity that occur as seeds enter or leave dormancy. As noted above, Batlla & Benech-Arnold have identified changes in light sensitivity and water potential thresholds due to chilling in *P. aviculare*, and Allen and coworkers showed that changes in water potential thresholds were associated with the loss of dormancy in *Bromus tectorum* seeds during dry afterripening (Christensen *et al.*, 1996). Similar results were found for true potato (*Solanum tuberosum*) seeds in response to afterripening and dormancy-breaking chemicals (Alvarado & Bradford, 2005). Loss of dormancy in *Aesculus hippocastanum* seeds was associated with a lowering of the minimum temperature for germination during stratification (Steadman & Pritchard, 2004). Alvarado & Bradford (2002) and Rowse & Finch-Savage (2003) demonstrated that the reduction in germination that occurs between the optimum and the maximum germination temperatures is a consequence of an increase in the water potential threshold for germination as temperature increases. Thus, shifts in the median sensitivity of a seed population to environmental factors, along with the variation among seeds in their individual sensitivities, can account for a wide array of seed germination and dormancy phenotypes.

Population responses to light

This integrative aspect of population-based threshold models can be illustrated by further examining data presented by Batlla & Benech-Arnold (2005). The responses of germination to light intensity as a function of accumulated stratification thermal time from their fig. 3 are reproduced here (Fig. 1, symbols). The light intensity is quantified as the ratio of the far-red-absorbing form of phytochrome to total phytochrome (Pfr/P). They fit a trilineal model to these data that describes an initial unresponsive period, a linear increase in sensitivity to light and then a maximum response for a given Pfr/P ratio (see fig. 3 of Batlla & Benech-Arnold, 2005). The extension of the population-based threshold concept to these data provides an alternative modeling approach. Assume that there is a range of sensitivities to light (i.e. of threshold Pfr/P ratios required for germination) within the seed population, illustrated here by a normal frequency distribution (Fig. 2). Without chilling, all of the seeds require very high (unattainable) Pfr/P ratios, so that the seeds are
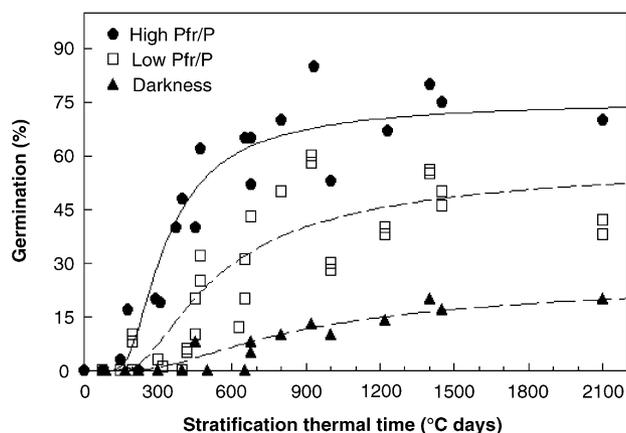
Fig. 1 Germination of *Polygonum aviculare* seeds after different periods of chilling (expressed on a stratification thermal time scale) and at light levels that result in different ratios of the far-red-absorbing (Pfr) form of phytochrome relative to total phytochrome (P) (from Batlla & Benech-Arnold, pp. 445–452). The symbols are the experimental data, and the curves are predicted based upon the population distributions and shifting light requirement thresholds in response to chilling.
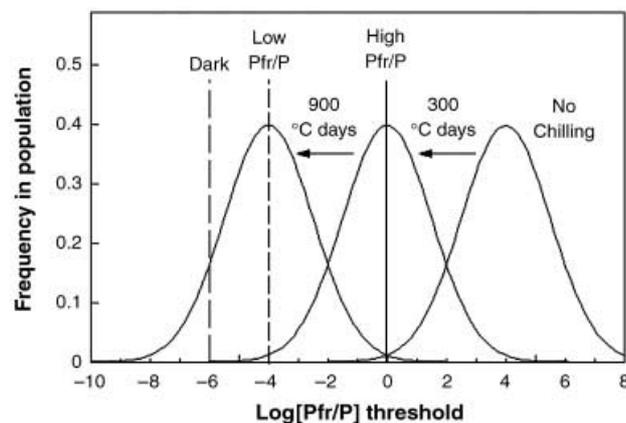
Fig. 2 Theoretical threshold distributions of the sensitivity of the seed population to the Pfr/P ratio. The sensitivity to light is shown as a normal frequency distribution. Initially, the sensitivity to light is low (i.e. a very high (unattainable) Pfr/P ratio would be required to stimulate germination). With the accumulation of chilling, the sensitivity distribution shifts toward lower Pfr/P ratios (i.e. the seeds become more responsive to light). The vertical lines indicate the approximate Pfr/P ratios that correspond to the different light treatments. The fractions of the sensitivity distributions that are to the left of these lines correspond to the fractions of the seed populations that are able to germinate at those Pfr/P ratios.

