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# FIRE ECOLOGY OF PACIFIC NORTHWEST FORESTS

*James K. Agee*

ISLAND PRESS
WASHINGTON, D.C. ❑ COVELO, CALIFORNIA

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Library of Congress Cataloging-in-Publication Data

Agee, James K.
Fire ecology of Pacific Northwest forests / James K. Agee.
p. cm.
Includes bibliographical references (p. ) and index.
ISBN 1-55963-229-1
1. Forest management—Northwest, Pacific. 2. Fire ecology—Northwest, Pacific. 3. Forest fires—Environmental aspects—Northwest, Pacific. I. Title.
SD144.A13A55 1993
574.5'264—dc20 93-2071
CIP

Printed on recycled, acid-free paper.

Manufactured in the United States of America

10 9 8 7 6 5 4

CHAPTER 5

# FIRE EFFECTS ON VEGETATION

FIRE HAS VARIABLE BUT PREDICTABLE EFFECTS on individual plants. Translating these from the physical to the physiological helps us understand how fire affects vegetation not only at the level of the individual plant but also at the levels of the plant community and the landscape. Further, vegetation provides the fuel that makes fire possible, so we can view fire effects on vegetation as an interaction rather than just a unidirectional effect.

This chapter first describes mechanisms of fire damage to individual plant parts. The differential response of plants may be due to fire variation or to specific adaptations of plants to survive as individuals. Some species with clear adaptations to fire may appear to increase the flammability of the community within which they grow, but the issue of fire-dependent ecosystems is a controversial topic on which debate is likely to continue. Also controversial, at least historically, has been the role of fire in plant succession theory. In recent years the emphasis has moved away from the development of all-encompassing theories of vegetation development to

the construction of process-oriented ecological models. These dynamic models can incorporate fire as an ecological process, and several models applicable to the Pacific Northwest are conceptually described in this chapter. Such models have value in linking physiological processes of individual plants to interactions at the community and landscape levels.

## FIRE AND THE INDIVIDUAL PLANT

Trees can be injured by fire in several ways. Foliage and buds can be killed in the crown of the tree, the bole can be heated to a point where part or all of the cambium is killed, or the roots can be heated and killed. Each of these types of damage depends upon lethal heat contacting live tissue. Although fire temperatures usually exceed 600°C in the flaming zone, plant tissue may be protected from these temperatures by insulation provided by the soil, by tree bark, or by location in the crown of the tree far above the flames and lethal heat.

There is no single critical temperature for tissue death, although duration of 60°C for 1 minute is often noted by researchers as a "standard" lethal time-temperature combination (Kayll 1968, Methven 1971). Others (Lorenz 1939, Seidel 1986), using water baths or dry heat, have shown limited survival of seedlings up to 65°C for 1 minute. Wright and Bailey (1982) reported that *Stipa comata* culms survived exposure to >60°C for 1 minute regardless of the moisture content. For most purposes the 60°C/1 min combination is an acceptable lethal heat criterion for breakdown of cell protoplasm. Heat experiments have primarily been made with seedlings, and when fire burns across a site, even if it is a low intensity underburn, it usually consumes the seedlings in its path. The use of seedlings in laboratory experiments, however, has been helpful in predicting effects on plant tissue. The results are applicable to mature plants, which may be subjected to lethal heat over only a portion of their leaves, stems, or roots.

## Crown Damage

Above every fire is a zone within which living tissue will be killed by the hot gases. The maximum height of the zone is related to fireline intensity (the rate of energy release per unit length of fireline; see chapter 1), the ambient temperature, and the windspeed (Van Wagner 1973). Increasing fireline intensity will increase scorch height as the energy release rate increases. As ambient temperature increases, less heat is needed from the fire to reach lethal temperatures. Increasing wind tends to level the convection column, reducing scorch height for a given fireline intensity. If wind is increased with other factors constant, this can cause fireline intensity to increase and scorch height to increase.

The no wind/25°C relation between fireline intensity (I, in kW $m^{-1}$) and scorch height ($h_s$, in m) is

$$h_s = 0.148\ I^{2/3}$$

(see Fig. 5.1). Corrections for different ambient temperature and windspeed conditions (Fig. 5.2A,B) can be graphically applied to the scorch height calculated from this equation (Van Wagner 1973; see Albini 1976 for English units).

In the derivation of this relationship, Van Wagner (1973) recognized that slightly higher temperatures might be required for dormant tissue to be killed. Variable sensitivity to temperature in the tree crown due to the dormancy effect and bud size was incorporated into a crown damage model for northern Rocky Mountain conifers (Peterson and Ryan 1986). Peterson and Ryan defined three levels of temperature considered lethal after one minute: 60°C, 65°C, and 70°C. The 60° level was applied to trees with small buds, such as Douglas-fir, during the growing season. The 65° level was applied to small-bud species during the dormant season and to large-bud species like ponderosa pine during the growing season. The 70° level was applied to large-bud species during the dormant season.

