CHAPTER 8

Concepts of Fire Effects on Plant Individuals and Species

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ABSTRACT

Plants are assumed to adapt to fire regime. The recurrence intervals and spatial patterns of fires in the boreal forest, plus the ubiquity of most plants, render it unlikely that species-wide adaptations to burning regimes of particular sizes, timings, and intensities can be detected. On the other hand, it is reasonable to expect the evolution of broad, overlapping strategies for coping with fire. Plants are grouped as invaders, evaders, avoiders, resisters, and endurers in order to examine presumed adaptive traits such as seeding from a distance, seed storage in 'banks', sprouting from protected tissues, and resistance to burning. The categories are relevant to forecasting succession, given knowledge of fire behaviour and terrain.

8.1 INTRODUCTION

This chapter examines the ecological role of fire in the adaptations of plants, focusing primarily on the vegetation of the boreal forest region in North America. Although the ecology of northern European forests is similar, only passing reference has been made to the literature of the Fennoscandian countries. The chapter begins with an examination of some characteristics of fires, and then the functional analysis of plant adaptations to fire is discussed. Concluding sections deal with problems of identifying evolutionary responses to environmental forces and with the relevance of autecological information in forecasting post-fire succession. The botanical names in the text and tables can be found with their authorities in Moss (1959), Hale (1969), and Crum (1973).

8.2 PATTERNS OF FIRE IN SPACE AND IN TIME

The large regional pattern of fires varies with macroclimatic regime while locally the pattern varies with terrain (landform-vegetation). Johnson (1979) proposed that the distribution of intervals between fires, regionally and
locally, could be fitted by the Weibull function. Van Wagner (1978a) showed that the age distribution of fire-generated patches of forest (constituting the same frequency distribution as the between-fire intervals) should in theory fit the negative exponential function (which is one form of the Weibull function), assuming random ignitions and equal probabilities of burning everywhere. Despite the unlikelihood of such simple assumptions for complex terrain, he demonstrated a reasonable fit to several sets of empirical data from northern forests.

As a working hypothesis, the negative exponential distribution has a number of appealing characteristics. Assuming random fires at a constant rate, the reciprocal of fire probability at any place equals the fire cycle or fire rotation period, which is also the mean of the ages of the fire-initiated patches. The fire cycle can therefore be calculated with ease from conventional forest inventory data. Common estimates of fire cycles for the boreal forest are 50 to 100 years (Kourtz, 1967; Heinselman, 1973; Woods and Day, 1977; Zackrisson, 1977; Van Wagner, 1978a).

The negative exponential model predicts that about two-thirds of a region will carry stands that are younger than the fire cycle and about one-third will carry stands that are older than the fire cycle. Thus a heterogeneous patchy forest is predicted as the regional norm, with some areas reburning at short intervals (because of random ignitions) while others escape burning for long periods.

The largest percentage of the annually burned area in northern forests is known to result from a few large fires (Rowe, 1979a). However, successive fires never coincide in area and this, plus the prevalence of unburned inclusions, confers on the regional vegetation its multi-aged character. Low-intensity fires that do not kill trees go undetected in age-class analyses, but they add further variation to the spatial mosaic at the understorey level.

Biomass accumulation is a function of time since last fire, so fire intensity depends, to some extent, on fire frequency (Kilgore and Taylor, 1979; Heinselman, 1981). The relationship is not linear because fuel availability does not parallel biomass (Van Wagner, 1979). However, if fire-to-fire frequencies for a major region such as the boreal forest or its sections fit the negative exponential distribution, then in a general way so should fire intensities. Also, assuming random ignitions the probabilities of fire recurrence and intensity at any given place are fitted by a Poisson distribution (Van Wagner, 1978a) as exemplified in Table 8.1.

It should be noted, however, that as a natural selection filter, fire intensity must be interpreted by its impacts on plants according to their phenologies. Daubenmire (1968) drew attention to the greater sensitivity to spring fires of cool-season grasses (such as *Poa pratensis*) compared with the later sprouting warm-season grasses (such as *Andropogon scoparius*). Phenological differences in the boreal flora also effectively modify the impact of fire intensity.
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Table 8.1 The probability that any given place within a region will experience N fires during one theoretical fire cycle of 60 years, according to the Poisson distribution where \( \bar{x} = 1 \) (average age of stand equals 1 fire cycle) and \( P_N = e^{-1/N} \). Fire intensity is measured in kilowatts per metre of fire front.

