Does pyrogenicity protect burning plants?

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Abstract. Pyrogenic plants dominate many fire-prone ecosystems. Their prevalence suggests some advantage to their enhanced flammability, but researchers have had difficulty tying pyrogenicity to individual-level advantages. Based on our review, we propose that enhanced flammability in fire-prone ecosystems should protect the belowground organs and nearby propagules of certain individual plants during fires. We base this hypothesis on five points: (1) organs and propagules by which many fire-adapted plants survive fires are vulnerable to elevated soil temperatures during fires; (2) the degree to which burning plant fuels heat the soil depends mainly on residence times of fires and on fuel location relative to the soil; (3) fires and fire effects are locally heterogeneous, meaning that individual plants can affect local soil heating via their fuels; (4) how a plant burns can thus affect its fitness; and (5) in many cases, natural selection in fire-prone habitats should therefore favor plants that burn rapidly and retain fuels off the ground. We predict an advantage of enhanced flammability for plants whose fuels influence local fire characteristics and whose regenerative tissues or propagules are affected by local variation in fires. Our "pyrogenicity as protection" hypothesis has the potential to apply to a range of life histories. We discuss implications for ecological and evolutionary theory and suggest considerations for testing the hypothesis.

Key words: adaptations; ecosystem engineering; evolution; fire ecology; heat; Mutch hypothesis; niche construction; plant flammability; pyrogenicity as protection; resprouting; serotiny.

Concepts of Pyrogenicity

Fire-prone ecosystems are characterized by plants whose aboveground tissues burn. Some of these flammable plants are pyrogenic—they promote fires by burning especially intensely, in some ecosystems even under nondrought conditions ("self-immolators," sensu Zedler [1995]). Pyrogenic plants have physical and chemical characteristics that facilitate their combustion, such as fine leaves and branches with high volatile oil content, fuels that resist packing and decomposition, and dead leaves and branches that remain off the ground (Mutch 1970, Philpot 1977, Rundel 1981, Bond and Midgley 1995, Zedler 1995, Schwilk 2003, Behm et al. 2004, Scarff and Westoby 2006). The prevalence and oftentimes dominance of pyrogenic plants in grasslands, savannas, and woodlands around the world suggest that increased flammability is advantageous in fire-prone ecosystems (Mutch 1970, Bond and Midgley 1995, Zedler 1995, Platt 1999, Schwilk and Ackerly 2001, Behm et al. 2004).

Pyrogenicity as an adaptation to fire has been a popular but controversial idea. Mutch (1970) first hypothesized that traits conferring enhanced flammability were adaptive based on his dual observations that: (1) fuels of different plant species vary greatly in their degree of flammability; and (2) highly flammable plants are prevalent in fire-prone communities. Snyder (1984) criticized his hypothesis, noting that enhanced flammability might result from selection for other, directly beneficial traits such as drought tolerance or defense against herbivores. Troumbis and Trabaud (1989) and Whelan (1995) pointed out that Mutch's hypothesis for pyrogenic plant communities invoked group selection because it required that fires spread across the landscape via continuous fuels of numerous individual plants, often of different species. Despite these perceived

problems, numerous empirical observations have continued to fuel the idea that plants with pyrogenic traits might have some advantage in fire-prone habitats.

How might pyrogenicity evolve through individual-level selection despite steep perceived costs to the self-immolating individual? Some hypotheses assume that pyrogenicity is tied to unspecified traits that confer fitness benefits (Bond and Midgley 1995, Kerr et al. 1999) or incorporate kin-selected altruism (Schwilk and Kerr 2002). If post-fire environments are conducive to the growth or establishment of pyrogenic plants' offspring, then pyrogenicity constitutes "ecosystem engineering" or "niche construction" (Platt et al. 1988, Bond and Midgley 1995, Platt 1999, Schwilk and Kerr 2002, Schwilk 2003). This idea presumes that when the more flammable individuals burn, they alter the environment in some way that enables adaptation to the post-fire environment by their descendants (e.g., Kerr et al. 1999). Some pyrogenic plants produce more seeds immediately after fires than at other times, possibly because their seedlings establish at higher rates in the open spaces or mineral soil exposed by recent fires (Brewer and Platt 1994, Platt 1999).

