Nordic Society Oikos

Kill thy neighbour: an individualistic argument for the evolution of flammability

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Bond, W. J. and Midgley, J. J. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. – Oikos 73: 79–85.

The idea that flammability has evolved in many fire-prone communities has been criticised for being group-selectionist. However flammability may enhance inclusive fitness if the resulting fires kill neighbouring less flammable individuals and also open recruitment possibilities. We modelled the evolution of flammability using cellular automata to simulate neighbourhood effects of burning. For plants that survive fire only from unburnt canopies (non-sprouters), increased flammability would cause them to burn to death. Flammability traits can evolve in such species only if they result in fire spreading to kill less flammable neighbours and only if they carry additional fitness benefits. In species that resprout from roots or stem bases after fire, flammability can evolve merely by increasing neighbour mortality but is more likely to do so if the associated traits had other benefits. Most flammability-enhancing traits, both structural and biochemical, are likely to have such additional benefits. We predict that flammability traits will be associated with dense populations where the effect on neighbours is most marked and suggest several tests. Fire has been a key, but neglected, evolutionary force. Alteration of the fire regime through the evolution of flammability, even in a single species contributing heavily to fuel loads, would result in the selective exclusion or admission of other species to an ecosystem depending on the compatibility of their pre-existing traits with fire.

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Many vegetation types depend on fire for their continued persistence. Without fire, these communities are replaced by non-flammable forests and scrub. Mutch (1970) argued that fire-prone vegetation may have evolved characteristics which increase flammability and thereby contribute to the perpetuation of fire-dependent communities. He argued that though ignition may occur "accidentally or randomly, the character of burning is not random. ... Fire dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favoured development of characteristics that make them more flammable".

Mutch's hypothesis has been widely cited by fire ecologists since it seems to provide an evolutionary rationale for the differences between fire-prone and fire-free communities. For example, studies on pines and oaks have shown that pine litter is more flammable than oak litter and that without fire pines are replaced by oaks. This has been taken as evidence that flammability has evolved in pines as part of its competitive armoury (Williamson and Black 1981, Rebertus et al. 1989). However despite its wide appeal, the Mutch hypothesis is flawed (Snyder 1984, Christensen 1985, Troumbis and Trabaud 1989). Although communities that burn more readily may be more flammable than those that do not, the differences in flammability may be purely coincidental. Alternative selection pressures such as herbivory, nutrient retention or drought tolerance may be more plausible determinants of "flammability" traits (Snyder 1984, Troumbis and Trabaud 1989). Mutch also presented his hypothesis at the
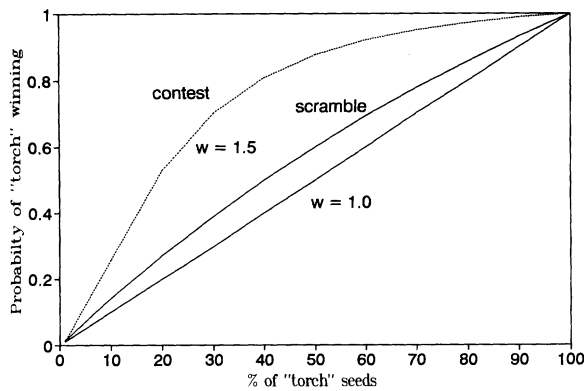
Fig. 1. The effect of different forms of seedling competition on the outcome of biased lotteries where more than one seed occupies a gap. The weighting, w, represents the fitness of a flammable seedling relative to non-flammable seedlings. A weighting of 1 produces an unbiased lottery while $w > 1$ indicates additional fitness advantages associated with flammability. Solid line = scramble, dashed = contest.

level of species or community – for example pines are assumed to have evolved flammability to avoid replacement by oaks – and the hypothesis has been criticised for being group selectionist (Snyder 1984). The difficulty is in seeing how a trait which increases the risk of injury to a plant would spread at the expense of related individuals less likely to suffer injury. The intraspecific costs of enhanced flammability seem to override possible benefits in interspecific interactions.