<table>
<thead>
<tr>
<th>N</th>
<th>Probability</th>
<th>Average interval fire-to-fire (years)</th>
<th>Expected fuel buildup fire-to-fire</th>
<th>Fire intensitya</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0.3</td>
<td>12</td>
<td>Sparse</td>
<td>Light surface fires &lt;300 kW m(^{-1})</td>
</tr>
<tr>
<td>4</td>
<td>1.5</td>
<td>15</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>6.1</td>
<td>20</td>
<td>Moderate</td>
<td>Surface or crown fires 300–1500 kW m(^{-1})</td>
</tr>
<tr>
<td>2</td>
<td>18.4</td>
<td>30</td>
<td>Intense crown fires</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>36.8</td>
<td>60</td>
<td>Heavyb</td>
<td>Intense crown fires &gt;1500 kW m(^{-1})</td>
</tr>
<tr>
<td>0</td>
<td>36.8</td>
<td>60+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

aSee McArthur and Cheney (1966); Van Wagner (1978b).
Conversion to Btu/sec/ft = kW/m x 0.289.
bHeavy fuel buildup may relate to deadfall from a previous fire and not simply to post-fire ‘new growth’.

Furthermore, the actual release of energy as a fire passes, expressed as kilowatts per metre of fire front (Van Wagner, 1978b), may bear little relation to the survival of perennating plant parts buried in the soil. The important parameters are depth of burn in the duff and soil temperature profile, related to fire residence time (duration) or ‘burnout time’ (McArthur and Cheney, 1966).

Fire severity is the appropriate descriptor of the degree of organic removal and of soil heating. Thus, on sandy soils a fire of low intensity (low energy release) may nevertheless be of high severity (all organic cover removed and near-surface seeds, rhizomes, and roots killed). On the other hand, summer and autumn fires, when the duff is dry, tend to be more severe than spring fires when duff is moist, and the effects on the survival and resprouting of particular species can be quite different (Miller, 1977). Some of the most intense fires recorded in the boreal forest have had little effect on subsequent vegetation because they occurred when the soil was still wet or frozen in the spring (Kiil and Grigel, 1969).

There is a strong likelihood that fire cycles calculated for regions are composites of variable fire cycles at the local site level where terrain is relatively uniform. Zackrisson (1977) reported that dry lichen-heath sites
burned three times as often as moister blueberry-herb sites, and he found the same ratio of fires in a comparison of south-facing and north-facing moraine slopes. Similar observations have been reported by Rowe and Scotter (1973) and by Tande (1979). This means that a 100-year fire cycle for a large area might comprise upland cycles of 60 and 80 years on sandy and clay substrates plus lowland cycles of 120 and 140 years on bog borders and deep peat, respectively. The relevance to fire ecology of ecological land classifications that identify terrain units of combined vegetation-landform at regional and subregional levels is therefore apparent (Rowe, 1979b).

The variable patterns of boreal fires in space, time, and intensity are important. They cast doubt on the wisdom of searching for species-wide selection pressures such as may result in other regions and on other continents from consistent predictable patterns of short-interval low-intensity fires, or long-interval high-intensity fires. This seems particularly pertinent where wide-ranging species—the majority of the boreal and low arctic flora—are concerned.

The serotiny of *Pinus banksiana*, for example, shows a statistical increase northwards (Schoenike et al., 1959), but even among the most serotinous populations a few open-cone individuals testify to the variability of the selection process. Young pines of most populations tend to be non-serotinous, suggesting that seed storage in closed cones is advantageous only when stands are closed and mature. Referring to papers of Lotan (1976) and Schoenike (1976), Gill (1981) suggested that the serotiny of *Pinus contorta* is an adaptation to good sites, where high productivity produces rapid fuel accumulation and encourages fires of high intensity. This implies that in other places where fires are fewer, and especially on low-productivity areas, selection is for non-serotinous cones (Smith, 1970). The sites of non-serotinous pine described by Lotan (1976) appear to agree with the hypothesis.

Specific adaptations of plants to fire, if they are to be found, must be at the local ecosystem level where in the context of their immediate experiences the fit are separated from the unfit.

### 8.3 LIFE-FORMS, FUNCTIONS, AND FIRE

In order to relate plants to the fire environment, those morphologic and developmental traits advantageous for survival must first be identified. The conventional life-form classification (Raunkiaer, 1934) based mainly on position of the perennating organs relative to the soil surface, is relevant insofar as location of buds and seeds in the vertical plane matches a gradient of energy release during fire. Obviously the life-forms with aerial perennating parts—the phanerophytes and chamaephytes—are most susceptible to destruction by burning, while the surface and sub-surface types—the hemi-
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cryptophytes and cryptophytes—are moderately and well protected. Many forbs (broad-leaf herbs) are cryptophytes and, as noted by Vogl (1979), most grasses are hemicryptophytes. This helps to explain the observation (Daubenmire, 1968) that frequent fires favour forbs over grasses. Therophytes—surviving the unfavourable season in the seed stage—share the advantages of hemicryptophytes or of cryptophytes depending on whether their seeds lie at the surface or within the soil.

