Fire and Dwarf Mistletoe (*Arceuthobium* spp.) Relationships in the Northern Rocky Mountains

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THE geologic record indicates that fire has been a major factor in the development and succession of vegetation in terrestrial environments of temperate climatic zones. From earliest times, natural fires ignited by lightning or volcanoes often destroyed large areas of vegetation at random. The fate of such fires was determined by the combination of interacting natural environmental factors. Apparently, primitive man was quick to realize some beneficial aspects of fire because his use of fire became a vital characteristic of his habitat. Although he undoubtedly caused changes in vegetation through his use of fire, only 20th Century man has developed adequate technology to prevent and suppress unwanted fires in the environment. This technology has begun to reveal the significant role of fire as an ecological factor in vegetational development. Perhaps nowhere are we more cognizant of this fact than in the northern Rocky Mountains where vast areas of fire-regenerated coniferous forests exist.

The pioneer and seral tree species within the many forest ecosys-

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tems of the northern Rocky Mountains definitely reflect the longtime inclusion of fire as a factor of environmental selection. Many adaptations, such as serotinous cones, fire-resistant bark, rapid growth, short life cycle, and natural pruning, are readily observed among these species. After only 50 years or so of successful fire prevention and suppression in these forest ecosystems, we are already encountering some difficult problems of regeneration and pest management; problems that tax the capability and technology of man as the steward of the earth. The relationships of fire to forest vigor and hygiene are only now being recognized.

Dwarf mistletoes (*Arceuthobium* spp.) are one of the most serious pests within the coniferous forests of the northern Rocky Mountains. Adverse growth impact (mortality and growth reduction) due to these pests was recently estimated at 1.5 billion board feet annually within these forests. Directly and indirectly, fire has a significant effect upon the population dynamics of the dwarf mistletoes; and, indirectly, through their effects on the coniferous host plant, the dwarf mistletoes have a significant effect upon fire behavior. These relationships have been little studied and quantitative information is largely lacking, but empirical observations are frequently recorded. A review of this subject by Alexander and Hawksworth (1975), which reflects the highly empirical nature of our knowledge, has been very helpful to the authors in preparing the present paper.

In this paper, we present a qualitative discussion of some interrelationships of fire and four major species of dwarf mistletoes, *Arceuthobium americanum* on lodgepole pine, *A. campylopodum* on ponderosa pine, *A. douglasii* on Douglas-fir, and *A. laricis* on western larch in the northern Rocky Mountain forest ecosystems. Because fundamental knowledge of (1) the biology and ecology of the dwarf mistletoes, (2) the ecology of the common hosts as related to the forest ecosystems of the northern Rocky Mountains, and (3) the effects of fire on forest vegetation is essential to an understanding of these interrelationships, some pertinent aspects of these topics are also reviewed.

We have adopted the synecologic perspective, terminology, and forest ecosystem classification of Daubenmire (1968) and Daubenmire and Daubenmire (1968). The taxonomic treatment by Hawksworth and Weins (1972) is used for the dwarf mistletoes.

BIOLOGY AND ECOLOGY OF DWARF MISTLETOES

The dwarf mistletoes are obligate parasites that attack only coniferous plants. They are chlorophyllous, dioecious, seed plants (angiosperms), but can synthesize little, if any food. Three major aspects of their biology and ecology are pertinent to this paper: (1) definite host affinities; (2) method and rate of spread; and (3) effect upon the host.