Flammability itself is a difficult concept to define in relation to evolution by natural selection because it is influenced by many different and apparently unrelated plant properties (Troumbis and Trabaud 1989). For our purposes, it is the probability that one plant burns more readily and with greater intensity than another in the same population. Structural traits causing increased flammability include high surface area to volume ratios (fine foliage, thin branches), branching patterns that carry fire from the ground to the canopy and scleromorphic leaves (Rundel 1981, Papio and Trabaud 1991). Chemical correlates of flammability include high cellulose rather than lignin content and high levels of ether extractive secondary constituents such as terpenes and waxes (Rundel 1981). Both sets of traits are likely to have other effects on plant function besides enhancing flammability (Snyder 1984).

Modelling the evolution of flammability in a population

Flammable individuals should make dangerous neighbours in a fire because they increase the risk of mortality. We develop the argument that traits enhancing flammability could evolve if the result is high neighbourhood mortality, even if the flammable plant is also killed,

through freeing up space for recruitment opportunities. We wish to explore conditions under which inclusive fitness benefits (Hamilton 1964) for offspring exceed the cost for flammable parents. We use trees and shrubs as examples since fire is often patchy in woody vegetation and some canopies escape burning. Plants have diverse ways of surviving fire (e.g. Gill 1975). We consider two modes of fire survival: non-sprouters – where plants are killed by intense fires and regenerate only from seeds; and sprouters where plants respond to destruction of foliage by sprouting from the roots or from epicormic buds (Gill 1975, Rundel 1981). Levels of fire-induced mortality in non-sprouters vary. All individuals in some species are routinely killed by burning. In others, plants are killed only by intense fires which destroy shoot apices or kill the stem. We first consider the apparently improbable case of these fire-resilient non-sprouters where increased flammability would result in the death of the plant.

Assume a population of a woody plant with the following characteristics: gap-phase regeneration so that recruitment occurs only in gaps created by the death of adult plants; the population experiences regular ground fires but individuals are killed only in intense canopy burns. Plants are protected from cambial damage by insulating layers of bark, have no capacity for root crown sprouting, and canopies recover only if shoot apices are not burnt; gaps created by plants dying in a fire are filled from seeds dispersed from surrounding plants between fires.

This kind of life history is common among many conifers and also in some angiosperm families that occur in fire-prone systems. In Cape fynbos, for example, several members of the Proteaceae show these characteristics (Yeaton and Bond 1991). *Leucospermum conocarpodendron* is a 4–5 m sclerophyllous shrub which lacks the capacity to sprout from roots. However, it has thick bark and plants survive fires if the canopy is not completely scorched (Rourke 1972). *Protea lepidocarpodendron*, which co-occurs with the *Leucospermum*, is 2–3 m tall, has thinner leaves, and denser branching producing a canopy that is highly flammable. The species is also a non-sprouter but is thin-barked and always killed by fire. Variability in fire response, matching this pattern but at the intraspecific level, has been reported for conifers (Critchfield 1957, Stott et al. 1992).

Under what conditions could a single flammable ("torch") mutant invade an ancestral less-flammable ("damp") population? Gaps formed by death of the "torch" could potentially be colonised by seedlings of both forms. Since the surrounding seed source would initially all be "damps", it seems unlikely that the flammable mutant could invade. However, if the torch mutant burnt so fiercely that it killed adjacent "damp" plants as well as itself, more space would be created for occupation by its seedlings potentially increasing the chance of the "torch" mutant invading.

Successful colonization of a gap by a torch seedling

may be affected by other fitness benefits associated with increased flammability. Although most emphasis has been placed on alternative benefits of chemical traits, structural plant attributes which enhance flammability may also have large effects on plant performance. Fire tends to maintain early successional species at the expense of slower growing, taller late successional elements (e.g. Jackson 1968, Mutch 1970). Increased allocation of resources to early and prolific branching promotes rapid initial growth and increased fecundity (Grime 1979, Tilman 1988) but also increases the risk of crown fires. We quantify these alternative effects of traits that enhance flammability as increased "torch" fecundity, or as biased recruitment lotteries in either scramble or contest competition between "torch" and "damp" seedlings (Fig. 1).