insensitive to light. With accumulated thermal chilling time, this sensitivity distribution shifts to lower Pfr/P ratios, such that some seeds can now germinate in the light, and the higher the Pfr/P ratio, the larger the fraction of the population for which the threshold is exceeded and which can therefore germinate. With further chilling, the sensitivity distribution shifts even lower, to the extent that some seeds
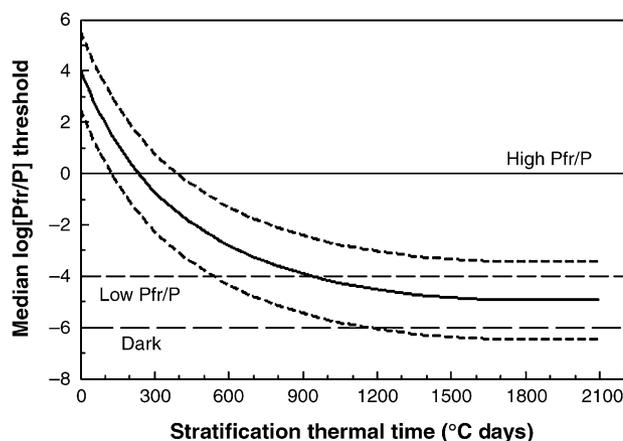
Fig. 3 Theoretical change in sensitivity to Pfr/P ratio as a function of stratification thermal time. As the sensitivity of the seed population to light increases with chilling time, the median threshold shifts to lower Pfr/P ratios (solid curve). The dashed lines indicate one standard deviation around the median to represent the variation among seeds in their thresholds. The horizontal lines correspond to different Pfr/P ratios. The fraction of the seed population that is below these horizontal lines (i.e. has a sensitivity threshold lower than the Pfr/P ratio established by the light conditions) corresponds to the percentage that can germinate at each light level.

can germinate in the dark and the majority of seeds germinate in the light. The distribution of sensitivities among seeds in the population automatically accounts for the sigmoidal shape of the response curves. For any given light level (Pfr/P ratio), as the sensitivity threshold distribution shifts to lower values with thermal chilling time, the sigmoidal increase in germination response is automatically generated (curves in Fig. 1). Thus, to characterize the effects of chilling on the response to light, one needs only a single relationship between the accumulated stratification chilling time and the decrease in median threshold Pfr/P ratio (Fig. 3), along with the variation in light sensitivity within the seed population (the standard deviation of the frequency distribution). The smooth curve shown in Fig. 3 and the log Pfr/P axis of Fig. 2 may not be strictly correct, as germination responses to light are generally biphasic, corresponding to the VLFR and LFR response ranges (e.g. VanDerWoude, 1985). Thus, there may be more of a quantum change in light sensitivity rather than the quantitative change illustrated here. Nonetheless, the general concept of increasing fractions of the seed population becoming more sensitive to light with thermal chilling time can be adapted to different sensitivity scales.