Raunkiaer’s life-forms were designed with severity of regional climate in mind, and with the idea that life-form spectra would allow regional comparisons of climate. Therefore the classification is not fully appropriate for study of fire-induced responses and adaptations. Specific ecological problems require appropriate structural-functional concepts (Knight and Loucks, 1969).

Table 8.2 Descriptors of the ‘regeneration niche’ of plant species (modified from Noble and Slatyer, 1977)

<table>
<thead>
<tr>
<th>I. Mode of regeneration and reproduction—first vital process</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetative-based:</td>
</tr>
<tr>
<td>V species — able to resprout if burned in the juvenile stage</td>
</tr>
<tr>
<td>W species — able to resist fire in the adult stage and to continue extension growth after it (though fire kills juveniles)</td>
</tr>
<tr>
<td>Disseminule-based:</td>
</tr>
<tr>
<td>D species — with highly dispersed propagules</td>
</tr>
<tr>
<td>S species — storing long-lived propagules in the soil</td>
</tr>
<tr>
<td>C species — storing propagules in the canopy</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>II. Communal relationships—second vital process</th>
</tr>
</thead>
<tbody>
<tr>
<td>T species — tolerants that can establish immediately after a fire and can persist indefinitely thereafter without further perturbations</td>
</tr>
<tr>
<td>R species — tolerants that cannot establish immediately after fire but must wait until some requirement has been met (e.g., for shade)</td>
</tr>
<tr>
<td>I species — intolerants that can only establish immediately after a fire. Rapid-growth pioneers, they tend to die out without recurrent disturbances</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>III. Time scale of critical life history events—third vital process</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measured from time zero (most recent fire) and plotted using the following symbols on a linear time axis:</td>
</tr>
<tr>
<td>p — propagules arrive on burned site</td>
</tr>
<tr>
<td>m — reproductive maturity reached, production of propagules begins</td>
</tr>
<tr>
<td>l — loss of species from community by senescence</td>
</tr>
<tr>
<td>e — loss of propagules from stored sources (note e = ∞ for D species)</td>
</tr>
</tbody>
</table>
Autecological characters appropriate to the plant-fire interaction have been proposed by Lyon and Stickney (1976), Noble and Slatyer (1977), and Catellino et al. (1979). The last two papers emphasize three 'vital attributes' that constitute dimensions of the species 'regeneration niche': reproduction, competition, and life cycle. The scheme shown in Table 8.2 was inspired by the above concepts although a number of liberties have been taken in redesign for the subsequent discussion.

Note that first place is given to method of regeneration (vegetative extension) and reproduction. Although account is taken of competitive and symbiotic interactions, these are under emphasized relative to their heavy emphasis in population biology literature. In a pulsed environment, characteristics serving invasion, seed storage, and regrowth take precedence over those serving competition, for interspecies reactions may not develop before

Table 8.3 Mode of persistence of plants in the context of fire

<table>
<thead>
<tr>
<th>I. Disseminule-based, propagating primarily by diaspores</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Invaders</td>
<td></td>
</tr>
<tr>
<td>Highly dispersive, pioneering fugitives with short-lived disseminules (DI species of Table 8.2).</td>
<td></td>
</tr>
<tr>
<td><em>Ceratodon purpureus</em></td>
<td><em>Senecio congestus</em></td>
</tr>
<tr>
<td>Evaders</td>
<td></td>
</tr>
<tr>
<td>Species with relatively long-lived propagules that are stored in soil or in canopy (CI, SI, and ST species).</td>
<td></td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td><em>Rubus strigosus</em></td>
</tr>
<tr>
<td><em>Corydalis sempervirens</em></td>
<td></td>
</tr>
</tbody>
</table>

| Avoiders                                                 |  |
| Shade-tolerant species that slowly reinvade burned areas; late successional, often with symbiotic requirements (DT and DR species). |  |
| *Abies balsamea*                                         | *Goodyera repens* |

| II. Vegetative-based, propagating primarily by horizontal and vertical extension |  |
| Resisters                                                |  |
| Shade-intolerant species whose adult stages can survive low-severity fires (WI species). |  |
| *Pinus banksiana*                                        | *Eriophorum vaginatum* |

| Endurers                                                 |  |
| Re sprouting species, shade-intolerant or tolerant, with shallow or deep buried perennating buds (VI and VT species). |  |
| *Populus tremuloides*                                    | *Alnus crispa* |
another perturbation occurs. Grubb (1977) has argued persuasively that there are infinite possibilities for species' coexistence on the basis of differences in 'regeneration niche', provided that ecosystems continue to pulse. Thus competition may often be a relatively unimportant part of community niche structure, particularly in severe northern boreal environments.