Actual crown mortality requires the integration of crown scorch height with crown dimensions of an individual tree. (The ability of crowns to resprout from axillary or adventitious buds after being scorched or burned will be discussed later.) For completely scorched

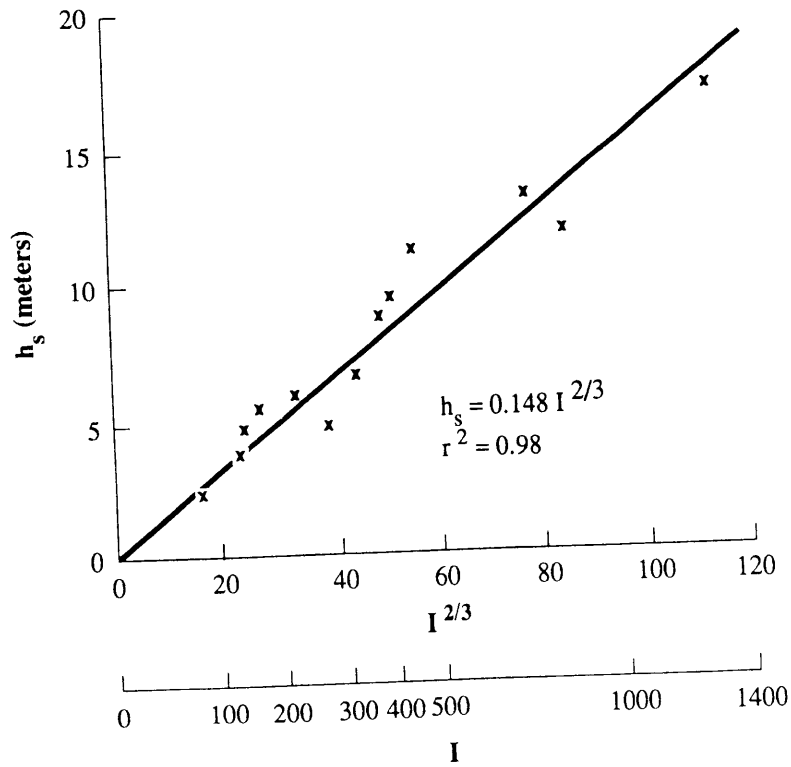


FIG. 5.1. *Experimental relation between scorch height, $h_s$, and fire intensity, I, in kW $m^{-1}$.*
(From Van Wagner 1973)

trees, crown morphology may not be relevant, as the entire crown may be killed. For taller trees, the base of the live crown, the shape of the crown, and the height of the tree will influence the proportion of the tree crown that is likely to be killed. Proportion of crown volume killed is a better predictor of postfire tree condition than scorch height (Peterson 1985), because the former is more highly associated with injury to the tree than the latter.

Geometric solids have been used to describe crown shape (Table 5.1), and crown volume can be calculated based on crown diameter and height. Specified solids may not accurately represent crown shapes, particularly if one crown shape is assumed to represent all individuals of one or more species. Scorch height may not be the same all around the tree, particularly on slopes, where scorch

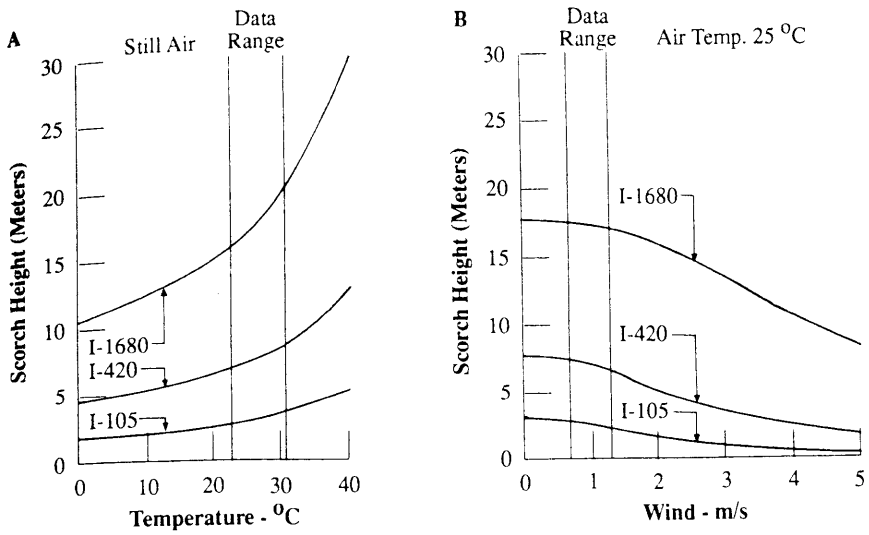


FIG. 5.2. A: *Theoretical relation between scorch height and air temperature for three fireline intensity levels.* B: *Theoretical relation between scorch height and wind at 25°C for three fireline intensity levels. Actual data range shown by vertical lines.*
(From Van Wagner 1973)

height will be higher on the upslope side of the tree (Peterson 1985). An average scorch height can be applied to estimate affected crown volume in this case (Fig. 5.3).

It is often desirable to reconstruct fireline intensity in postfire monitoring to compare fire effects in different fires or different areas of a single fire. Because scorch height depends on windspeed and ambient temperature as well as fireline intensity, some estimates of

TABLE 5.1. CROWN SHAPES OF SEVERAL PACIFIC NORTHWEST TREE SPECIES (PERCENTAGES)

| *Crown Shape* | *Douglas-Fir* | *Lodgepole Pine* | *Subalpine Fir* | *Western Redcedar* |
|---|---|---|---|---|
| Paraboloid | 78.0 | 41.1 | 23.8 | 57.1 |
| Cone | 16.0 | 33.0 | 48.8 | 18.2 |
| Ellipsoid | 5.0 | 22.3 | 22.7 | 24.7 |
| Cylinder | 1.0 | 3.6 | 4.7 | 0 |

SOURCE: Peterson 1985.