We propose a new hypothesis to explain how traits enhancing flammability provide intrinsic advantage to pyrogenic plants in fire-prone habitats. We start with three basic assumptions: (1) tissues of established plants ignite and sustain fire; (2) pyrogenicity is the result of increases in combustibility (the rate at which fuels are consumed after ignition), consumability (the proportion of fuels consumed by fire), or both (Anderson 1970, Martin et al. 1994); and (3) established plants or their nearby offspring might survive fires via belowground tissues or seed banks. We draw on prior studies to argue that traits associated with increased flammability should reduce the likelihood of damage to a plant's below-ground organs and propagules. Such risk reduction could operate independently or together with other consequences of pyrogenicity, such as altered post-fire environments that favor offspring. We argue that evolutionary discussions of pyrogenicity should consider that the manner in which a plant burns affects soil heating in that immediate vicinity, and thus, survival of that plant or its nearby propagules (i.e., potential offspring). We assert that the cost of pyrogenicity to the individual should be less than commonly perceived because most plants in fire-prone habitats risk damage to aboveground tissues in fires regardless of whether or how they burn. By indicating how pyrogenicity might be directly advantageous to individual plants, our hypothesis elucidates a novel mechanism by which traits related to pyrogenicity might invade plant populations.

We present five points that build the case for pyrogenicity as a form of self-protection in fire-adapted plants. The first three synthesize important observations of fire effects on soil and on plants, the fourth is a deduction that follows logically, and the fifth explains some implications of that deduction, including which

characteristics of plants should be adaptive in fires. We subsequently explore the potential generality of our "pyrogenicity as protection" hypothesis for different plant life history strategies and conclude by discussing some implications for ecological and evolutionary theory and ecosystem management.

PYROGENICITY AS PLANT SELF-PROTECTION IN FIVE POINTS

1. *The belowground organs and propagules by which plants might survive fires are vulnerable to elevated soil temperatures, especially near the soil surface.*—Soil insulates, and heat from fire decreases rapidly with soil depth (Steward et al. 1990, Bradstock and Auld 1995, Schimmel and Granstrom 1996, Choczynska and Johnson 2009). Insulation capacity of soil varies with soil type and moisture level, but such variation appears to be of minor consequence (Steward et al. 1990, Choczynska and Johnson 2009). Belowground organs and propagules are most vulnerable at the soil surface, and the likelihood of tissues surviving fires increases with depth (Flinn and Wein 1977, Hodgkinson and Oxley 1990, Bradstock and Auld 1995, Schimmel and Granstrom 1996, Odion and Davis 2000, Brooks 2002, Choczynska and Johnson 2009).

2. *The extent to which a given quantity of burning fuel heats the soil is determined mainly by how long it burns and by the fuel's proximity to the soil surface.*—Duration of combustion and its height above the ground are important determinants of temperatures at and below the soil surface during fires (Steward et al. 1990, Hartford and Frandsen 1992, Bradstock and Auld 1995). Conductive and radiative heat transfers are both strongly inversely related to distance and tend to drive soil heating during fires, whereas convective heat is typically less important because convection generally transfers heat upward and away from the soil (Aston and Gill 1976, Steward et al. 1990, Michaletz and Johnson 2007, Keeley 2009). As such, commonly used metrics like fireline intensity (the rate of heat transfer per unit length of the fireline in kilowatts per meter [Byram 1959]) are often not predictive of soil heating (Hartford and Frandsen 1992, Bradstock and Auld 1995, Schimmel and Granstrom 1996, Keeley 2009). Rate of fire spread may be inversely related to soil heating because faster fires tend to burn both with shorter residence times and higher above the ground than slower-moving fires (Stinson and Wright 1968, Bailey and Anderson 1980, Bradstock and Auld 1995, Whelan 1995).

3. *Fuels, fires, and fire effects are heterogeneous at small scales, meaning fuels produced by individual plants influence how long and how high fires burn.*—Fire temperatures, intensities, and residence times vary widely at small scales, as do resulting effects on vegetation (Stinson and Wright 1968, Bailey and Anderson 1980, Hodgkinson and Oxley 1990, Odion and Davis 2000, Brooks 2002, Thaxton and Platt 2006, Brewer et al. 2009). The quantity, composition, and vertical structure of plant fuels all affect fire intensity,

residence time and height of combustion (Smith and Sparling 1966, Stinson and Wright 1968, Williamson and Black 1981, Odion and Davis 2000, Schwilk and Ackerly 2001, Brooks 2002, Schwilk 2003, Thaxton and Platt 2006).