Perspectives

The case illustrated here by the work of Batlla and Benech-Arnold and those reviewed above show that threshold models for different environmental stimuli can be combined for greater explanatory power. In the example here, the

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.

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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 finding 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 southeast 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 CO_2 levels may have stimulated the development of fire-prone C_4 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 CO_2. 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
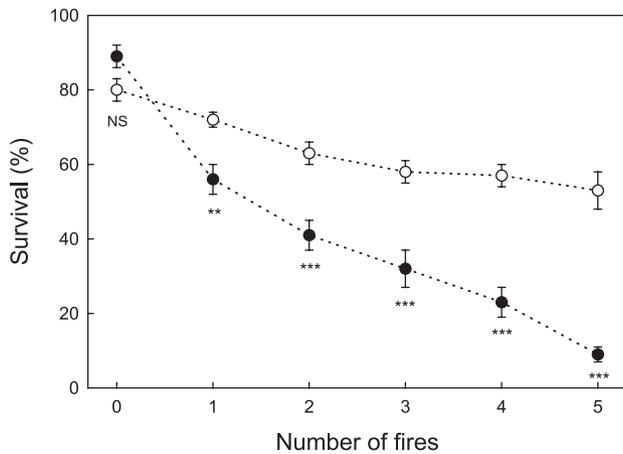
Fig. 2 Declining mean percentage ($\pm$ SE) of the survival of resprouting species in response to five successive fires in a previously fire-protected savanna fragment in north-east Queensland. Closed circles: rainforest species; open circles: savanna species. The physiological and morphological base 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
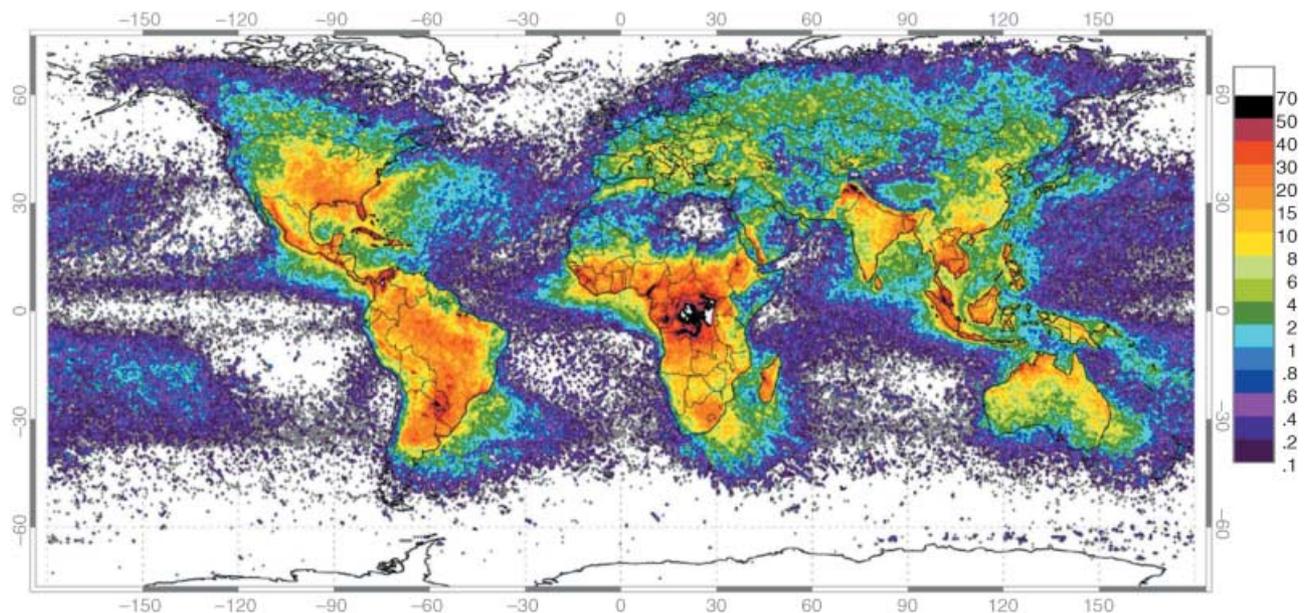
Fig. 3 Global lightning activity (number of flashes per km^2 per year). These data include both cloud-to-cloud and cloud-to-ground strikes. There is a general concordance between high lightning activity in seasonally dry climates and those areas identified by Bond *et al.* (2005) as susceptible to vegetation 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 CO_2 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.