8.4 FUNCTIONAL ADAPTATIONS OF PLANTS

The first two 'vital attributes' constituting a mode of persistence are summarized in five categories in Table 8.3. A few examples of boreal species in each category are given. The letter descriptors relate species groups to the 'regeneration niche' outlined in Table 8.2. For the discussion that follows, papers by Lutz (1956), by Ahlgren and Ahlgren (1960), and by Ahlgren (1974) proved particularly useful as sources of autecological information. Lyon and Stickney (1976) have given a useful list for the Rocky Mountains. Other sources are acknowledged in the appropriate sections. Many species cannot be specifically identified for one category nor is there any implication that they can be so identified in the future. An element of choice, based on my own experience in northern terrain, is expressed in the selected examples.

8.4.1 Invaders

These early arrivers owe success to the copious production of short-lived wind-disseminated propagules. They tend to be shade-intolerant pioneering 'fugitives', dependably present though in variable quantity after fire regardless of its cycle length and intensity. Once established, they usually flower and fruit profusely or spread vegetatively. These are good 'fireweeds'.

Examples of invaders on dry or freshly burned sites are:

- *Ceratodon purpureus*
- *Polytrichum piliferum*
- *Arctagrostis laifolia*
- *Betula papyrifera*
- *Salix bebbiana*

Examples of invaders on moist to wet burned sites are:

- *Funaria hygrometrica*
- *Marchantia polymorpha*
- *Agrostis scabra*
- *Calamagrostis canadensis*
- *Carex aenea*
- *Salix planifolia*
- *Senecio congestus*

For specific reference to members of these groups see Skutch (1929), Scotter (1964 and 1972), Crum (1973), Viereck (1973), Black (1977), Viereck and Dyrness (1979), and Archibold (1980).

Several special cases merit comment. The literature concerning *Epilobium angustifolium* is ambiguous, but evidence is strong that, like *Calamagrostis*
canadensis, it is both an enduring sprouter and an invader by seed. *Populus tremuloides* commonly invades by seed on the rocky terrain of the Precambrian Shield but elsewhere seedlings rarely survive and regeneration is by vegetative means.

### 8.4.2 Evaders

An interesting suite of species store seed in the canopy, humus, or mineral soil. Evasion of high temperature, with rapid subsequent germination, is the strategy. There are only a few boreal trees with seed banks in the canopy: *Pinus banksiana* and *P. contorta* with serotinous cones throughout the crowns, and *Picea mariana* with terminally placed clumps of semi-serotinous cones. Both respond to high temperatures with abundant seed release. Although *Picea glauca* retains small amounts of seed in its canopy for periods up to 10 months after cone ripening, it qualifies better as an invading semi-tolerant tree.

Pronounced dormancy mechanisms are necessary for those seeds that accumulate in the soil. It is likely that some plants in this category have hard or refractory seeds, triggered to germinate by fire-induced high temperatures (Uggla, 1958; Cushwa *et al.*, 1968; Vogl, 1974). Two kinds of ‘bankers’ can be distinguished: shade-intolerant early successional ephemerals and semi-tolerant to shade-tolerant perennials that persist in successional communities long after fire.

The short-lived ephemerals are often annual or biennial. In habit they resemble the mud flat ruderals described by van der Valk and Davis (1978) that lie over long periods between brief post-fire flowerings. During their short periods of abundance they make ‘one-shot’ seed deposits on the burned surface, which subsequently will form the base of the humus layer. As organic horizons are seldom completely burned away (and as some seed may work into the protection of the upper mineral soil), the propagules of such plants are favourably situated for survival even through intense and severe fires. The habits of these and similar species are referred to by Ahlgren (1960, 1979), Vierreck (1973), Ohmann and Grigal (1979). Examples are:

- *Corydalis sempervirens*
- *Aralia hispida*
- *Geranium bicknellii*
- *Polygonum cininode*

The semi-tolerant and shade-tolerant species, persisting into later successional stages, contribute to the seed store for a much longer period. Consequently their ‘banks’ are less localized. Seed is distributed through the humus as it accumulates and some may filter into the upper mineral soil (Moore and Wein, 1977). Mostly the species are berry-fruiting and the accumulating seed store results from bird and mammal vectors. Regeneration of such species is favoured by fires of low severity and short duration that
remove little of the surface organic layer. Examples of semi-tolerant and shade-tolerant seed-banking species are:

- *Geocaulon lividum*
- *Symphoricarpos* spp.
- *Prunus pensylvanica*
- *Ribes* spp.
- *Rubus strigosus*
- *Viburnum* spp.
- *Shepherdia canadensis*
- *Cornus stolonifera*

These and similar species have been commented on by Quick (1962), Marks (1974), Moore and Wein (1977), and Chapin and Van Cleve (1981).

### 8.4.3 Avoiders

Members of this third class of disseminule-based plants are farthest from any direct adaptations to fire. They are often listed in the literature as 'species occupying unburned areas', meaning that they arrive late in succession and prosper where fire cycles are long. As members of relatively old and unperturbed communities they tend to be mesophytic and tolerant, some requiring prior modification of the ecosystem (by humus accumulation or leafy shade) before they can invade by propagules and maintain themselves by vegetative means.