4. *Therefore, how a plant burns can influence local soil heating, and consequently, the chances that it or its nearby propagules survive fire.*—The three points above indicate that survival of a plant's belowground organs and nearby propagules during fire is to some extent a function of both the duration of fire and of how high above the ground the plant's tissues burn. We deduce that specific traits relating to differences in fuel flammability and position above the soil should thereby affect individual plant fitness. For example, in *Adenostoma*-dominated California chaparral, Odion and Davis (2000) observed that woody fuels that fell from the canopy onto the ground and smoldered long after fire passage increased local soil temperatures and reduced seed germination and resprouting at those same locations.

5. *We hypothesize that in fire-prone ecosystems, natural selection should often favor plants that burn up rapidly during fires and retain their fuels off the ground.*—If a plant's fuels affect its own or its offspring's survival probabilities (by affecting local fire characteristics), then traits that speed combustion and keep fuels off the ground should be directly advantageous to the individual plant or its nearby propagules. Compared with smoldering combustion of fuels on the ground, rapid flaming combustion of fuels off the ground should send more heat upward (via convection) and away from the soil, reducing fire residence times (Whelan 1995, Michaletz and Johnson 2007). In this way, pyrogenic tissues that burn rapidly and above the soil surface should reduce risk to a plant's belowground organs and nearby propagules during fires, and should therefore be favored by natural selection in many ecosystems depending on fire regime.

ELABORATING THE "PYROGENICITY AS PROTECTION" HYPOTHESIS

Our hypothesis proposes a novel explanation for pyrogenicity based on individual-level selection. It provides a clear evolutionary advantage by which related traits might increase in frequency over generations within populations. Many studies have suggested that pyrogenicity should be an advantageous trait at the level of populations because pyrogenic assemblages are observed to displace less flammable ones where fire sources are present (Williamson and Black 1981, D'Antonio and Vitousek 1992, Bond and Midgley 1995, Kerr et al. 1999, Platt 1999, Schwilk and Kerr 2002). Nonetheless, a mechanism by which enhanced flammability might increase in frequency in a population starting with a single mutant type has proven elusive. Instead, various studies have tended to treat pyrogenicity as an emergent property of communities (Philpot

1977, Snyder 1984, Troumbis and Trabaud 1989), while remaining tentative or unclear about how related traits might invade the population (however, see Platt et al. 1988, Bond and Midgley 1995, Schwilk and Kerr 2002). Protective pyrogenicity provides a solution to this conundrum without presupposing direct ties between enhanced flammability and an unspecified trait that confers increased fitness. It contrasts with previous explanations that treat enhanced flammability as a detriment to the individual (e.g., Bond and Midgley 1995, Schwilk and Kerr 2002).

We can predict when pyrogenicity should and should not protect plants during fires using the explicit mechanism within our hypothesis. We expect plants in fire-prone landscapes to combust quickly and to retain fuels off the ground if they: (1) produce enough fuel to influence local fire characteristics; and (2) resprout from shallow belowground organs or germinate from shallow seeds that remain close to parents; shallow organs and seeds are vulnerable to local soil heating. In contrast, we predict no protective advantage of pyrogenicity for plants whose fuels do not influence local fire characteristics or whose tissues or propagules are unaffected by local variation in fires. Examples include plants that resprout from deep belowground, produce seeds that are dispersed widely or stored deeply in the soil, are very small statured relative to nearby neighbors, or are located in places subject to large inputs of exogenous fuels that swamp their own contribution to the local fuel load. These plants should possess mechanisms for surviving fires (e.g., resprouting ability, heat-resistant seeds), but not pyrogenic fuels.