Some species of *Arceuthobium,* such as *A. douglasii,* have a rather narrow host range. Others, such as *A. laricis,* are capable of attacking a dozen or more conifers. However, each species exhibits a physiological adaptation of host preference; for each species, a single conifer host is far more susceptible to attack than any other. We often refer to this conifer as the "common host" for the species, and we recognize this adaptation in the specific epithet of many dwarf mistletoes. Thus, the common host for *A. laricis* is western larch (*Larix occidentalis*). Furthermore, without exception, any species of dwarf mistletoe has its greatest reproductive potential when growing on its common host. Concomitantly, we find greatest spread and intensification of the pest within and between individuals of these hosts. Such conditions normally result in high impact levels that bear directly on fire interrelations. On the other hand, reproduction by the dwarf mistletoes is often difficult, if not impossible, on many of their uncommon hosts. For example, *A. laricis* will attack *Pinus ponderosa* and *Abies grandis,* but reproduction on these hosts is rare. It also attacks *Picea engelmannii* but seldom produces aerial shoots, and reproduction on this host is unknown to us. *A. douglasii* will attack *Abies grandis* and stimulate the host to produce small, flat, witches'-brooms, but it rarely produces aerial shoots. We do not know it to be capable of reproduction on this host. Thus, even though the total range of hosts may be large, as for *A. laricis,* reproduction on them is often restrictive, as with *A. douglasii.* The attendant buildup is thereby commensurately reduced. Consequently, these parasites on certain hosts will either have little influence on fire behavior or be little affected by it.

Dwarf mistletoes reproduce through propagules borne in a berry-like fruit. Botanically speaking, the propagule of dwarf mistletoe is not a seed because no integuments are produced. However, these propagules are commonly referred to as seeds and, from a practical viewpoint, we do not find this objectionable. Seeds of all species mature in late summer and throughout the fall, depending on species, latitude, elevation, and climatic conditions. Seeds are forcibly ejected via an explosive mechanism in the fruit. Seed may be ejected for horizontal distances up to 21 m, depending on factors such as wind velocity, height of infection above ground, position of seed-producing infections within the crown of the host tree, and obstructions in the flight path of the seed. The average distance of unobstructed seed flight is probably closer to 5-8 m. Seed dissemination is almost completely dependent upon the explosive fruit; biotic factors are of little or no known significance to the parasite's spread within and between trees. The rate of spread of the dwarf mistletoes is most rapid from infected overstory trees into young regeneration. Horizontal spread within stands of a uniform stand structure and age class is rather slow, about 30-45 cm/year (Gill and Hawksworth, 1961; Hawksworth, 1958).

Dwarf mistletoes affect their hosts in several ways. They reduce the vigor, the growth rate, the quality and quantity of forest products produced, the quality and quantity of the tree seed produced, and predispose the tree to attack by insects and infection by fungi. They cause mortality, stimulate epicormic growth of host branches to produce numerous witches'-brooms (Hexenbessen), cause swellings and cankers on the trunk that may contain resin accumulations, and cause spike-tops. All of these, especially witches'-brooms, which are often enormous, increase the fire hazard by altering the quality, quantity, distribution, and flammability of fuel in the forest.

ECOLOGICAL STATUS OF THE COMMON HOSTS

Daubenmire and Daubenmire (1968) have described 21 habitat types (ecosystem basis) for classifying the northern Rocky Mountain coniferous forest vegetation. Pfister et al. (in preparation) define 58 habitat types for Montana and illustrate the relationship between the two classification systems. In all habitats in which western larch occurs, regardless of the classification system used, it is always pioneer or seral, denoting transitory and determinate occupancy of the habitat. Lodgepole pine, seral in northern Idaho habitat types, appears to be the potential climax in certain topo-edaphic environments of Montana and is keyed to five community types in which it is at least a persistent seral species or may even be climax (Pfister et al., in preparation). In five northern Idaho habitat types, Douglas-fir is a seral species, and ponderosa pine occurs as a seral species in three habitat types. However, in four habitat types, Douglas-fir is a component of the climax vegetation and ponderosa pine reaches climax in six habitat types (Daubenmire and Daubenmire, 1968). A climax status denotes a more permanent and continual occupancy of the habitat by the species than the seral status.

During development of the sere, certain natural events may delay succession temporarily and prolong occupancy of the habitat by pioneer or seral vegetation. Periodically repeated, such events may prolong this occupancy indefinitely, thus perpetuating the seral vegetation. When this occurs, the structure of vegetation of a seral stage may strongly resemble the structure of a climax vegetation. Tolerant seral species, such as Douglas-fir and ponderosa pine, may be represented in a mixture of age classes with continued reproduction dependent upon the repeated occurrence of the natural event. With intolerant species, such as lodgepole pine and western larch, the vegetation usually develops a mosaic pattern consisting of even-aged clusters or patches of irregular size and shape. However, either vegetation pattern may develop with any of these four coniferous species. In the northern Rocky Mountain forest ecosystems, the periodically repeated occurrence, intensity, and behavior of natural fires has been a prime factor in the development of such plant ecological situations and vegetative patterns.