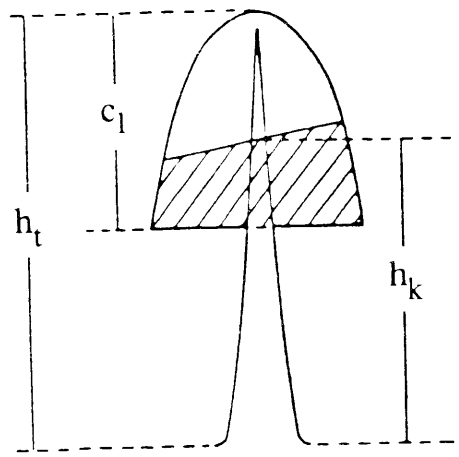


FIG. 5.3. *Fraction of crown volume killed calculated by height of crown kill ($h_k$), tree height ($h_t$), and crown length ($c_l$). Shaded area indicates crown kill.*
(From Peterson and Ryan 1986)

the windspeed and temperature are essential if a fireline intensity estimate within a narrow range is desired. In one experiment on loblolly and shortleaf pines (*Pinus taeda* and *P. echinata*), fireline intensity of underburns was underestimated by a factor of three when reconstructed from scorch height (Cain 1984).

## BOLE DAMAGE

Tree stems may also be damaged by fire, even though they often have a thick bark that insulates the cambium against the heat from forest fires. When a fire approaches a tree bole, it rarely produces an even distribution of heat around the stem. This uneven distribution of heat will sometimes result in the death of the cambium on one side of the tree, creating a fire scar; in other cases, enough heat penetrates the bark to kill the cambium around its entire circumference.

The uneven distribution of heat around a tree bole as a fire passes is caused by the presence of a cylinder (the bole) in three-dimensional air space. The cylinder effect was demonstrated by Gill (1974), who positioned metal rods of varying diameters at various distances from a stationary flame source. Maximum flame heights

were observed on the leeward side of the rods. The diameter of the rods also affected flame height, but only on the lee side. These results suggest that the lee side of the tree is more likely to receive higher heat loads at the bark surface, and that larger diameter trees may experience more heat than smaller diameter trees. This might help to explain a commonly observed pattern of fire scarring in ponderosa pine forests, where frequent, low intensity fires historically occurred. Some trees remain unscarred until they are perhaps 30–50 cm in diameter, and then become scarred and rescarred by most later fires at frequent intervals. The smaller trees, even with thinner bark, may not create enough of an eddy effect on their lee side to cause fire scars to form.

The flame experiment results of Gill (1974), which were collected in a laboratory setting, are consistent with temperature data collected around the bases of trees during wildland fires. Synthetic trees placed in a grassland with fuel 70 cm tall recorded highest temperatures on lee aspects and at a height of 40 cm (Tunstall et al. 1976). On trees surrounded by pine litter, Fahnestock and Hare (1964) found lee aspects to have the highest temperatures (Fig. 5.4). The highest temperature recorded (846°C) was from a headfire on the lee side of a tree at about 1 m above the ground.

Bark plates had higher temperatures than bark fissures, and more heat was applied by heading than backing fires to the lee side of the tree up to 1 m above the ground. In simulated fires at 0.3 m above a lighted wick around the tree bole, Hare (1965) found lee aspect temperatures of 538°C compared to 260°C on the windward aspect. Fire scars are more likely to occur on the upslope sides of tree boles because of the eddy effect from headfires, and also because headfires on a slope are usually of higher intensity than backing fires due to preheating of fuels ahead of the fire by radiation and convection. The upslope side of the tree may also act as a catchment for fuels rolling downslope between fire events, possibly increasing fire intensity on that side of the tree, but such fuel accretion is not necessary for accelerated fire behavior and fire scarring.

The effect of bole heating on the cambium depends on how well it is insulated from the heat applied to the exterior of the bark. Heat transfer through bark is a complex process, but with several simplifying assumptions it can be adequately modeled to predict passage of a temperature pulse through bark. Thermal diffusivity, by