Comprehensive theory regarding the evolution of pyrogenicity should consider potential roles of enhanced flammability both as a means of self-protection and of engineering growing space. Whereas our "pyrogenicity as protection" hypothesis suggests that rapid, intense combustion should reduce mortality of belowground organs and seeds, previous explanations emphasize opening space (via damage to competitors and consumption of organic litter) that facilitates regeneration (e.g., Platt et al. 1988, Bond and Midgley 1995, Schwilk and Kerr 2002). These two possibilities are not mutually exclusive, and testable predictions should indicate the circumstances under which each might contribute to the evolution of pyrogenicity. For example, plants that resprout from organs near the soil surface should benefit more from rapid combustion of fuels held off the ground than plants with organs deeper in the soil, regardless of whether space is opened for regeneration. Alternatively, if pyrogenicity is a means of opening space, plants should produce slow-burning fuels that spread outward along the soil surface to increase fire residence times and soil heating (e.g., Williamson and Black 1981, Platt 1999, Platt and Gottschalk 2001). Tests among different potential evolutionary drivers of enhanced flammability should examine the benefits of altering both local conditions during fires and the environment post-fire.

CONCEPTS & SYNTHESIS

Assumptions about Plants in Fire-prone Habitats

A necessary assumption of our hypothesis is that plants in fire-prone habitats burn. Only within plant lineages that burn periodically can there be selection for enhanced flammability leading to protective pyrogenicity. Fire-prone habitats are both productive enough that vegetation forms a continuous fuel matrix across the landscape, and periodically dry enough for recurrent fires to burn that vegetation. Some habitats contain almost continuous fine fuels (e.g., many grasslands and savannas); others are subject to periodic, extreme weather that drives intense fires (e.g., certain crown-fire systems [Moritz et al. 2004]). Both ensure that constituent plant lineages are periodically damaged by fire. Variation in fuels and weather conditions drive heterogeneity within and among fires, in turn driving variation in fire effects among plant species over space and time. We base our hypothesis on assumptions that recurrent fires burn in fire-prone habitats, and that plants are potentially damaged or killed during at least some of these fires.

Oftentimes the actual cost of pyrogenicity incurred during a fire by a highly flammable plant may be small relative to that incurred by a nonpyrogenic plant. We argue that pyrogenicity confers a direct benefit in the form of reduced risk to belowground tissues, because in many cases soil heating should be less. Pyrogenicity also has a cost in the form of potential tissue lost from any increased likelihood of burning. The expected benefit of pyrogenicity must outweigh this cost. For a given location, that net benefit or cost will be a function of how fast fuels accumulate (i.e., site productivity vs. decomposition rate) relative to the fire return interval. This interplay will determine any advantage, for example, in retaining flammable fuels above the ground. Where fuels are continuous and fires are recurrent, plants risk damage to aboveground tissues in the heat of passing fires regardless of how or even whether their tissues combust. In this context, the relative cost of pyrogenicity in fire-prone habitats might be less than previously assumed (e.g., see Bond and Midgley 1995, Schwilk and Kerr 2002).

Pyrogenicity and Different Plant Life Histories

Our hypothesis has potential to apply to different types of plants in a variety of ecosystems. To illustrate its generality, we discuss three life histories that characterize flammable plants as examples of how pyrogenicity might confer protection.

Most plants in high fire-frequency ecosystems are resprouters. Such plants commonly survive aboveground immolation via underground organs (Collins and Gibson 1990, Platt 1999, Higgins et al. 2000, Vesk and Westoby 2004, Brewer et al. 2009). The relationship of soil heating to fire residence time and height of combustion should apply to ecosystems with a continuous ground layer of resprouting plants that regrow quickly and can thus reburn shortly thereafter (often within 1–2 years, e.g., marshes, grasslands and savan-nas). For resprouters that produce enough fuel to influence local fire characteristics, we predict selection for pyrogenic traits such as fuels held off the ground. We thus expect the large-statured graminoids that dominate the groundcover of these systems to exhibit enhanced combustibility and consumability during frequent, low-intensity fires (e.g., Platt et al. 1991).

