New Phytologist

Commentary

Dimensions of plant flammability

Introduction

Fire is a ubiquitous phenomenon that shapes vegetation pattern and even global biome distribution. Plants fuel fire, but the degree to which plant traits, rather than climate, weather, or simply total fuel load influence fire behavior is a matter of ongoing debate (Mutch, 1970; Troumbis & Trabaud, 1989; Bond & Midgley, 1995; Schwilk, 2003; Fernandes & Cruz, 2012; Pausas *et al.*, 2012). Scaling from plant traits to ecosystem effects is a fundamental goal of functional ecology and fire is among the most dramatic ecosystem processes shaping vegetation globally. The mechanistic basis for scaling from traits to fire behavior, however, has remained elusive because the flammability of individual plant parts in isolation is not a good predictor of the flammability of either whole plants or of natural fuels comprising leaf litter and downed woody material. In this issue of *New Phytologist*, Cornwell *et al.* (pp. 672–681) present an important study of litter flammability traits that was both experimental and comparative across many species of gymnosperm.

'Scaling from plant traits to ecosystem effects is a fundamental goal of functional ecology and fire is among the most dramatic ecosystem processes shaping vegetation globally.'

This paper contains three important contributions. First, Cornwell *et al.*'s results confirm previous work demonstrating that larger litter particles (i.e. larger leaves or abscised branches) create less dense litter which burns with faster spread rates. Second, this work shows that existing variation across plant species influences litter flammability along two axes. Finally, this work finds that a set of ecologically important species, the non-*Pinus* Pinaceae, which tend to drop small needles singly, have litter of especially high density and low flammability in comparison with other gymnosperms. Together, these findings not only have implications for understanding trait influences on fire in contemporary communities, but may also provide context for interpreting past fire regimes and the evolutionary history of litter trait effects on fire.

Fuel-bed density and flammability

Wildfire is categorized as either surface or crown fire, but this distinction is only clear in forests with multiple levels of vegetation. In vegetation types with little vertical fuel separation such as grasslands and shrublands, all fire is crown fire fueled by some combination of dead and live canopy material and plant litter. To understand how canopy architecture, leaf traits and wood traits might influence fire behavior, it is helpful, therefore, to distinguish between traits influencing the flammability of the whole plant canopy and those traits which influence the flammability of the litter to which they contribute.

Although crown fires and grassland fires dominate the global annual area burned (Mouillot & Field, 2005), litter-driven surface fires are an important component of many temperate forests. These fires consume leaf and twig litter, larger downed woody material, and living understory plants. Litter driven fire is often extraordinarily patchy and species leaf trait differences may contribute to this patchiness. Canopy flammability is influenced by the ratio of dead to live material in the crown, live fuel moisture and possibly by volatile compounds in living tissue (Rundel, 1981). Litter-driven fire, however, depends on the 'afterlife' effects of dead plant material (Scarff & Westoby, 2006; Schwilk & Caprio, 2011).

Properties of the air/fuel mix determine fire behavior, and if we hold fuel chemistry constant, then the spatial arrangement of fuels is the main fuel determinant of fire behavior. Fuel arrangement is often expressed as either fuel bulk density (mass of dry fuel per volume of air/fuel bed) or as a packing ratio (volume of fuel per volume of air/fuel bed). At very high densities and packing ratios, fire is oxygen limited. At such densities, decreasing density leads to increased aeration, faster spread rates and greater fire intensity (Scarff & Westoby, 2006). As density decreases further and oxygen is less limiting, however, heat transfer through the fuel mix, which is necessary to propagate fire, becomes more important (Fig. 1).

Leaf traits effects on flammability: past and present

Cornwell *et al.*'s results add to a growing consensus that litter flammability is strongly influenced by litter particle size with larger particles leading to greater aeration, faster flame spread rates, and higher rates of heat release (Scarff & Westoby, 2006; Kane *et al.*, 2008; van Altena *et al.*, 2012; de Magalhães & Schwilk, 2012). Because coexisting plant species can differ dramatically in the size of their leaves, leaflets or branches shed and also differ in the decomposition rate of those parts, leaf traits have 'afterlife' effects on an important ecosystem process. This has implications for current fire management in forests undergoing shifts in community composition, but also has implications for past fire regimes. Cornwell *et al.* find that there are very different litter flammabilities within the Pinaceae that are controlled by the size of abscised