Methods

Non-sprouters

We modelled the spread of a torch mutant in an arena of cellular automata with varying mortality of neighbours, dispersal attributes, seed production and seedling competition. Cellular automata models have been increasingly used in plant ecological studies (Auld and Coote 1981, Hobbs and Hobbs 1987, Green 1989, Silvertown et al. 1992, Colasanti and Grime 1993) though seldom to address evolutionary questions.

Our model consisted of a lattice of 20 × 20 square cells representing a finite patch of 400 plants. A single "torch" mutant was introduced at the centre of the margin of a population of "damps" simulating a likely scenario where a flammable community abuts a less flammable one. Each iteration of the model represented a fire. Mortality was induced by fire simulated by "killing" the "torch" mutant and plants in neighbouring cells. Enhanced flammability causes more intense fires in a canopy which may then spread to neighbouring canopies. The neighbourhood effects of increased flammability were simulated by generating "kills" at increasing distances from a torch cell up to a maximum of 4 cells. Seed dispersal from adjacent cells into each resultant "gap" was calculated as:

$$S = Cd^{-k}$$

where S is the number of seeds, C is a constant representing the size of the seed crop, d is the distance of the source cell in cell units from the empty cell, and k is a constant determining dispersal distance. The sum of seeds from all neighbouring cells within dispersal distance (to a maximum of 4 cells) gave the total size of the seed pool for damp and torch genotypes at the target cell. Recruitment was assumed to occur from seeds surviving the fire.

Competition between seedlings for a gap was simulated in two ways reflecting different biological circumstances. The simplest is to assume a form of scramble

competition between seedlings of torch and damp genotypes:

$$p_t = \frac{wS_t}{wS_t + S_d}$$

where p_t is the probability of a torch seedling winning the space, S_t is the number of torch seeds in the cell, S_d is the number of damp seeds in the cell and w is the fitness of a torch seedling relative to a damp seedling. A weighting of 1 produces an unbiased lottery where flammability has no other effects on seedling survival or growth while $w > 1$ indicates a fitness advantage for the flammable genotype. This form of lottery counts competitive advantage simply by weighting the seed number (Fig. 1). Plant competition is often asymmetric (Weiner 1990) resembling more a contest where the fastest growing seedlings have a disproportionate advantage over their competitors, even if they are in the minority. We express this form of competition as:

$$p_t = \frac{S_t^w}{S_t^w + S_d}$$

which places less emphasis on relative seed number and more on fitness differences (Fig. 1).

Spread of the torch mutant was iterated through repeated "fires" until either "torch" or "damp" forms were extinct. Sensitivity of the model was assessed using a variety of dispersal, mortality and fitness parameters (representing dominant shrubs in Cape fynbos and similar Mediterranean-type shrublands). Simulations with each set of parameters were repeated 50 times. Mortality and dispersal parameters were held constant for each simulation but probabilities of seedling regeneration were simulated stochastically.

Sprouters

Sprouting life histories are generally much more common than non-sprouting life histories in fire-prone woody communities. Sprouter mortality increases with increasing fire intensity (e.g. Moreno and Oechel 1993) so that a more flammable plant, and its neighbours, should experience higher mortality rates. We modelled the possible spread of a flammability "gene" using the same basic approach as that for non-sprouters. However, sprouters were assumed to survive fires unless they were "torches" or damps neighbouring "torches" when survival was assumed to occur with probability $m_t \leq 1$ for torches and $m_d \leq 1$ for damps. Pleiotropic effects on survival were simulated as $m_d < m_t$. The same basic assumptions were used for regeneration: a) gap-phase regeneration so that seedling recruitment occurs only in gaps created by the death of adult plants b) gaps created by plants dying in a fire are filled from seedbanks accumulated by dispersal from surrounding plants between fires. For the sprouter
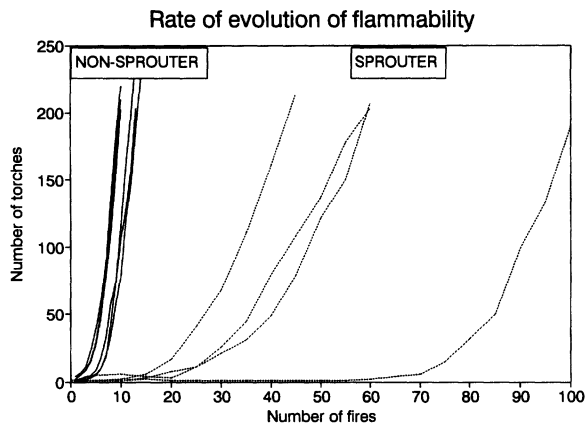
Rate of evolution of flammability