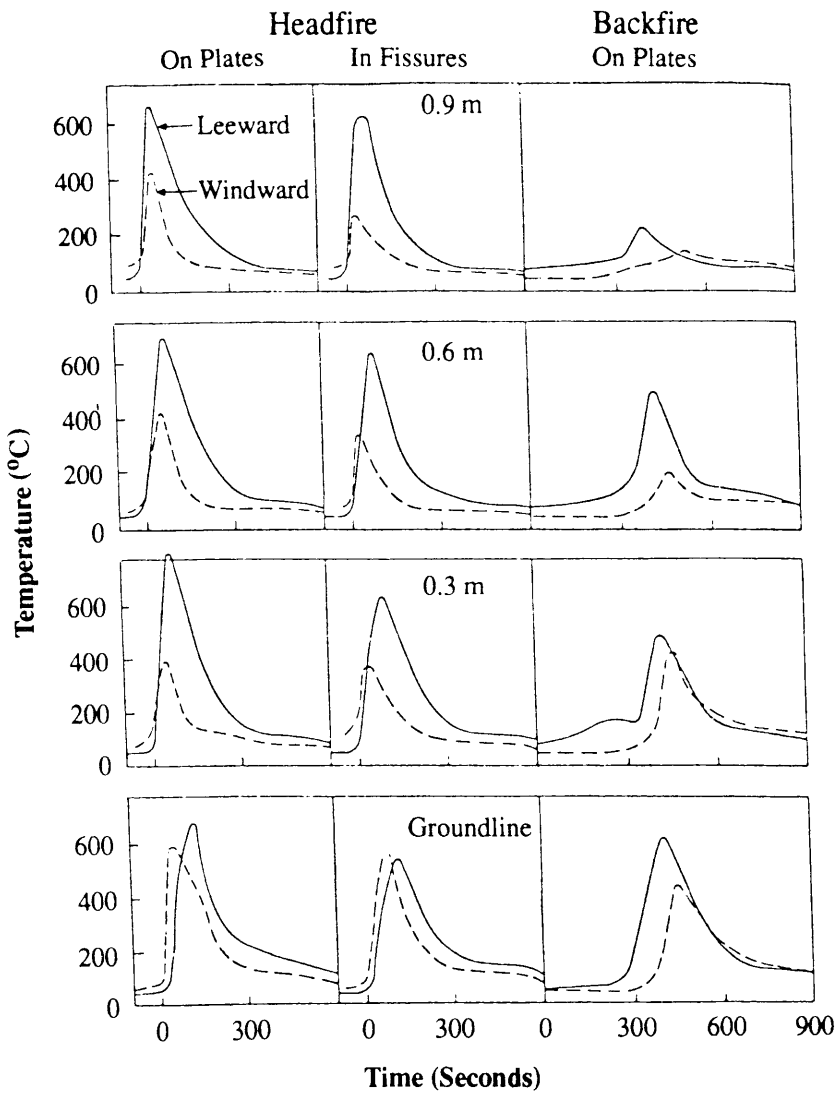


FIG. 5.4. *Mean time-temperature regimes at the bark surface of three trees in headfires and three trees in backfires. Top graphs are at roughly 1 m above ground line, and bottom graphs are at ground level.*
(From Fahnestock and Hare 1964)

Fourier's equation for heat conduction (Brown and Marco (1958, is the rate at which a temperature pulse moves through a material:

$$a = \frac{k}{c\,p}$$

where

$a$ = thermal diffusivity ($cm^2\ sec^{-1}$)
$k$ = thermal conductivity ($cal\ cm^{-1}\ sec^{-1}\ deg^{-1}$)
$c$ = heat capacity ($cal\ gm^{-1}\ deg^{-1}$)
$p$ = density of material ($g\ cm^{-3}$)

Thermal diffusivity increases as conductivity increases, but decreases as density or heat capacity increases. Because diffusivity is the ratio of several quantities, its dimensions are not readily interpretable in a physical sense (Spalt and Reifsnyder 1962). A good insulating material, such as asbestos, has a thermal diffusivity of $2.5 \times 10^{-3}\ cm^2\ sec^{-1}$. An average thermal diffusivity for bark is about $1.1–1.3 \times 10^{-3}\ cm^2\ sec^{-1}$ (Martin 1963, Reifsnyder et al. 1967), which makes bark more efficient than asbestos as an insulator. Bark, however, is a composite of several different materials: the bark solids, entrapped cells of air, and a seasonally varying moisture content. Thermal diffusivity might vary considerably based on bark structure, surface texture, and moisture content, particularly with the high thermal conductivity and high heat capacity of water.

As moisture is added to bark, thermal diffusivity does indeed decrease, primarily due to the high heat capacity of water (Fig. 5.5). Reifsnyder et al. (1967) suggested that the actual moisture content of the outer bark of red pine (*Pinus resinosa*) does not seasonally vary as widely as the limits in Figure 5.5. Therefore, differences in cambial heating resulting from thermal diffusivity changes due to bark moisture content or species-specific bark structure are expected to vary by a factor of 1.5–2 at most. There appears to be a much more important factor involved in cambial protection: bark thickness.

The thickness of the material through which the temperature pulse is moving has a large effect on the temperature experienced at the inner edge of the material. Bark thickness is the most important bark characteristic in assessing cambial protection from fire (Martin

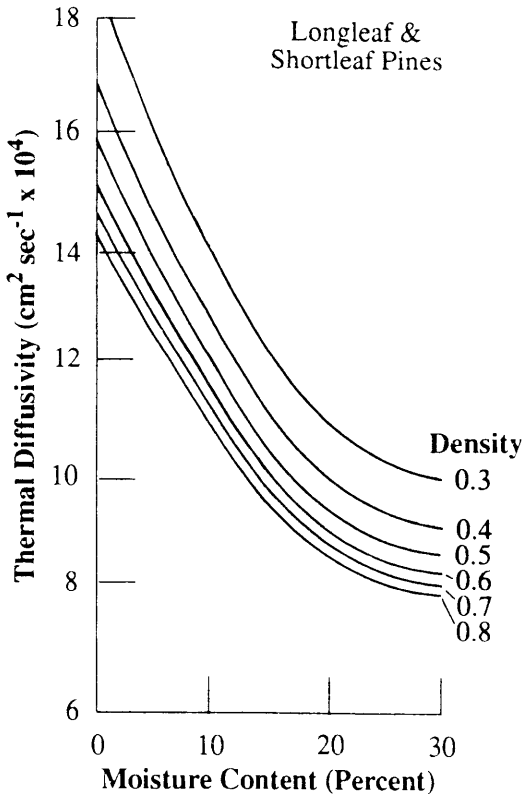


FIG. 5.5. *Thermal diffusivity of bark as a function of moisture content and dry density.*
(From Reifsnyder et al. 1967)

1963, Reifsnyder et al. 1967, Uhl and Kauffman 1990). Protection increases with the square of the bark thickness. Ryan and Reinhardt (1988) found a 40-fold difference in computed bark thickness for seven Pacific Northwest conifers, implying differential susceptibility to injury from fire. Bark thickness can be predicted from diameter of outside bark (Table 5.2), so that cambial damage from a given fireline intensity can be predicted from stand-level information.

A critical time for cambial kill can be derived as a function of tree diameter (Fig. 5.6). This relationship is based on bark thickness as a function of species and diameter. Peterson and Ryan (1986), using the work of Hare (1965) and Spalt and Reifsnyder (1962) and assuming a fire temperature of 500°C, developed the equation:

$$t_c = 2.9\ x^2$$

where

$t_c$ = critical time to cambial kill (minutes)
$x$ = bark thickness (cm)

For example, a species with a bark thickness of 0.6 cm could survive for about 1 minute, while a tree with bark thickness of 2.6 cm could survive for about 20 minutes, independent of other deleterious effects of the fire.