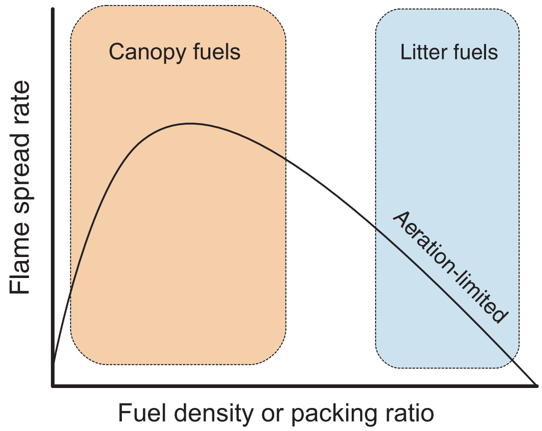

Fig. 1 Hypothetical relationship between fuel-bed density (or packing ratio) and the first axis of flammability measured by flame spread rate. There is now repeated evidence that litter fuels are aeration limited, that this effect is well-captured by litter-bed density, and that litter particle size (especially leaf size) therefore has a controlling positive effect on litter flammability. The effect of bulk density on canopy flammability is more complicated. There is evidence that fire spread is negatively associated with bulk density for crown fuels because that density acts as a heat sink, but at some point, very low densities will result in fuel too sparse to carry fire. See references in Fernandes & Cruz (2012).

needles and branches. The fact that these clades with differing flammability were present in the Cretaceous, combined with recent suggestions that surface fire regimes were important in the Cretaceous (Bond & Scott, 2010; He *et al.*, 2012), suggests that species effects on litter flammability may have influenced fire regimes during this period. Cornwell *et al.* suggest that abscised particle size, when available in the fossil record, may be an important trait from which to infer past forest litter flammability.

Although small litter particles produce more tightly packed and less flammable litter, smaller particles have greater surface-area-to-mass ratios and can promote fire in well aerated samples. But the burning characteristics of well-aerated samples do not simulate natural litter fuels, and litter-bed flammability studies find that the litter density effect outweighs any countervailing influence of surface-area-to-mass. Leaf size, however, most likely plays the opposite role in canopy flammability. Narrow leaves with high surface area to mass burn with high ignitability and intensity. Plant species with small leaves have fine and highly branched canopies as well and these tightly spaced leaves and twigs, at densities well below those that cause oxygen limitation, allow efficient heat transfer. Therefore, plants with low flammability leaf litter may have highly flammable canopy structure (Scarff & Westoby, 2006).

What are the axes of flammability?

Flammability, the general ability of vegetation to burn, is a product of the plant traits and those other fuel characteristics that influence fire behavior. It is not a single axis of variation, however. Historically, authors have followed the definitions as outlined by Anderson (1970) and considered flammability as comprising ignitability, sustainability, consumability and combustibility. But there is little empirical support for these as separate axes when considering natural variation across plant species. Cornwell *et al.* and previous work (e.g. de Magalhães & Schwilk, 2012; and others) are consistent in demonstrating that litter-driven fire has two major dimensions: one related to the rate of heat release and the other representing total heat release and often captured by proxy measures such as integrating temperature over time. These correspond approximately to Anderson's (1970) 'combustibility' and 'sustainability', respectively. Both have important implications for fire effects on living organisms. The first of these axes is strongly controlled by litter packing as described earlier and is often tightly correlated with flame spread rate (Scarff & Westoby, 2006; de Magalhães & Schwilk, 2012; Cornwell *et al.*). High values along the second axes, total heat release, are often associated with long smoldering combustion, and can predict soil heating and damage to well insulated plant parts.

In litter fire at least, this second axis is not completely orthogonal to the first; spread rate and total heat release are partly negatively correlated (see Cornwell *et al.*, Fig. 4; de Magalhães & Schwilk, 2012; Fig. 1). Slow burning fires can result in significantly more soil heating than fast fires. In crown fire, especially where there are both canopy and surface fuels, these axes may be completely independent as rapid spread and high intensity can be followed by long smoldering combustion. In past work, researchers have used 'flammability' to refer either to traits that increase rate of heat release or to those characteristics that increase total heat release. The degree which these axes of flammability are independent or negatively correlated may vary by fuel type.

Future directions

In part because the litter fire experiments are tractable, trait effects on litter flammability have been better studied than trait effects on canopy flammability. Understanding how plant traits influence crown fire is still a major challenge. The flammability of individual, separate, plants parts does not well predict the flammability of litter beds and is also a poor predictor of canopy flammability (Fernandes & Cruz, 2012; Bowman *et al.*, 2014, and references cited therein). While some authors have attempted to use small-scale laboratory measurements to predict differences among canopy flammabilities, the difficulty of large-scale crown fire experiments have led other authors to infer flammability from trait measurements and general models of flammability (e.g. Behm *et al.*, 2004). Fewer studies have measured whole plant flammability in natural conditions or under detailed laboratory measurements. These shortcomings in past work prompted Fernandes & Cruz (2012) to suggest physical-based fire models as the best route to understanding plant flammability.