We would also expect that enhanced flammability might serve a protective function for many species whose adults die in fires but that persist via seeds stored in the soil or canopy. In crown-fire habitats like shrublands and woodlands, reseeding perennials can constitute a substantial proportion of plants (Lamont et al. 1991, Ojeda 1998), and fires are typically more intense but less frequent than in the grasslands and savannas dominated by resprouters. For species with seeds stored in the soil, we expect selection for pyrogenic characteristics in those whose seeds remain near both the parent plant and the soil surface. (Note that short-distance dispersal is the most likely outcome for various dispersal syndromes [e.g., Gomez and Espadaler 1998 for myrmecochory]). Rapid combustion of parents that retain fuels off the ground should reduce local heating of the soil and any seeds therein. Other species retain seeds in the canopy, including serotinous pines (sensu Critch-field 1957, Keeley and Zedler 1998) and proteas (Lamont et al. 1991). Seeds in serotinous cones are also vulnerable to prolonged heating during fires (Bradstock et al. 1994, Mercer et al. 1994), and those near the ground are more vulnerable than those higher up (Bradstock et al. 1994, Whelan 1995). How parent plants burn should thus influence seed survival rates; rapid combustion of parents that retain seeds off the ground should reduce risk. Consistent with this idea, Despain et al. (1996) determined that crowns of lodge-pole pines (*Pinus contorta* Laws.) require just 15–20 seconds on average to burn up entirely, based on video footage from the Yellowstone wildfires of 1988.

Pyrogenic litter may serve a protective function for species, like some savanna trees, that routinely survive low-intensity ground-fires with relatively minor damage. If their litter should accumulate over prolonged periods, the boles and surficial roots of such species can become increasingly vulnerable to fires that smolder in packed fuels (Varner et al. 2005, Michaletz and Johnson 2007). Fires spread via pyrogenic fuels and simultaneously consume those fuels (Williamson and Black 1981, Scarff and Westoby 2006); thorough consumption in fire precludes litter from accumulating over multiple fire intervals (Platt 1999). Although pyrogenic litter has been suggested to offer competitive advantage to savanna and woodland trees (Williamson and Black 1981, Scarff and Westoby 2006), it might also serve to protect individuals from excessive heating of the soil when fires smolder in dense, accumulated duff. Because packed litter often retains moisture longer than aboveground fine fuels, flammability of these two fuel types can decouple (Armour et al. 1984, Michaletz and Johnson 2007).

We would expect flammable litter to confer protective advantage for plants in habitats otherwise at risk of smoldering duff fires.

IMPLICATIONS AND CAVEATS

Our hypothesis for protective pyrogenicity is for species in the context of their historical fire regimes over evolutionary time. We note that extreme fires can act as potent evolutionary filters. Predicting whether and to what extent pyrogenicity should evolve requires knowledge of the full range of variation in a given fire regime. Fire regimes are dynamic over time; they change along with environmental conditions and species composition. Thus, current pyrogenicity should reflect some range of historical fire regimes along with ongoing changes in environmental conditions.

Modern fire regimes are often novel. Humans exert new control over fire regimes in many ecosystems, both directly and via human-modified climate (Bowman et al. 2009). Discrepancies between current and historical fire regimes can complicate our ability to make inferences about selection pressures that past fires would have exerted on fire-adapted plants. We expect changing modern fire regimes in fire-prone habitats to drive changes in the composition and architecture of plant tissues, with the potential to send species on new evolutionary trajectories. We propose that where restoration and conservation of fire-prone ecosystems is a goal, land managers should strive not only to burn, but to do so in ways that are consistent with historical, climate-driven fire regimes.

Expected fire behavior is an integral part of this evolutionary hypothesis. Fire behavior is highly variable and dependent on synoptic weather and the quantity, moisture content, composition, and configuration of fuels. For a host of reasons, modern prescribed fires can be substantially different in behavior and effect from fires typical during prior evolutionary history (Moritz and Odion 2004). Fuel consumption, especially on the ground, is likely to be markedly different (i.e., less) during controlled burning as compared to natural wildfires during extreme weather. We would expect some of the same traits that render plants less flammable during low-intensity prescribed fires (e.g., self-pruning, production of high bulk-density fuels) to pose risks during high-intensity wildfires that burn fuels more completely. For example, during comparatively "cool" prescribed fires, self-pruned fuels lying on the ground might not burn at all, whereas during wildfires in drought times, these same fuels might burn easily. (For plants that retain their branches above the ground, these fuels might burn in either case.) To offer valid insights, it is imperative that any tests of this hypothesis incorporate fires that are typical of the evolutionary history of given habitats. Admittedly, this imperative may pose a challenge where natural fire occurrence was driven primarily by cyclical, extreme weather events difficult to match under prescription (e.g., Moritz et al. 2004, Gagnon 2009).

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CONCEPTS & SYNTHESIS