Bark thickness is not uniform around the tree; instead, it is thicker along some radii and thinner along others. The so-called bark fissures, comprising younger bark, will experience lower temperatures in a fire (Fahnestock and Hare 1964), but often have a higher probability of cambial kill due to the thinner bark. On thick-barked species, such as Douglas-fir, the fissures are likely places for repeated cambial kill along the same bole radius (Fig. 5.7). Species with rough-textured bark may experience lower average temperatures at the bark surface than smooth-barked species (Uhl and Kauffman 1990).

If the heat pulse is sufficient to kill the cambium but of limited spatial extent on the bole, fluid movement within the tree's inner bark or xylem may translocate heat sufficiently to prevent cambial kill (Vines 1968). It was not clear from Vines's experiment whether this reaction was a physiological response on the part of the tree or a

TABLE 5.2. SINGLE BARK THICKNESS (BT) AS A FUNCTION OF DIAMETER OUTSIDE BARK (DOB) FOR SEVEN WESTERN NORTH AMERICAN CONIFER SPECIES

| *Species* | *Equation (cm)* | *Source* |
|---|---|---|
| Douglas-fir | BT = 0.065 DOB | Monserud 1979 |
| Western larch | BT = − 0.1143 + 0.0629 DOB | Faurot 1977 |
| Engelmann spruce | BT = 0.189 + 0.022 DOB | Smith and Kozak 1967 |
| Lodgepole pine | BT = 0.0688 + 0.0143 DOB | Faurot 1977 |
| Subalpine fir | BT = 0.015 DOB | Finch 1948 |
| Western redcedar | BT = 0.386 + 0.021 DOB | Smith and Kozak 1967 |
| Western hemlock | BT = 0.056 + 0.043 DOB | Smith and Kozak 1967 |

SOURCE: Ryan and Reinhardt 1988.

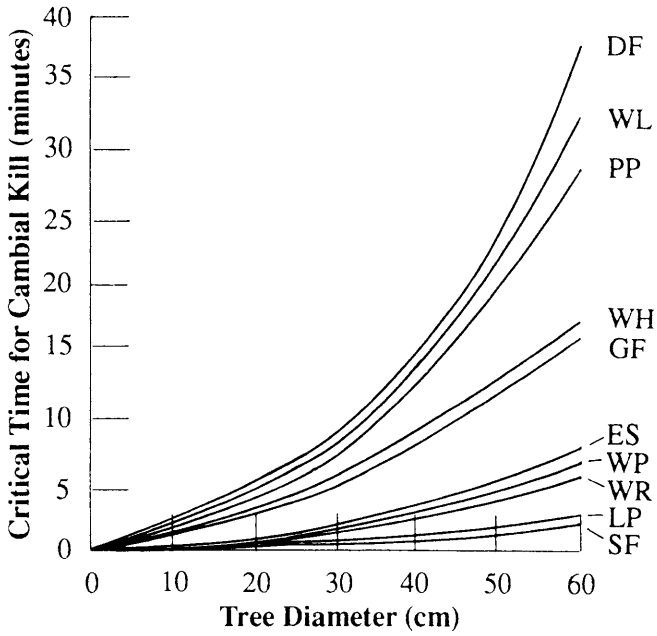


FIG. 5.6. *Critical time for cambial kill as a function of tree diameter and species. Species are Douglas-fir (DF), western larch (WL), ponderosa pine (PP), western hemlock (WH), grand fir (GF), Engelmann spruce (ES), western white pine (WP), western redcedar (WR), lodgepole pine (LP), and subalpine fir (SF).* (From Peterson and Ryan 1986)

physical effect of heating the bark. A factor that can have the opposite effect is bark flammability. If the bark catches fire, it will produce heat that can affect the cambium at the same time as its thickness—and insulating ability—is being reduced (Gill and Ashton 1968, Vines 1968).

Height of bark char has been used to estimate flame height (not length) and fireline intensity (McNab 1977). An experiment in loblolly and shortleaf pine (Cain 1984) demonstrated that height of bark char underestimated flame length for both heading and backing fires. If the bark is flammable or has heavy lichen cover, the height of bark char may exceed flame height on the landscape, resulting in overestimates of fireline intensity.

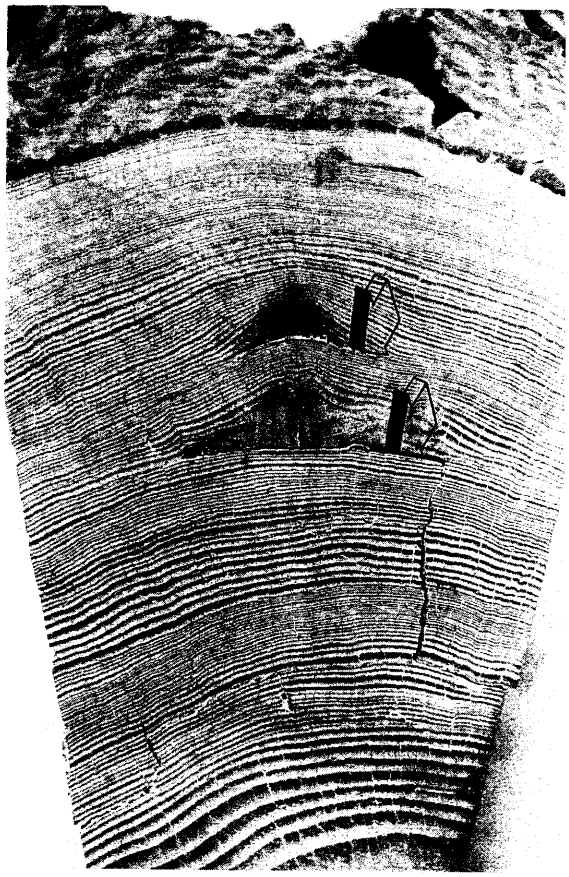

FIG. 5.7. *Douglas-fir showing two grown-over fire scars (arrows). Note the thinner bark at the intersection of the tree circumference with a radius drawn through the two scars.*

## ROOT DAMAGE

Damage to roots from prescribed or wild fires has not been studied intensively. Small-diameter (fine) roots are more susceptible to damage than larger roots because of thinner bark. Root damage usually accompanies bole damage, so its effects may be confounded with heating of the basal portion of the tree stem. However, roots

can be killed at some distance from the stem while the stem is unaffected by heat.