Examples of tolerant avoiders are:

- *Abies balsamea*
- *Linnaea borealis*
- *Picea glauca*
- *Mitella nuda*

Dependent avoiders include many saprophytic vascular plants as well as shade-requiring mosses and lichens:

- *Circaea alpina*
- *Corallorhiza* spp.
- *Goodyera repens*
- *Monotropa uniflora*
- *Hylocomium splendens*
- *Peltigera aphthosa*

References to these and related species have been given by Ahlgren (1960), McLean (1969), Flinn and Wein (1977), and Zackrisson (1981).

*Arceuthobium americanum* is the interesting case of an intolerant obligate seeder without fire-evading or fire-enduring mechanisms. Its survival depends on fire avoidance, yet it parasitizes the fire-dependent pine. Its refuges are very dry open sites where its fruits are not attacked by the fungus *Wallrothiella arceuthobi* Ros. (Dowding, 1929) and where crown fires are uncommon due to low forest density and sparse fuel accumulation. From such foci it spreads between fires to surrounding forests (Alexander and Hawksworth, 1975). Paradoxically, infected trees are more susceptible to crown fires than uninfected trees, because the parasite causes 'brooming' and the retention of needles (Dowding, 1929).

### 8.4.4 Resisters

The aboveground parts of only a few intolerant northern species can
successfully resist fire. Usually this ability is low in juvenile stages but increases with age. Examples are:

*Pinus banksiana* and *P. contorta*

**Eriophorum vaginatum**

At maturity, the relatively thick bark of the pine protects against creeping ground fires, while the lack of ladder fuel (due to self-pruning and peripheral foliage) reduces the frequency of crown fires. Pine is the only boreal tree that survives repeated scarring. *Picea mariana*, *P. glauca*, and *Larix laricina* infrequently live through single fires but rarely do they double scar and survive. Mature *Eriophorum vaginatum* resists fire by its dense tussock form (Wein and Bliss, 1973).

Tall shrubs such as *Alnus crispa* and dwarf shrubs such as *Vaccinium* spp. are occasionally pruned by low-intensity fires without total killing of branch tissue. However, the accumulation of leaves under fruticose plants usually assures sufficient fire intensity to kill the cambium at the ground surface, thus killing all higher parts as well. Consequently shrubs are sprouting endurers rather than resisters of fire.

### 8.4.5 Endurers

Plants able to resprout after the passage of fire comprise a large and diverse group of phoenix species. As juveniles or adults they regenerate from stem bases, rhizomes, root crowns, roots, and other belowground organs. Such 'V-species' include many of the hemicryptophytes and cryptophytes that in the northern forests and tundra make up two-thirds to three-quarters of the flora (Whittaker, 1975: 64). Their importance has led some to conclude that there is little successions of the species-replacement type in certain boreal forests since, with a few notable exceptions among the trees and the cryptogams, the post-fire vegetation simply sprouts from the pre-fire stock (Smith and Sparling, 1966; Black and Bliss, 1978). The endurers should not be confused with tolerant sprouting 'avoiders' that maintain themselves vegetatively in late successional communities as long as fire does not visit them.

Survival of sprouting species in the fire environment depends greatly on vertical positioning of the perennating parts in the insulating humus and mineral soil. A study by McLean (1969) showed that the proliferation of at least some leguminous species after fire is due to their deep, well protected perennating buds. However, there are difficulties in categorizing species as to depth of sprouting buds except in a site-specific way. For example, *Vaccinium vitis-idaea* has been described as having shallow subterranean runners in Sweden (Uggla, 1958), as rooting in the moss layer in Alaska (Chapin and Van Cleve, 1981), and as deep-rooted in northern Manitoba (Ritchie, 1959). It is very susceptible to destruction by fire according to the first two reports, but resistant and enduring according to the third.
In addition to the ecotypic and phenotypic differences that can be expected in wide-ranging species, the positioning of underground buds is also influenced by the thickness of the humus layer. As forests and shrublands increase in biomass, the rooting systems of constituent plants tend to migrate upwards into the thickening duff layer (Siren, 1955). The probable reason is that the zone of maximum biological activity and nutrient release also migrates upwards during succession (Viereck, Chapter 11, this volume). Species initially rooted in mineral soil may, if they survive into the matuer community, be rooted in the H or F humus layers where their susceptibility to fire damage in dry years is greatly increased. From this there follows the interesting implication, supported by observations of fire effects in old forests, that deep burning long-interval fires may virtually eliminate sprouting species while clearing the ground for invading species. On shorter fire cycles with low fuel buildup and fire intensities, species tend to stay rooted in mineral soil where they survive and contribute to the early stages of recolonization after fire (Flinn and Wein, 1977; Chapin and Van Cleve, 1981).