Fig. 2. Simulated dynamics of invasion of a flammable mutant into a non-flammable population. Solid lines indicate the population growth of non-sprouters and dashed lines of sprouters. Several simulation runs are shown to indicate the variance in rates of spread.

case, fitness differences in fecundity and seedling survival were not simulated. Each simulation was run until only one morph survived. Simulations were repeated 50 times for each set of parameters.

Results

Non-sprouters

Simulated population dynamics of the torch mutants show that torches either went extinct or rapidly invaded the non-flammable population (Fig. 2). Analysis of repeated runs shows that a flammability "gene" cannot invade a non-flammable population unless it kills its neighbours (Fig. 3). Furthermore, even if the "torch" mutant burns so fiercely that it kills neighbouring plants, it cannot spread unless flammability is associated with additional fitness benefits expressed, for example, as increased fecundity C, or competitive advantage w. The model was most sensitive to changes in w, the fitness factor weighting the seedling lottery. Simulated contest competition produced the greatest probability of a flammability gene spreading (Fig. 3A). It was less likely to spread under scramble competition (Fig. 3A) and least likely to spread when benefits were expressed as fecundity differences, C, (Fig. 3B) under the set of rules used in the model. We could not envisage a situation where the dispersal constant, k, could be linked to flammability and have not simulated different k's for the two genotypes.

Sprouters

Results differ from the non-sprouting case firstly in the dynamics of invading populations of flammable mutants (Fig. 2). Mutant sprouters persist at low densities for far

longer than non-sprouters, have much slower rates of spread and much greater variance in rates, largely because of the long persistence time of individuals (Fig. 2). In this respect sprouters behave rather like sexual apomicts hoarding mutations. Secondly there is a significant probability of flammability spreading, without additional fitness advantages, as long as it results in fire spreading to neighbours (Fig. 4). This result appears to be due to a storage effect (Chesson and Warner 1981) where a rare favourable regeneration episode is "stored" over subsequent unfavourable episodes because the new recruits persist by sprouting. Thirdly, flammability is very likely to spread in a population if there are even slight survival
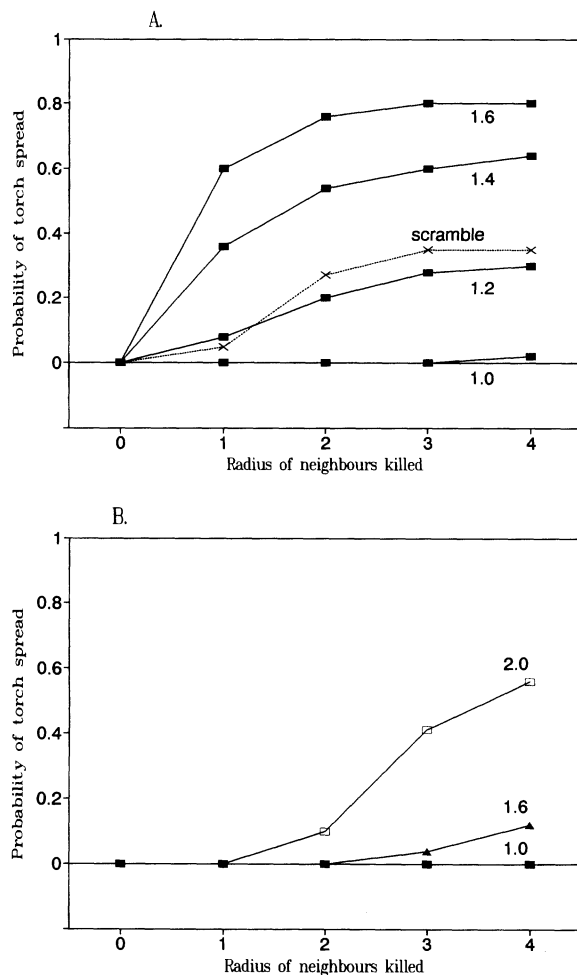