Early reports of fine-root kill to 2.5 cm soil depth in southern pine (Heyward 1934) concluded that little harm was done, because many of these roots die annually anyway. More recent reports have documented fine-root mortality from low intensity underburns and have linked the root effects to growth reductions in young ponderosa pine stands (Grier 1989) and to tree mortality in low vigor, old-growth ponderosa pine stands (Swezy and Agee 1991). The impact on the tree from fine-root kill may also depend on season of burning; trees may be less dependent on fine roots in autumn, a time of natural root turnover, than in spring while entering the season of drought. Both ponderosa pine studies measured fine-root impact from spring burning; surveys of old-growth pine burned in autumn months found no increased levels of tree mortality over a 10 year postfire period (Swezy and Agee 1991).

## Fire Adaptations

Methods of categorizing tree response to fire were developed early in the history of American forestry. The U.S. Geological Survey published the first table of relative fire resistance for species in the Cascade Mountains (Gorman 1899). A more detailed description of fire resistance of common species of the Pacific Northwest was available by 1925 (Flint 1925). This system was slightly expanded by Starker (1934) in a more national survey (Table 5.3). These systems were based on the relative resistance of mature individuals to fire.

The first treatment of fire adaptations in an ecology textbook came in 1947 with Daubenmire's *Plants and Environment.* Fire was recognized as an environmental "factor" equivalent to light and water "factors," and distinct from other effects of the "temperature factor." Daubenmire (1947) defined seven adaptational features that facilitated woody plant persistence under repeated burning. Although Daubenmire's work marked an important beginning to the classification of plant adaptation to fire, these seven adaptations are not all exclusively related to fire, and at least one may have little to do with fire.

1) *Germination.* Some shrubs possess hard-coated seeds that lie dormant in the soil until a fire passes. Density of snowbrush (*Ceanothus velutinus*) in the soil may exceed 12 million $ha^{-1}$ (Weatherspoon 1988). Some seeds are consumed by fire, but others are scarified, which later allows them to imbibe water and germinate in a nutrient-rich and competition-free environment. Such seeds are common in *Ceanothus* (Fig. 5.8), *Arctostaphylos,* and *Rhus* (Daubenmire 1959), and these seeds are thought to remain viable in the soil for several decades (Quick 1977). Kauffman and Martin (1991) reported optimum scarification temperatures for deerbrush (*Ceanothus integerrimus*) of 75–100°C, with wet heat more effective than dry heat at 4–8 min exposure. Exposure above 120°C for 4–8 min caused significant mortality, suggesting a heat threshold above which survival is low to absent. This is why such seedlings will not be found within the perimeter of small burn piles in mixed-conifer forest but will germinate in profusion around the edge.

2) *Rapid growth and development.* Some woody species have life history characteristics that enable them to complete a life cycle quickly. This enables them to provide seed in the event of two closely spaced fires. Bishop pine (*Pinus muricata*) along the California coast can produce viable seed at a young age (Daubenmire 1959). Longleaf pine (*Pinus palustris*) in the Southeast undergoes a "grass stage" where it resembles a perennial grass for several years while developing a deep root system (Fig. 5.9). The terminal bud remains in the center of this cluster of foliage, protected from the typical frequent, low intensity fires that burned through the region. The shoot then begins to grow rapidly, carrying the terminal bud above the zone of lethal heat injury. A similar adaptation is present in the Mexican pines *Pinus montezumae* and *Pinus michoacana* (Perry 1991). An example of a developmental adaptation to fire is an increase in flowering (Biswell and Lemon 1943). In the Pacific Northwest, Thurber's needlegrass (*Stipa thurberiana*) and Great Basin wildrye (*Elymus cinereus*) show increased flowering after burning (Wright and Klemmedson 1965, Kauffman 1990).

3) *Fire-resistant foliage.* Daubenmire defined this adaptation on the basis of absence of high resin or oil content, so that normal foliar moisture content could stop a fire encountering the plant.