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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 (Dombrovska & 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.
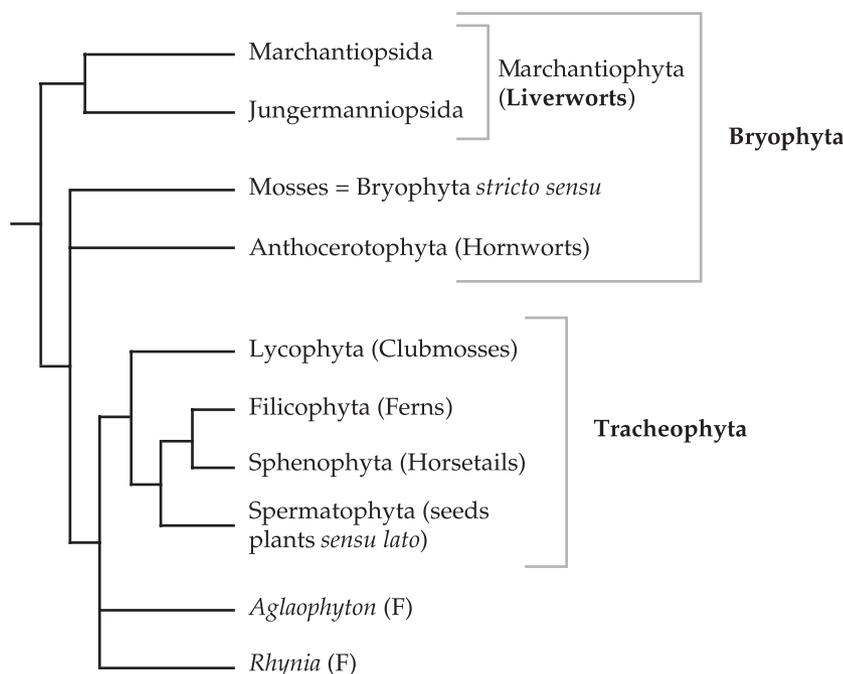
Fig. 1 A phylogeny of land plants (Embryophyta; Dombrovska & Qiu, 2004; Groth-Malonek *et al.*, 2004), including vascular (Tracheophyta) and nonvascular groupings. Note that the basal tree topology is still debated (Goffinet, 2000; Nishiyama *et al.*, 2004). See He-Nygren *et al.* (2004) for a phylogenetic tree of liverworts. (F), fossil groups.

Table 1 Liverworts and their fungal symbioses (note that all species in each order may not necessarily harbour fungi). B, association with basidiomycetes; G, association with glomeromycetes (arbuscular associations); A, rhizoid-associated ascomycetes; M, mycoheterotrophic species, i.e. achlorophyllous but using fungal carbon; –, no fungal association found. Modified from Boullard (1988) and Nebel *et al.* (2004).

Class	Order	Fungal symbioses
Marchantiopsida	Marchantiales	G
	Ricciales	–
	Monocleales	G
	Sphaerocarpales	–
Jungermanniopsida	Lepicoleales	B
	Jungermanniales	B or A
	Porellales	–
	Radulales	–
	Pleuroziales	–
	Haplomitriales	G
	Blasiales	–
	Treubiales	G
	Fossombroniales	G
	Metzgeriales	G, A or B (M in Aneuraceae)