Fig. 3. Probability of spread of a flammable non-sprouter in relation to the radius of neighbours burnt calculated as the proportion of 50 simulations in which "damps" went extinct. A. Flammability linked to seedling advantages expressed in contest (solid lines) or scramble (dashed line) competition. Values indicate varying fitness, w, relative to the "damp" genotype for contest competition and $w = 1.6$ for scramble competition. Fecundity and dispersal held constant ($S = 8d^{-2}$). B. Flammability linked to fecundity advantage. Values indicate fecundity relative to the damp genotype ($C = 8$). Dispersal held constant, ($k = -2$) with an unbiased lottery ($w = 1$).
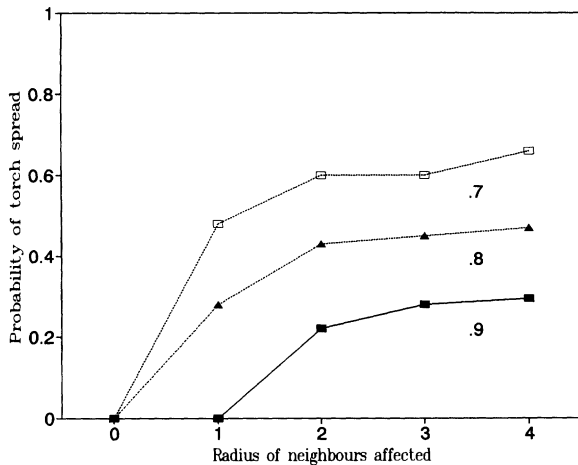
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Fig. 4. Probability of spread of a flammable sprouter in relation to the radius of neighbours affected. Values indicate m_d, the probability of "damp" neighbours surviving burning compared to 0.9 for torch genotypes. Fecundity and dispersal were held constant ($S = 8d^{-2}$) in an unbiased lottery ($w = 1$).

advantages ($m_t = 0.9$, $m_d = 0.8$) for the flammable genotype.

Discussion

Two general points emerge from this analysis of the evolution of flammability: flammability can evolve only if 1) fire is propagated to neighbours, and 2) if traits that promote flammability confer additional fitness benefits. These results hold for both sprouting and non-sprouting fire life histories. We first consider the effect of increased flammability on neighbours. In woody plants, crown fires which burn the canopy are more likely to damage neighbouring plants than surface fires. In the *Protea/Leucospermum* example cited earlier, Yeaton and Bond (1991) showed that *Leucospermum* plants with canopies touching neighbouring flammable *Protea* individuals had a much higher probability of burning to death (79%) than isolated individuals (44%). Our results imply that flammability would evolve only in dense populations so that flammability-enhancing traits should be found only in species regularly occurring in dense stands. We predict that intraspecific variation in flammability traits should follow density gradients with the least flammable plants in sparse populations. In fynbos Proteaceae, the emergent small trees and tall shrubs with non-sprouting but fire surviving life histories and low flammability (e.g. *L. conocarpodendron*, *Mimetes fimbriifolius*, and *Leucadendron argenteum*, Rourke 1972, Williams 1972) occur in sparse populations whereas the overstorey of high flammability, fire-killed, non-sprouting shrubs usually occur in dense stands (Bond et al. 1984). We would predict similar relationships between density and flam-

mability in North American conifers. Flammability traits would not be expected in savanna trees since tree densities are typically too low for fire to spread between canopies of neighbouring trees.

The simulation results show that flammability is most likely to evolve where flammability-enhancing traits have additional benefits. Alternatively a mutation conferring these benefits (e.g. enhanced growth or survival) would be more likely to spread if it also enhanced flammability to the extent of killing neighbours thus creating space for its progeny. What is the likelihood of such a syndrome of traits occurring and can fire ever be disentangled from other forces as a selective agent?