EFFECTS OF FIRE ON FOREST VEGETATION

The effects of fire on vegetation are highly variable. Many are extremely difficult to measure or predict because of the complexity of numerous interacting environmental factors known as the environmental complex. The effects may be direct in that vegetation is killed by high temperatures of the fire and combustion proceeds to reduce the litter to ash, or they may be indirect and not involve the temperature factor. The direct effects on forest vegetation are often spectacular, immediate, readily observed, and are of considerable economic concern because they are more readily measured and evaluated in terms of tangible products or benefits lost and can be easily translated into monetary units or other values. The full economic impact of this loss is concentrated in a short time period and absorbed by the "now" generation. Any residual economic impact is rapidly changed by time and often becomes obscure in a fluctuating economy. In fact, immediate economic concern so fully occupies man's thinking that it overshadows the biologic and ecologic aspects of fire. This is exemplified by the dogma that has developed in the United States during the past 50 years that natural fires can be only detrimental to the desires of mankind.

Indirect effects of fire are gradual, dynamic, and interactive, and involve alteration and modification of all aspects of the environment. These effects largely represent the biologic and ecologic aspects of fire. Their impacts are distributed over indefinite time periods to be partially absorbed not only by the "now" generation but by future generations.

The effects of fire on a forest ecosystem will be determined largely by the type of fire. Likewise, the environmental complex will determine the habit of the fire and this habit will change as the complex changes. Daubenmire (1959) describes the three types of fires, ground, surface, and crown, referred to in this paper.

Most of the conifers growing in the northern Rocky Mountains, including the four species emphasized here, require exposure of mineral soils for natural regeneration. Man has found it extremely difficult to obtain natural regeneration of these species without a seedbed of exposed mineral soil and has used prescribed burning after harvest operations as one method to achieve such a seedbed (Pechanec, 1971). However, fires have been the major natural ecological factor providing this condition for regeneration of coniferous forests of the past and present. To us, then, a characteristic requiring a mineral seedbed most likely represents an ecological adaptation to the periodic and repeated occurrence of fire for eons in the habitat.

INTERRELATIONSHIPS OF FIRE AND DWARF MISTLETOES

The direct relationships of fire to dwarf mistletoes are of little known significance to man in his attempts to develop strategies for management of these pests. The dwarf mistletoe plants are killed by fire; their tissues are oxidized and reduced to ash. However, fire exhibits no selective action against these undesirable obligate parasites; in the process of killing the dwarf mistletoes, fire indiscriminately kills desirable vegetation, including hosts, that may be of enormous ecologic, aesthetic, spiritual, and economic value. Likewise, the direct relationships of dwarf mistletoes to fire and its behavior are of little significance when the potential total fuel and energy produced by the parasites are considered in terms of the total biomass.

The indirect relationships between fire and dwarf mistletoes are significant to us here because they are potentially useful in managing these pests and the forests infested with them. Fire, being a prime ecological factor in the development of the coniferous forests of the northern Rocky Mountains, also has a major influence on the distribution, frequency, constancy, and fidelity of dwarf mistletoes because of their obligate nature and physiological adaptations. Such influences are not unidirectional; they may be beneficial or detrimental to propagation of the pest, depending upon the environmental complex, particularly those aspects related to the nature and behavior of the fires. Thus, Alexander and Hawksworth (1975) stated, "Wildfires play a multiple role in the distribution of dwarf mistletoes."