Examples of early successional shade-intolerant sprouters are:

*Populus tremuloides*  
Arctostaphylos uva-ursi

*Apocynum androsaemifolium*  
*Maianthemum canadense*

*Arctostaphylos uva-ursi* is variable: listed by some as a sprouter (Scotter, 1972) but by others as incapable of vegetative reproduction from underground parts (Lutz, 1956) or as susceptible to fire because its ‘fibrous roots and stolons’ are in the humus (McLean, 1969). In northern Saskatchewan the species sprouts strongly from golfball-sized basal burls (lignotubers) in the mineral soil (personal observation). Further, its name suggests an animal vector, implying the likelihood that it is a seed-banking species (SI). Uggla (1958) reported that its thick-shelled seeds survive fire in the upper soil and are stimulated to germination by the momentary high temperatures of passing fires.

Examples of semi-tolerant to shade-tolerant late successional sprouters are:

*Alnus crispa*  
*Equisetum sylvaticum*

*Aralia nudicaulis*  
*Pteridium aquilinum*

*Cornus canadensis*

The last group, and others like them (see Ahlgren, 1960; McLean, 1969; Heinselman, 1973; Beasleigh and Yarranton, 1974; Archibold, 1979, and Viereck and Dyrness, 1979), comprise a group of ‘superspecies’ whose prevalence attests to their adaptability. Able both to endure burning and to maintain themselves under a canopy, they epitomize success almost regardless of fire cycle length. However, their mesophytism confines them to environments with relatively longer fire cycles than those of the intolerant sprouters.

Ericaceous chamaephytes, and dwarf shrubs with similar habits such as
Table 8.4  Suggested adaptations of species groups to fire cycles

<table>
<thead>
<tr>
<th>Short fire cycle</th>
<th>Intermediate fire cycle</th>
<th>Short, intermediate, or long fire cycle</th>
<th>Very long fire cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Endurers</strong>&lt;sup&gt;a&lt;/sup&gt;</td>
<td><strong>Resisters</strong>&lt;sup&gt;VI species&lt;/sup&gt;</td>
<td><strong>Invaders</strong>&lt;sup&gt;DI species&lt;/sup&gt;</td>
<td><strong>Avoiders</strong>&lt;sup&gt;DT species&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td><em>Pinus banksiana</em></td>
<td><em>Ceratodon purpureus</em></td>
<td><em>Abies balsamea</em></td>
</tr>
<tr>
<td><em>Apocynum androsaemifolium</em></td>
<td><em>Eriophorum vaginatum</em></td>
<td><em>Polytrichum piliferum</em></td>
<td><em>Picea glauca</em></td>
</tr>
<tr>
<td><em>Arctostaphylos uva-ursi</em></td>
<td><em>Evaders CI species</em></td>
<td><em>Epilobium angustifolium</em></td>
<td><em>Linnaea borealis</em></td>
</tr>
<tr>
<td><em>Maianthemum canadense</em></td>
<td><em>Pinus banksiana</em></td>
<td><em>Calamagrostis canadensis</em></td>
<td><em>Mitella nuda</em></td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Evaders</strong>&lt;sup&gt;SI species&lt;/sup&gt;</td>
<td><strong>Evaders</strong>&lt;sup&gt;ST and SI species&lt;/sup&gt;</td>
<td><strong>Endurers</strong>&lt;sup&gt;VT species&lt;/sup&gt;</td>
<td><strong>Avoiders</strong>&lt;sup&gt;DR species&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>Corydalis sempervirens</em></td>
<td><em>Rubus strigosus</em></td>
<td><em>Alnus crispa</em></td>
<td><em>Goodyera repens</em></td>
</tr>
<tr>
<td><em>Geranium bicknellii</em></td>
<td><em>Comandra livida</em></td>
<td><em>Aralia nudicaulis</em></td>
<td><em>Circaea alpina</em></td>
</tr>
<tr>
<td><em>Aralia hispida</em></td>
<td><em>Prunus pensylvanica</em></td>
<td><em>Cornus canadensis</em></td>
<td><em>Hylocomium splendens</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Equisetum sylvaticum</em></td>
<td><em>Peltigera aphthosa</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pteridium aquilinum</em></td>
<td></td>
</tr>
</tbody>
</table>

Dry  Moisture gradient  Moist

<sup>a</sup>Letter symbols as in Table 8.2.

*Betula glandulosa* and *Empetrum nigrum*, also qualify as species whose main stratagem is vegetative regeneration. The rarity of buried viable seeds associated with these species in the southern forests and in the subarctic have been reported by Moore and Wein (1977) and by Johnson (1975). *Vaccinium myrilloides*, *V. vitis-idaea*, *V. uliginosum*, *Ledum palustre*, and *L. groenlandicum* are examples of ericads that thrive as resprouters in the frequently burned forest ecosystems of the southern boreal and the subarctic.