In the context of our study, the important traits are those which have fitness benefits while at the same time increasing flammability. Secondary chemicals which enhance flammability are thought to act also as defences against herbivores (e.g. Rundel 1981, Snyder 1984). There are several structural traits that could enhance both carbon gain and flammability, especially in well lit early post-burn conditions. Early and prolific branching will maximise lateral spread, reduce allocation to supporting stems, resulting in increased relative growth rates (Grime 1979, Givnish 1988, Tilman 1988) while at the same time increasing the probability of fires spreading into the canopy (Kercher and Axelrod 1984). As a result one would expect flammable genotypes to branch earlier and have shorter stature than less flammable relatives. Architectural changes leading to increased carbon gain could also influence flammability through the allometric relationship between branch number and branch thickness (White 1983, Bond and Midgley 1988). More branches allow more efficient use of light in well-lit post-fire conditions but the allometric consequence of branching prolifically would be thinner branches with higher surface area to volume ratios and increased flammability (Rundel 1981).

Fire survival by sprouting carries an allocation cost. Any flammability-enhancing trait that also increased carbon gain could improve fire survival if the carbon was allocated to survival structures. For example, Pate and co-workers (Pate et al. 1990, 1991) have shown that resprouting Australian shrubs and monocots have high carbon allocation costs to root reserves compared to nonsprouters allowing increased capacity for sprouting after fire. Similar costs can be anticipated in the production of thick fire resistant bark.

The difficulty lies in distinguishing the importance of fire from other forces as selective agents for enhanced flammability (Snyder 1984, Christensen 1985, Troumbis and Trabaud 1989). One possibility is to explore variation in the retention of flammability-enhancing structures after they have served their alternative function. Trees vary greatly in the degree to which they shed shaded branches (Millington and Chaney 1973). Though early branching may enhance carbon gain, there can be no physiological advantage in retaining these branches when they have been shaded by subsequent growth. However the reten-

tion of branches increases the likelihood that fires will be carried up to tree canopies. The capacity to self-prune may thus be a useful trait for exploring the evolution of flammability. We predict that in comparisons of flammable and less flammable species of co-occurring trees, or intraspecific variants, the least flammable will self-prune and occur at low densities while the most flammable will retain dead branches and occur in dense stands. Similar patterns may occur in delayed leaf fall and retention of dead leaves in the canopy.

A second possibility is to explore the association between fire-adapted reproductive traits and flammability. Serotiny is the retention of seeds in woody structures in the canopy of a plant until fires stimulate their release (Critchfield 1957, Gill 1975, Lamont et al. 1991). Serotiny is associated with large stand-destroying fires (Muir and Lotan 1985) and should therefore correlate well with flammability. The degree of serotiny is under genetic control in at least some species (Perry and Lotan 1979) and shows intraspecific variation in conifers (Critchfield 1957, Givnish 1981) and *Banksia* species (Cowling and Lamont 1985). We predict an association between serotiny and canopy architecture in these species such that strongly serotinous populations should have more flammable architectures, including reduced height and retention of dead canopy material, and generally occur in denser populations than weakly serotinous ones.

Conclusions

As sessile creatures, plants have limited effects on their neighbours. By exploiting fire, they can extend those effects. We have shown that structural and biochemical traits in fire-prone environments can evolve to increase flammability while also serving other functions. We predict that the frequency of these traits should differ in populations with consistently sparse populations and those in dense stands because of the selective advantage of killing neighbours. However an unequivocal demonstration that a flammability enhancing trait evolved under selection by fire may prove at least as difficult as untangling the importance of herbivores from other selective forces in the evolution of plant "defensive" traits (Coley et al. 1985, Grubb 1992).

Our simulation model suggests that flammability can evolve for individual benefit. However, the importance of fire in the evolution of floras goes far beyond individualistic selection. Vast tracts of the earth carry the vegetation they do because of the prevailing fire regime (Heinselman 1973, Gill 1975, 1981, Romme 1982, Booysen and Tainton 1984, Stott et al. 1992). Fire acts as a powerful selective filter excluding or admitting species to an ecosystem depending on whether pre-existing traits conform to the prevailing fire regime. The evolution of flammability, even if only in the few species that dominate the fuel, would be one factor instrumental in determining fire regimes and therefore the access of species to these fire-prone biomes which today cover millions of square kilometres.

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