Several workers have reported their observations on the relationship of fire to the distribution of dwarf mistletoes. Dowding (1929) stated that fire was the major factor limiting the distribution of *Arceuthobium americanum* on *Pinus banksiana* in the sandhill areas of central Alberta. Baranyay (1970) asserted that fires have functioned as an effective natural control of dwarf mistletoes in the pine forests of Alberta. Andrews (1957) felt that fires have been important in reducing dwarf mistletoe populations and recognized the tremendous costs in time and trees. Hawksworth (1961), Roth (1953), Graham (1961), and Tinnin and Knutson (1973) have related the distribution of dwarf mistletoes on ponderosa pine and Douglas-fir to fire. Fire is believed to be the major factor limiting the spread of dwarf mistletoes in spruce stands in the Lake States (Anderson, 1949; Heinselman, 1973). Several workers have expressed their opinion that fire control in the lodgepole pine forests has resulted in an increase in *A. americanum* (Kimmey, 1957; Baranyay, 1970; Heinselman, 1970; Loope 1971; Frykman, 1972; Hawksworth, 1974). Shea (1966) commented on the role of fire in reducing *A. tsugense* in the western hemlock forests of western Oregon and Washington. Opinions must eventually be tested and validated or invalidated with facts.

The reports cited above are based on observations covering short and definite time frames. They may reflect the old adage that "people see what they want to see." A sequel is found in a report by Kuijt (1955) that the present abundance of *A. americanum* in the northern Rocky Mountains is due to the role of fire in maintaining the extensive forests of lodgepole pine. In this statement, perhaps we see an early recognition of the complex nature of the ecological role of fire in the forest ecosystem when considered over an indefinite period. This statement was substantiated by Parmeter and Scharpf (1963) who reported that fires have destroyed many acres of white and red fir forests and their dwarf mistletoes in California, but that the long-range, ecological consequences of such fires have perpetuated the pest.

Weir (1916a, 1916b) was one of the first to suggest the use of fire in managing the dwarf mistletoes. As a result of the numerous subsequent observations on the relationships of fire and dwarf mistletoes, controlled burning has been frequently recommended, but infrequently used, as a possible tool for managing these pests. Alexander and Hawksworth (1975) have adequately reviewed the literature on this subject and we refer you to their paper for historical aspects.

Some of the earliest reports of the indirect relationships of dwarf mistletoes to fire were by Weir (1916a, 1916b) when he commented on the effects of spike-tops, witches'-brooms, burls, and "cat faces", caused by dwarf mistletoes, on fire behavior. Like so much of Weir's effort on dwarf mistletoes, however, his advice has gone largely unheeded. LeBarron (1948) and Boyce (1961) allude to these relationships. In his report concerning natural resistance of ponderosa pine to dwarf mistletoes, Roth (1966) referred to the indirect relationships of dwarf mistletoes to fire. Brown (1974) discussed some relationships of dwarf mistletoes to fire on the basis that they cause alterations in the distribution and quality of fuels. We suspect that many fire-fighting foresters, while suppressing fires in the northern Rocky Mountain forests, have witnessed results of the indirect effects of dwarf mistletoes on fire behavior without realizing the ecological consequences.

We have observed some forested areas in the northern Rocky Mountains where the ecological effects of fire have effectively curtailed, at least temporarily, development of the parasites and many areas where fire has provided for their intensification and perpetuation. The time frame, in which the effects of fire on the forest is considered, is very important. We cannot provide quantitative documentation of sequential development of the relationships between fire and dwarf mistletoes for any of these areas; nor can we document the nature, behavior, or history of fire or the population dynamics of the dwarf mistletoes. However, we appreciate this opportunity to present our views on the interrelationships between fire and dwarf mistletoes. Such relationships are the product of a highly interactive environmental complex, so we will relate our views of them in terms of ecosystem and habitat type concepts for each of the four conifers and its respective dwarf mistletoe growing within the northern Rocky Mountains.

In our opinion, the greatest potential for development and perpetuation of the dwarf mistletoe is in those habitat types where its common host achieves climax status. This opinion is based on observations of many populations of the parasite in different habitat types where its host may occur as a climax or seral species. However, adaptations or certain environmental factors may partially compensate for potential deficiencies of a common host of seral status.

Climax Species: Ponderosa Pine and Douglas-fir

Older ponderosa pine and Douglas-fir are relatively resistant to fire because thick layers of bark on the lower portion of the stem provide sufficient insulation to protect the cambium from injury caused by high temperatures. Ponderosa pine is the only conifer that occurs in the *Pinus ponderosa* series of habitat types (Daubenmire and Daubenmire, 1968). This series may be divided into a grassy and a shrubby group that coincide with differences in growth rate, reproductive behavior, and disease resistance of the pine (Daubenmire and Daubenmire, 1968). We believe that such a division also may coincide with differences (1) in the nature and behavior of fires because of variations in moisture and the quality, quantity and distribution of fuels, and (2) in the manifestation of *Arceuthobium campylopodum* because of variations in structure of the pine population.