### 8.5 SUCCSSION

A suggestion as to how the species groups are adapted to fire cycles of different lengths is shown in Table 8.4. Frequent fires (short cycle) favour sprouting shade-intolerant species and those ephemerals that bank seed at the
mineral soil surface. A fire cycle of intermediate length allows species that are resistant in the adult stage to mature and survive, along with those that bank seeds in the canopy or in the humus layer. Prospering under short, intermediate, or long fire cycles are the pioneering invaders and the shade-tolerant sprouting 'superspecies'. With long fire cycles, the disseminule-based tolerant and symbiotic species develop in 'climax' communities.

Note that increasing fire cycle length, from the left side of Table 8.4 to the right, matches an apparent moisture gradient, as might be expected. Thus short fire cycle plants tend to be xerophytes, while long fire cycle plants tend to be mesophytes. Anderson and Bailey (1980) reported that annual burning in the aspen parkland of Alberta increases xerophilic species.

The relevance of the adaptations generalized in Tables 8.2, 8.3, and 8.4 to prediction of succession is obvious, given knowledge of fire cycle lengths. On this pattern, papers by Lyon and Stickney (1976) and by Cattelino et al. (1979) have explored the possibilities of modelling the multiple pathways of succession in western North American forests.

Beyond recognition that post-fire species-site interactions are complex (Shafi and Yarrantan, 1973), the fact that, in principle, succession can never be successfully predicted and modelled on the basis of autecological information alone needs emphasis. The populations and communities in which man is interested are only components of ecosystems, and the process of succession expresses adjustments between all the components. For example, animal depredation of seed and other propagules is often a critical factor. Questions as to whether succession is endogenous or exogenous (Bormann and Likens, 1979; White, 1979) are strictly academic. Succession must be more than an autogenic process, for ecosystems are not closed. Each tract of the earth’s surface is an open geographic system, exchanging energy and materials (including disseminules) with its neighbours. In short, each landscape ecosystem has an ecology that comprises the web of relationship with the ecosystems that surround it, as well as an internal physiology. To understand and predict the behaviour of organisms on any area (i.e., in any ecosystem) therefore requires attention to their broader environmental matrix, which is most easily conceptualized and identified as terrain.

The problem of predicting vegetation succession is sharply focused in those instances where community composition following fire is derived almost completely from the stand's environment. Suppose that a very old forest, from which intolerant species have disappeared, finally burns after a dry summer. The thick humus layer is consumed down to mineral soil, destroying most of the stored seed population and those persistent resprouting species whose perennating buds have moved upwards into the organic layer. The early successional community will then comprise invading species. The likelihood of their arrival, in what proportions and abundance, can only be
assessed from prior knowledge of the surrounding terrain (landforms, soils, biota) and climatic regime (winds, snow cover, moisture regime).

It follows that predictive models of organism succession have to find ways of linking the components (plants, animals) with their spatial matrix. This bringing together of two levels of organization can be accomplished through the chorologic (spatial) appreciation of terrain and its biotic relationships as expressed in maps. If practical ecological purposes are to be served, the concentration on species, populations, and communities as 'things in themselves' (rather than as ecosystem components in an ecosystem matrix) must be avoided.

8.6 DISCUSSION

Analyses of plant responses to environmental forces can take many routes. Population biologists, for example, have proposed hypotheses concerning evolutionary strategies based on non-competitive and competitive (r and K) relationships (Pianka, 1970), or on interactions between competitiveness, stress tolerance, and unspecified environmental disturbance (Grime, 1977). The difficulty in testing and making sense of such systems reflects the problems of relating functionally labile individuals and populations to one another along continua whose two- or three-dimensional axes cannot be rigorously defined. On the other hand, less theoretical ecological approaches serve specific purposes. For example, Vogl (1974) has suggested that grassland species under the influence of fire be understood not as occupants of successional stages but simply as increasers, decreasers, neutrals, invaders, or retreaters, reflecting responses similar to those from grazing pressure (Stoddart et al., 1975). Such practical schemes position species securely relative to each other on particular sites, but they do not address questions of adaptation. The attempt in this chapter to key adaptive traits (plant-morphogenetic characters of known ecological importance) to a specific environmental force (fire) is perhaps a useful middle ground.

 Harper (1977) has pointed out the difficulties of relating ecological (proximate) and evolutionary (ultimate) effects. 'Adaptation is always retrospective,' he says (p. 776). Wise after the evolutionary fact, we examine the ecological relationships of today's survivors and project them into the past as success stratagems. The philosophical difficulty is the ease with which ecological evidence can be adduced to support theory, when history has swallowed up the circumstances of evolution. Conjecture must therefore constitute a large part of the reasoning about plant adaptations to fire, and about fire effects on plants.