TABLE 5.3. RELATIVE FIRE RESISTANCE OF THE MOST IMPORTANT TREES OF OREGON AND WASHINGTON IN ORDER OF GREATEST RESISTANCE

| *Species* | *Bark Thickness of Old Trees* | *Root Habit* | *Branch Habit* | *Canopy Cover* | *Lichen Growth and Color* | *Foliage Inflammability* | *Most Common Way of Killing* |
|---|---|---|---|---|---|---|---|
| Western larch | very thick | deep | high & open | open | light/black | low | most resistant |
| Douglas-fir | very thick | deep | high & dense | dense | none–heavy/ gray | high | crown fires |
| Ponderosa pine | thick | deep | moderately high & open | open | light/black | low | crown fires |
| White/grand fir | moderately thick | shallow | low & dense | dense | none–heavy/ gray | medium | root char, crown fire |
| Western redcedar | thin | shallow | low & dense | dense | none–moderate/ gray | high | root char, crown fire, burn down |
| Mountain hemlock | medium | medium low | low & dense | dense | none–moderate/ gray | high | root char, crown fire |
| Noble fir | moderately thick | medium thick | high & dense | dense | medium–heavy/ gray | high | foliar scorch or crowning, core burn |
| White pine | medium | medium | high & moderate | dense | moderate/ gray & heavy | medium | scorching cambium or crowning |
| Lodgepole pine | very thin | deep | moderately | open | moderate–heavy/ | medium low | scorching |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Lodgepole pine | very thin | deep | moderately low & open | open | moderate–heavy/ gray, black | medium low | scorching cambium or crowning |
| Western hemlock | medium | shallow | moderately low & dense | dense | none–heavy/ gray | high | root char, crown fire, core burn |
| Engelmann spruce | very thin | shallow | low & dense | dense | none–heavy/ gray, black | very high | root char, scorching cambium, crowning |
| Sitka spruce | very thin | very shallow | moderately high & dense | dense | none–heavy/ gray, yellow | high | root char, occasional crowning |

SOURCE: Starker 1929.

FIG. 5.8. *Snowbrush* (Ceanothus velutinus) *plant that has germinated at the edge of a circle of burned debris.*

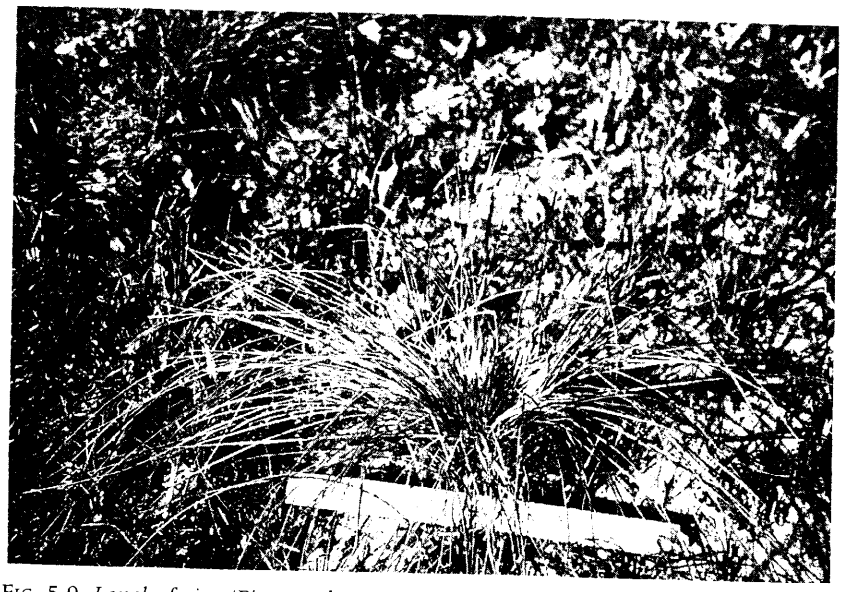

FIG. 5.9. *Longleaf pine* (Pinus palustris) *of the southeastern United States in the grass stage.*

In fact, this is not an adaptation to fire at all. Considerable debate has accompanied a hypothesis that some fire-dependent communities may have evolved flammable characteristics in response to natural selection (Mutch 1970), but to propose that absence of such traits constitutes a fire adaptation is without basis. Some plants (e.g., *Atriplex* spp.) possess higher than average levels of chemicals (particularly silica-free ash content and the sum of calcium plus phosphorus content) that inhibit the combustion process (Philpot 1970, Nord and Green 1977), but alternate explanations for such compounds may be more easily defended than the proposition that these are fire-derived traits. High moisture content of foliage clearly reduces the probability of foliar ignition, but this trait appears to be more a function of site and leaf age than an adaptation to fire.

4) *Fire-resistant bark.* Bark thickness, as noted earlier, can be a critical factor in determining plant survival. Western larch, Douglas-fir, and ponderosa pine all have bark thicker than associated species (Fig. 5.6), and are more likely to survive fires of low to moderate severity. Even thinner bark on mature trees, such as Oregon white oak (*Quercus garryana*), is sufficient to withstand cambial kill in savanna environments, where fires tend to be flashy and of low duration.

5) *Adventitious or latent axillary buds.* Many shrub species and a wide variety of tree species can regenerate crowns after fire by sprouting of buds along the stem, at the stem base, or from lateral roots (Fig. 5.10A–C). Epicormic sprouting from aerial buds depends on whether the crown was scorched or consumed. In crown fires, buds behind thin bark on fine branches will be killed, and epicormic sprouting will occur only along branches and stems exceeding a certain diameter, representing the lower limit of bark thickness that withstood the lethal temperatures. Such "fire columns" are common in *Eucalyptus* spp. and pitch pine (*Pinus rigida*) in the eastern United States. Coast redwood (*Sequoia sempervirens*), bigcone Douglas-fir (*Pseudotsuga macrocarpa*), and the oaks (*Quercus* spp.) commonly sprout new crowns after crown scorch or consumption. Basal sprouting may occur (*Betula, Arbutus, Lithocarpus, Quercus, Ceanothus* spp.) if aerial foliage and buds, or the cambium of the

FIG. 5.10. *Three types of sprouting response to fire.* A: *Sprouting along the stem in oak* (Quercus *spp.*). B: *Root suckering in aspen* (Populus tremuloides). C: *Sprouting from the root crown in chamise* (Adenostoma fasciculatum).
(Aspen photo courtesy Dr. L. Brubaker)

main stem of the tree, are severely injured or killed. Size and age are likely to influence the ability of a plant to sprout after fire (Kauffman 1990). Species like quaking aspen (*Populus tremuloides*) or Oregon white oak can produce sprouts from lateral roots after the death of the main stem. Such clonal development can be a primary regeneration mechanism for some species.