Mycorrhizal relationships vary among tracheophytes: most of them associate with biotrophic fungi, the Glomeromycetes (Schüßler *et al.*, 2001), to form arbuscular mycorrhizas diagnosed by intracellular arbuscular hyphae (Smith & Read, 1997). This association is ancestral in tracheophytes (Selosse & Le Tacon, 1998), because Siluro-Devonian fossils already display arbuscular mycorrhizal (AM) associations, for example *Rhynia* or *Aglaophyton* (Fig. 1; Boullard & Lemoigne, 1971). As vascular plants diversified, so did their interaction with symbiotic fungi. Perhaps as an adaptation to various soil conditions, some taxa switched to asco- and basidiomycetes that form mycorrhizas with extracellular colonization (ectomycorrhizas, for example on temperate trees) or cell penetration by hyphal pelotons (in *Ericaceae* and orchids) (Smith & Read, 1997). At a functional level, carbon flux reversed in some lineages of achlorophyllous plants recovering carbon from their fungi (mycoheterotrophy). All these transitions are highly homoplasic, i.e. occurred several times (Selosse & Le Tacon, 1998).

Liverworts and their fungi

Reports of colonization of liverworts by fungi date back to the 1800s (Stahl, 1949; see Boullard, 1988 for a review). Investigations of ultrastructural features and fungal identities resumed in the 1980s. The colonization is restricted to the vegetative thallus, except for the meristematic apices, and results in a symbiotic structure that is homologous to neither a root nor a cormus. It is therefore best called a 'mycothallus' (Boullard, 1988). Colonization of gametophytes does not in itself distinguish them from tracheophytes, as gametophytes of some Lycophyta and Filicophyta (Fig. 1) also form mycothalli (Read *et al.*, 2000). However, characteristics of true mycorrhizas appear at closer inspection.

Ascomycetes colonize swollen rhizoids of some leafy Jungermannopsida species (Table 1; Duckett *et al.*, 1991; Turnau *et al.*, 1998), sometimes forming ingrowth pegs into surrounding cells (Boullard, 1988; Kottke *et al.*, 2003). Their dense intracellular growth resembles ascomycetous pelotons occurring in ericoid mycorrhizas. Indeed, strains of the ericoid

partner *Hymenoscyphus ericae* were isolated from *Cephaloziella exiliflora* (Chambers *et al.*, 1999), and *H. ericae* strains can colonize liverwort rhizoids *in vitro* (Read *et al.*, 2000). Reciprocally, ascomycetous isolates from rhizoids form ericoid mycorrhizas (Duckett & Read, 1991).

Basidiomycetes colonize leafy and thalloid Jungermannopsida species (Table 1). They form intracellular hyphal pelotons that finally undergo a lysis in the host cells (Ligrone *et al.*, 1993), in a way reminiscent of basidiomycetous hyphae in orchid mycorrhizas. Indeed, the basidiomycetes involved are mycorrhizal on tracheophytes: Aneuraceae species (Metzgeriales) appear to be colonized by ectomycorrhizal *Tulasnella* spp. (Bidartondo *et al.*, 2003; Kottke *et al.*, 2003); symbionts in *Lophozia* spp. and *Calypogeia muelleriana* (Jungermanniales) are related to Sebacinales, an orchid mycorrhizal taxon (Kottke *et al.*, 2003). Notably, the achlorophyllous Aneuraceae *Cryptothallus mirabilis* is mycoheterotrophic and derives carbon from its *Tulasnella* partners (Bidartondo *et al.*, 2003).