The problem is that the influence of fire on plants cannot be sharply set off from that of other agitations. Morphologic characters that appear to have been selected for survival in the fire environment may be attributed equally
well to biotic or to climatic-soil stresses. Also, presumed adaptations may be fortuitous. The high concentrations of volatile substances in leaves and twigs, attributed by some to selection pressure of herbivory (Chapin and Van Cleve, 1981) or to sympyrosis (Mutch, 1970), may reflect the metabolic necessities of plants in nutrient-poor environments, where assimilates are shunted into hydrocarbons rather than into carbohydrates and proteins (Forrest, 1971).

Furthermore, such adaptations as do serve species survival under fire regimes may represent preadaptations, developed under the influence of earlier and different selective forces. It is conceivable, for example, that the growth habit of grasses and sedges, characterized by high root/shoot biomass ratios (Wein and Bliss, 1973; Clark, 1977), is primarily an adaptation to the need for efficient recycling of nutrients in a dry environment and secondarily to the effects of top 'grazing' by fire and by animals.

Such caveats having been stated, and they are repeated in several outstanding review papers on plants, fire, and evolution (Gill, 1981; Keeley, 1981), there can, however, be little doubt that fire in environments such as the boreal forest has been and continues to be a potent ecological and evolutionary force. On this assumption, the comparative lengths of fire cycles and of organism life cycles assume significance.

Plants whose life cycles are long relative to fire-free episodes must successfully meet the full range of environmental vicissitudes, including fire. The optimum compromise may be phenotypic plasticity (Bradshaw, 1965) that fits the species to survival both of fire and of the ensuing successional stages of the encompassing ecosystem. Species with relatively short life cycles face different problems. If they reproduce sexually between fires, selective pressures may render them unfit for fire survival or for any early post-fire versus a late post-fire role. The solution is either to adopt the fugitive pioneering stratagem or to 'rest over' the inter-fire episodes as dormant seeds or buds, effect lengthening the life cycle relative to the fire cycle in the interests of maintaining genetic integrity.

The fire pulse can either act directly on organisms—when presumably they are selected for resistance to flame, heat, and smoke—or indirectly, where the post-fire environment with its particular physical and chemical components eliminates the unfit. From one viewpoint, fire is the predator seeking out and consuming plants as its energy source, while they either avoid it in the sanctuary of 'escape terrain' or respond on their home ground by erecting defences and safely sequestering their viable resources. From another viewpoint, certain plants can be considered active searchers after fire, tracking down and scavenging burned-over ground whenever it appears, moving quickly and efficiently to profit from newly available resources. Compared with the 'stay-at-homes' these are the fugitives, the active pyrophiles whose numbers rise and fall with the fire cycle like the lynx population tracking the ups and downs of the snowshoe hare. Of course, the
stratagems of survival by escaping fire, by coping with it, or by pursuing it are not mutually exclusive, for all may be practised to some extent by individuals and populations in the course of their life cycles.

8.7 CONCLUSIONS

A search of the literature shows a very large number of articles reporting in various ways and with variable insight how species behave when subjected to periodic fires. The significance of fire as an evolutionary force remains practically unknown. The difficulties of gaining a better understanding of fire-plant relationships centre on the following points which need to be taken into account in pursuing the fascinating study of responses and adaptations:

(1) Fire is one of many periodic perturbations in ecological systems. Its various effects, direct and indirect, interact with other strong selective forces in the environment. Fire is not, for example, the only ‘pruner’ of plant aerial parts, nor the only destroyer of perennating organs in the surface humus layer.

(2) Assuming as a tentative hypothesis that the patterns of fires over large northern regions and in the context of evolutionary time are a random series, then the search for plant species adaptations to particular sizes, timings, and intensities of burning may not be realistic, especially for ubiquitous species.

(3) Within large regions, fires undoubtedly occur more frequently on some terrain types than on others. At this local site level, particularly where short fire cycles are the norm, ecotypic adaptations can be expected.

(4) The search for adaptations to fire should utilize structural-functional criteria, such as those life-form characteristics that bear on the ability of species to persist and regenerate by the stratagems of invasion, evasion, avoidance, resistance, and endurance.

(5) Phenotypic plasticity of perennial species complicates the categorization of plants as single structural-functional types. Species frequently display two or more stratagems between perturbations. Also, morphologic and physiologic changes are usual as plants age, particularly if they are long-lived perennials. In short, complexity rather than simplicity should be expected in the adaptations of organisms to pulsing ecosystems.

(6) Given the functional role of organisms in ecosystems, it is unrealistic to attempt explanations of post-fire succession solely by reference to the autecology of plant species.

8.8 ACKNOWLEDGEMENTS

It is a pleasure to acknowledge stimulating correspondence that included

### 8.9 REFERENCES