6) *Lignotubers.* A lignotuber is a basal swelling at the interface between root and shoot that contains buds and food reserves (James 1984). When the shoots are killed by fire, dormant buds insulated by the soil remain alive and are stimulated to sprout, using the stored food reserves. Lignotubers in Australian eucalyptus have exceeded several meters in diameter, but commonly are much smaller in the western United States. The issue of when a normal root crown with buds becomes a lignotuber has been debated since Jepson (1916) first described these root crown "burls." From local observation, species with lignotubers (*Arctostaphylos, Adenostoma*) typically have a spherical mass of tissue from which roots emerge on one side and shoots on the other (Fig. 5.11), in contrast to nonlignotuberous species that may have individual shoot- or root-related basal swellings (e.g., bitterbrush [*Purshia tridentata*]). Lignotubers may maintain dominance of the individual in the commmunity over several generations, until the dormant buds at the surface of the lignotuber are pushed from the soil by growth of the lignotuber or exposed by erosion of soil around the base; a succeeding fire can then kill the buds and the plant will die. I have observed this in chamise (*Adenostoma fasciculatum*) in coastal California chaparral.

7) *Serotinous cones. Serotinous* means "late opening," and this adaptation refers to cones that retain seeds in the tree canopy for a long time (Fig. 5.12). Viable seed has been removed from lodgepole pine (*Pinus contorta* var. *latifolia*) cones 75 years after cone maturation (Clements 1910). Not all cones within a tree or species are typically serotinous, so that the species may respond to other disturbances, such as insect attack. For example, much of the lodgepole pine in the pumice region of south-central Oregon and the Cascades and Sierra Nevada (*P. contorta* var. *murrayana*) is nonserotinous (Stuart et al. 1989). Fires burning through the crown melt the resin

FIG. 5.11. *Manzanita* (Arctostaphylos *spp.*) *with lignotuber as an aid in sprouting response. The chamise plant of Figure 5.10C has a lignotuber too.*

seal on serotinous cones, and they open soon after. Perry and Lotan (1977) found 100 percent of heavily serotinous cones of lodgepole pine opening after treatment in a water bath at 60°C for two minutes, but many cones from less serotinous trees opened at room temperature. The California closed-cone pines, such as knobcone pine (*Pinus attentuata*), bishop pine, and Monterey pine (*Pinus radiata*); the Mexican closed-cone pines; Baker cypress (*Cupressus bakeri*) in the Siskiyou and Klamath Mountains; and semi-serotinous black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) of the boreal forest are other examples of species with serotinous cones.

A broad biological classification of plant response to disturbance was developed by Rowe (1983). He defined five categories of plant response based on life-history characteristics of species. Some of the categories may not be exclusively related to fire, but characteristics of fire regime are incorporated into this system (e.g., *resister* category):

FIG. 5.12. *Serotinous cones of lodgepole pine opening the day after a wildfire. Seeds blow through the air and become buried in fresh ash from the fire.*

1. *Invaders.* Highly dispersive, pioneering fugitives with short-lived disseminules. Plants such as fireweed (*Epilobium angustifolium*), Scouler's willow (*Salix scouleriana*), and cottonwood (*Populus* spp.) are typical *invaders,* generally needing disturbance to occupy a site.
2. *Evaders.* This category includes species with relatively long-lived propagules that are stored in the soil or canopy. The species thus evades elimination from the site. Daubenmire's "germination" and "serotinous cone" adaptations both fit the *evader* category.
3. *Avoiders.* These are generally shade-tolerant, late successional species that slowly reinvade burned areas and have essentially no adaptation to fire. Hemlocks (*Tsuga* spp.), western juniper (*Juniperus occidentalis*), and subalpine fir (*Abies lasiocarpa*) are good examples of *avoider* species. Herbaceous species with reproductive parts in the litter layer are likely to be killed even by low intensity fires (Flinn and Wein 1977), and would also be classified as *avoiders.*
4. *Resisters.* These are species that can survive low intensity fires

relatively unscathed. Thick-barked species, such as Douglas-fir, ponderosa pine, and western larch, are *resisters*.

5. *Endurers*. These species have the ability to resprout from the root crown, lateral roots, or the aerial crown. Oaks, Pacific madrone (*Arbutus menziesii*), and various shrub species are among the many species classed as *endurers* in the Pacific Northwest.

This system is a useful way to broadly classify the species on a site, and it may be used to develop generalized responses to fire regimes: a low severity fire will favor *resisters*, while a high severity fire will favor *invaders*, *evaders*, and *endurers*. Fire suppression will generally favor *avoiders* by allowing late successional species to eventually occupy the site.

Some species may fit more than one category because of multiple adaptations or changes in morphology or physiology over time. For example, lodgepole pine may be an *invader* in terms of its rapid colonization of sites after fire, but it can also be an *evader* due to its serotinous cones. Douglas-fir is an *avoider* when young but a *resister* when mature. *Ceanothus* has an evader strategy with refractory seeds, and an endurer strategy because it sprouts after fire. Researchers should evaluate the possibility of dual classification when considering each species on a site.

Another universal life-form classification was developed in Australia by Gill (1980), but it has the disadvantage of assuming 100 percent leaf death before entering the classification key (Table 5.4). Species in fire regimes of moderate to low severity (particularly *resisters*) are not well classified by this system, and although it may fit the Australian experience, it is less universal than the system developed by Rowe.

## FIRE AND PLANT COMMUNITIES

The adaptations discussed so far focus on characters of individual species that allow them to respond to disturbance. Observations that communities with many fire-adapted species are also more "flammable" because of chemical or physical properties of fuels led Mutch (1970, p. 1047) to propose the following hypothesis of