In the grassy group of habitat types in the *Pinus ponderosa* series, herbs and shrubs are largely absent and the undergrowth union is xerophytic grasses. The accumulation of litter on the forest floor is too sparse to support ground fires. It consists mainly of pine needles and grasses, and decomposition is rather slow. The quantity and vertical distribution of fuels are inadequate to support crown fires. The thin layer of litter represents flash fuel in that it ignites readily and burns rapidly when dry, and it remains dry for 6-7 months of the year. During much of this dry period, the grasses aestivate and their aerial parts contribute to the quantity of flash fuel. Such ecological conditions support the rapid spread of surface fires that expose the mineral soil and may kill young pine regeneration, but inflict little damage to the older pines because the temperatures generated by such fires are not so high and are of short duration in their direct action on a given pine.

Occasionally, in areas of dwarf mistletoe infections, crowns of individual trees become so heavily infected that they are a vertical series of loosely formed, pendulant witches'-brooms. Where these trees are relatively open-grown, natural pruning does not occur and some of these brooms may be very close to or even in contact with the ground. Such crowns form an effective vertical ladder of fuel whereby a surface fire may torch the crowns of individual trees and kill them. Normally, these brooms do not break from the crowns of ponderosa pine and fall to the ground, as is common in Douglas-fir and western larch. A few may break and fall during periods of high wind, but the branches of ponderosa pine are very resistant to breakage and the loose character of witches'-broom formation is not favorable to the accumulation of large amounts of debris, snow, or ice that would increase breakage. Therefore, it is unusual to find accumulations of dead, fallen witches'-brooms around the base of an infected ponderosa pine that would concentrate fire effects at that point and kill the tree. Surface fires in the grassy group exhibit irregular, spotty, or finger-like patterns because the fuel over much of the area is insufficient to maintain the fire. Therefore, some of the young pine regeneration will survive. Evidence suggests that, before the development of efficient fire protection and suppression technology, surface fires frequently occurred in these habitat types. Fires in these habitat types seldom result in complete clean burns. Most often, they result in a scattered residual population with a staircase structure. Any abatement of the dwarf mistletoe population is minimal, localized, and temporary because it is dependent on the frequent occurrence of fires that destroy the young regeneration. A residual population of a common host with an open or patchy staircase structure forms a super highway for the movement and perpetuation of its dwarf mistletoe. Examples of such situations are to be seen in many of the ponderosa pine forests in Spokane County, Washington.

In the shrubby group of the ponderosa pine series, the distribution of the pine is more continuous, the density of stocking is usually more uniform throughout the habitat type, the population exhibits a much lower frequency of vertical structuring, and moisture is higher than in the grassy group. Reproduction is sparse, scattered, and relatively continuous. The undergrowth is dominated by layers of low, deciduous shrubs that are often very dense. Litter layer accumulations are greater, more diffuse, more uniformly distributed, and the quality is different than in the grassy group. The fire season is usually shorter than in the grassy group, but surface fires are more intense and burn more uniformly and completely. Fires often completely eliminate stands of pine and understory vegetation over large areas of these habitat types. Or, they may kill the undergrowth but kill few pines other than the young reproduction. Seldom do they leave an open residual population of several pines scattered throughout the burned area. Shrubs and herbs regenerate rapidly from subterranean organs, but it may be several years before seed crops in adjacent pine stands are adequate for regeneration of the burned area. Such regenerated pine stands are rather uniform in size and age classes. Consequently, the pine population exhibits less frequent vertical structuring than that of the grassy group; and, we know that the rate of spread of dwarf mistletoes is greatly reduced in stands of uniform structure. Fire has the potential for destroying entire dwarf mistletoe infection centers, thereby eliminating effective sources of inoculum. However, we cannot report on the observed behavior of *A. campylopodum* in the shrubby group because of the rare occurrence of the parasite within them. Daubenmire and Daubenmire (1968) report that the *A. campylopodum* has never been seen parasitizing ponderosa pine on a normal site in these habitat types. We are not certain how to interpret this statement. However, we know of small areas in Spokane County, Washington, representing the *Pinus ponderosa-Symphoricarpus* habitat type, where the pine is infected by the parasite. These areas are surrounded by the *Pinus ponderosa-Festuca* h.t. and occupy topographic depressions. We do not know if these areas are normal or abnormal sites, but on the basis of the evidence available, we cannot conclude that the shrubby group habitat types are resistant to the dwarf mistletoe—they may be escapes.