Finally, many liverworts form arbuscular associations with Glomeromycetes (Table 1; Boullard, 1988). This is reported from thalloid (Ligrone & Lopes, 1989) as well as leafy species (*Haplomitrium*; Carafa *et al.*, 2003). In several instances, the fungus also has AM 'abilities', as shown by *in situ* hyphal links to arbuscular mycorrhizas (Turnau *et al.*, 1999), or by synthesis of the association with an AM fungus (Read *et al.*, 2000). In this issue, Russell & Bulman report on the first identification of arbuscular associates from *Marchantia foliacea* (Marchantiopsida) based on structural and molecular investigations. Parenchyma cells are colonized by an intracellular arbuscule-forming fungus that was identified by its ribosomal DNA sequences (18S and ITS). All sequences, recovered from 10 populations, clustered within the *Glomus* group A (*sensu* Schüßler *et al.*, 2001). Such specificity is unexpected: although some host preference may exist in the field, as discussed by Russell & Bulman, arbuscular associations are often nonspecific (Smith & Read, 1997). During their investigations, Russell & Bulman found other fungal sequences in *M. foliacea*, which add to the various endophytic fungi already reported from liverworts (Davis *et al.*, 2003; Jumpponen *et al.*, 2003). This opens the Pandora's box of the 'mycothallosphere', i.e. microbes growing within and on liverworts.

Liverworts and early land plant symbioses

What is the evolutionary meaning of the resemblances between liverworts associations and mycorrhizas of tracheophytes, which often involve identical fungal partners? Resemblances between two lineages can arise in the three following ways.
1 Symplesiomorphy: the shared trait (a true homology) is retained from a common ancestor.
2 Convergence: the shared trait arose twice, in separate ancestors (the common ancestor did not have it).

3 Reversion: the common ancestor had the shared trait, and transmitted it to one lineage, whereas the second lineage lost it and then acquired it again.

Convergence between liverworts and tracheophytes most likely accounts for similarities in associations involving asco- and basidiomycetes. Because of the distinct patterns of rhizoid colonization, Duckett *et al.* (1991) already proposed independent origins for ascomycetous associations in liverworts. In addition, even if basal basidiomycetes associate simultaneously with liverworts and tree roots (Nebel *et al.*, 2004), mycorrhizal asco- and basidiomycete taxa may not be sufficiently old (Berbee & Taylor, 2001) to have colonized Ordovician embryophytes. Fungal host shifts may have shaped these similarities; indeed, opportunity of meeting (and creating symbiosis with) a new species is high, because (1) mycorrhizal fungi largely explore soil around their hosts and (2) a high concentration of fungal inoculum is required for horizontal transmission of the symbiosis. Even without such features, host shifts are common in the evolution of fungal symbioses with the termites and ants (Mueller & Gerardo, 2002). A similar scenario was proposed for the sharing of *Xylaria* endophytes by liverworts and angiosperms (Davis *et al.*, 2003).

Because (i) arbuscular associations are ancestral in tracheophytes, (ii) some hornworts (Fig. 1) also have arbuscular mycorrhizas (Boullard, 1988; Schüßler, 2000) and (iii) Glomeromycetes date back to the Ordovician (Berbee & Taylor, 2001), it is commonly assumed that arbuscular associations in liverworts are inherited from the ancestor to all embryophytes. Many losses would have occurred in evolution, for example among liverworts (Table 1) or for the whole mosses (Fig. 1) that have no symbiotic fungi. Because of this, arbuscular liverworts are often viewed as living fossils of early land plant fungal symbioses (e.g. Boullard, 1988; Carafa *et al.*, 2003). This is tempting, but time elapsed since the common ancestor is the same in all lineages and early-branching ones are not necessarily more 'ancestral'. All extant species may mix ancestral and derived characters.

Indeed, some derived (i.e. secondarily evolved) features may occur in arbuscular liverworts. Firstly, specificity with *Glomus* group A observed by Russell & Bulman in *M. foliaceae* is derived, as group A originates late in Glomeromycetes phylogeny (Schüßler *et al.*, 2001) – certainly later than the early land plants. (Specificity is also reported for liverworts associated with basidiomycetes (Nebel *et al.*, 2004) and can be viewed as an evidence of host shifts performed by isolated fungal lineages.) Secondly, different patterns of arbuscular infections exist in liverworts: in *Haplomitrium* and *Treubia*, fungi enter intercellularly, through plant mucilage secretion (Carafa *et al.*, 2003), whereas in Marchantiales, they enter intracellularly, through rhizoids (Ligrone & Lopes, 1989; Read *et al.*, 2000; Russell & Bulman). Infection also differs in hornworts, where rhizoids are free of fungi (Schüßler, 2000). Therefore, extant features of arbuscular mycothalli do not

allow unequivocal reconstitution of an ancestral association, because some (or all) features are derived. For similar reasons, it is even uncertain that all arbuscular associations in liverworts are symplesiomorphic with tracheophytes: at least some could be reversions or convergences.