Mechanistic fire modeling efforts may be very useful in helping to determine which traits are likely to be influential, and some recent modeling frameworks are including more and more trait-type structural information. An alternative intermediate scale experimental approach is to conduct experimental burns of portions of a plant canopy (Jaureguiberry *et al.*, 2011). Such an approach, when conducted with a portable apparatus, may allow rapid measurement of many species while sacrificing the precision of full laboratory whole plant methods (e.g. Weise *et al.*, 2005). We currently lack the sort of large comparative examination of canopy flammability that Cornwell *et al.* have provided for gymnosperm litter flammability.

There is increasing evidence that trait variation influences fire behavior and that coexisting species can vary in these traits. How and when such trait effects on fire behavior might have feedback effects on individual selection is a more complicated problem: no traits exclusively influence flammability (Bowman *et al.*, 2014). Cornwell *et al.* point out that their study does not provide evidence for or against the idea that selection has led to traits that promote fire (Mutch, 1970). Our increased understanding of flammability's role in plant evolution will require both a tighter link between traits and fire behavior as well as better ancestral character state reconstructions that inform the relative evolutionary order of fire suppressing, fire enhancing, and fire response traits.

Dylan W. Schwilk

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA
(tel +1 806 834 0902; email dylan.schwilk@ttu.edu)

References

van Altena C, van Logtestijn RSP, Cornwell WK, Cornelissen JHC. 2012. Species composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in Plant Science* **3**: 1–10.

Anderson H. 1970. Forest fuel ignitibility. *Fire Technology* **6**: 312–319.

Behm AL, Duryea ML, Long AJ, Zipperer WC. 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface. *International Journal of Wildland Fire* **13**: 355–365.

Bond WJ, Midgley JJ. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* **73**: 79–85.

Bond WJ, Scott AC. 2010. Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* **188**: 1137–1150.

Bowman DMJS, French BJ, Prior LD. 2014. Have plants evolved to self-immolate? *Frontiers in Plant Science* **5**: 590.

Cornwell WK, Elvira A, van Kempen L, van Logtestijn RSP, Aptroot A, Cornelissen JHC. 2015. Flammability across the gymnosperm phylogeny: the importance of litter particle size. *New Phytologist* **206**: 672–681.

Fernandes PM, Cruz MG. 2012. Plant flammability experiments offer limited insight into vegetation–fire dynamics interactions. *New Phytologist* **194**: 606–609.

He T, Pausas JG, Belcher CM, Schwilk DW, Lamont BB. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist* **194**: 751–759.

Jaureguiberry P, Bertone G, Díaz S. 2011. Device for the standard measurement of shoot flammability in the field. *Austral Ecology* **36**: 821–829.

Kane JM, Varner JM, Hiers JK. 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. *Forest Ecology and Management* **256**: 2039–2045.

de Magalhães RMQ, Schwilk DW. 2012. Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* **100**: 1153–1163.

Mouillot F, Field CB. 2005. Fire history and the global carbon budget: a 1 × 1 fire history reconstruction for the 20th century. *Global Change Biology* **11**: 398–420.

Mutch RW. 1970. Wildland fires and ecosystems – a hypothesis. *Ecology* **51**: 1046–1051.

Pausas JG, Alessio GA, Moreira B, Corcobado G. 2012. Fires enhance flammability in *Ulex parviflorus*. *New Phytologist* **193**: 18–23.

Rundel PW. 1981. Structural and chemical components of flammability. In: Mooney HA, Bonnicksen TM, Christensen NL, Lotan JE, Reiners WA, eds. *Proceedings of the conference on fire regimes and ecosystem properties*. USDA Forest Service General Technical Report WO-86, 183–207.

Scarff FR, Westoby M. 2006. Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology* **20**: 745–752.

Schwilk DW. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist* **162**: 725–733.

Schwilk DW, Caprio AC. 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology* **99**: 970–980.

Troumbis AS, Trabaud L. 1989. Some questions about flammability in fire ecology. *Acta Oecologica – Oecologia Plantarum* **10**: 167–175.

Weise DR, White RH, Beall FC, Etlinger M. 2005. Use of the cone calorimeter to detect seasonal differences in selected combustion characteristics of ornamental vegetation. *International Journal of Wildland Fire* **14**: 321–338.

Key words: fire, flame spread rate, flammability, gymnosperms, litter, plant evolution, plant functional traits (PFTs).