So, do arbuscular mycothalli tell us anything about early land plants? Although the earliest undoubted fossil liverworts are Upper Devonian, late Silurian early land plant remains have structural affinities with liverworts, both in vegetative parts (Edwards *et al.*, 1995) and spore walls (Wellman *et al.*, 2003). However, note that the very earliest land plants are only known as fossil spores and predate by 60 Myr the Siluro-Devonian arbuscular associations (Boullard & Lemoigne, 1971). If one admits that liverworts are morphological analogues of early land plants, then fungal associations could have occurred, and should be searched for, in early land plants. Extant mycothalli suggest an ancestral predisposition to fungal symbioses in Embryophyta. Indeed, fungal symbioses were claimed to be common during land conquest: the enigmatic and widespread Devonian *Spongiophyton* and *Prototaxites* are likely symbioses between fungi and algae of unknown affinities (Selosse, 2002). Theoretically, fungal hyphae are well preadapted to three-dimensional exploitation of soils; similarly, algae, and possibly early land plants, are well preadapted to fluid exploitation (i.e. capture of light and atmospheric CO_2). An early land plant–fungus symbiosis would thus be adapted to terrestrial life, at the soil–atmosphere interface (Selosse & Le Tacon, 1998). The finding of underground fossil parts of early land plants may verify such predictions – unfortunately, however, soils rarely undergo fossilization, due to erosion.

Future directions

Evolutionary implications of similarities between liverworts and tracheophytes will certainly benefit from advances in Embryophyta phylogeny; recent papers challenge our view, even claiming monophyly for Bryophyta (Nishiyama *et al.*, 2004). More curiously, the physiology of mycothalli remains a mystery. Except in the very particular mycoheterotrophic *Cryptothallus mirabilis* (Bidartondo *et al.*, 2003), no work goes beyond fungal identification and/or morphological analysis. How does a mycothallus function? Is it a true functional imitation of a mycorrhiza?

The fungus probably recovers carbon, as suggested by glycogen accumulation in hyphae (Carafa *et al.*, 2003) and biotrophic *Glomus* achieving their life cycle on hornworts (Schüßler, 2000). However, the fact that the fungus is mycorrhizal on other plants does not imply that it furnishes the same nutrients to the liverworts. The biotrophic interaction, as well as the reproducible and limited pattern of fungal colonization, as observed by Russell & Bulman, suggests that coevolution (in a broad sense) occurred, but gives no clues about the exchanges. This does not invalidate a neutral to weakly

parasitic fungal behaviour (Read *et al.*, 2000); equivalently, abuse by the plant, i.e. use of fungal carbon, is possible at least for Aneuraceae species related to the mycoheterotrophic *C. mirabilis*. As noted by Read *et al.* (2000), 'there is an urgent need to test such hypotheses'. Claims that *Marchantia nepalensis* cannot reproduce sexually without fungi (Chauduri & Rajaram, 1926, in Boullard, 1988) or that increased colonization in polluted soils could be protective (Turnau *et al.*, 1998) need careful investigation. All tools are now available to analyse exchanges: axenic thalli can be obtained from spores, and symbioses can be synthesized *in vitro* (Read *et al.*, 2000; Schüßler, 2000). It is now possible to transpose experimental designs already used for investigation of mycorrhizal functioning. And, beyond exchanges, microcosms and *in vitro* cultures could ultimately assess the fitness of each partner, demonstrating which profits from the coexistence.

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