In two of the three habitat types where Douglas-fir reaches climax status, it forms an association with shrub unions of undergrowth; in the third, the undergrowth union is grass. A segregate phase of the grass union is recognized. Western larch, ponderosa, and lodgepole pines are seral invaders of the habitat types of the *Pseudotsuga menziesii* series. Ponderosa pine is more drought resistant than Douglas-fir in the seedling stage, but, in areas moist enough for its seedlings to become established, Douglas-fir exhibits a greater competitive capacity than the three seral species. Ponderosa pine is the most frequent seral in the two habitat types with shrub unions, and lodgepole pine is the most frequent seral where the grass union occurs (Daubenmire and Daubenmire, 1968).

Arceuthobium douglasii does not infect western larch, ponderosa, or lodgepole pines, nor do their common dwarf mistletoes infect Douglas-fir. However, populations of *A. douglasii* attain their highest development in the *Pseudotsuga menziesii* series of habitat types.

Development of the shrubs in the *Pseudotsuga menziesii-Symphoricarpus albus* and *Pseudotsuga menziesii-Physocarpus malvaceus* habitat types is not as great as in their counterparts of the *Pinus ponderosa* series. The shrubs are smaller and less densely stocked, and they infrequently occur in the *Pseudotsuga menziesii-Calamogrostis rubescens* habitat type. Therefore, differences in distribution and quantity of fuel between the grass and shrub unions of this series are not as great as those in the *Pinus ponderosa* series. Surface fires, common in the *Pseudotsuga menziesii* series, usually result in spotty, irregular, incomplete burning because of the quantity and distribution of fuels and the fire resistance of Douglas-fir. Consequently, a scattered residual of groups or individual Douglas-fir remain, particularly, on dry ridges of shallow soils, screes, talus, or outcrops of rock.

In areas where the Douglas-fir is infected by *A. douglasii,* it is common to find large accumulations of dead, fallen brooms around the bases of older trees. These are dense brooms composed of numerous fine branches and debris. An accumulation of brooms concentrates the effects of fire at the base of the tree, which may kill an older tree. Such accumulations also provide the initial step in the vertical ladder for surface fires to torch a tree or trigger a crown fire.

Occasionally, surface fires may not occur for long periods. Fuels accumulate and Douglas-fir becomes rather uniformly and moderately to heavily stocked over large areas. When weather conditions are highly favorable for burning, surface fires within such areas may develop into crown fires. The probability of this happening is greatly enhanced if the Douglas-fir is infected by *A. douglasii* and the characteristic witches'-brooms have developed and established the vertical distribution of fuels to support crown fires and increase "spotting" potential. These fires may kill all conifers within the burned area and greatly reduce the existing population of the parasite. However, a few dwarf mistletoe-infected Douglas-fir along the border of burns invariably exist and serve as inoculum sources of the parasite.

Following fires, shrubs and grasses regenerate rather rapidly from underground organs. Conifers reinvade the burn more slowly. The order, intensity, and combination of conifers that reinvade the burn are largely dependent upon the availability of seed. However, the effects of burning on soil moisture regimes within the burned area also influence conifer reinvasion and may determine the time, intensity, and combination of such reinvasion. Once the area is stocked with conifers and the canopy becomes closed, seral species cease to reproduce. Douglas-fir continues to reproduce and, barring further disturbances, will eventually achieve dominance because it is more competitive. Thus, the highway is provided for *A. douglasii* to reinvade the burned area.

SERAL SPECIES: WESTERN LARCH, LODGEPOLE PINE, DOUGLAS-FIR, AND PONDEROSA PINE

Western larch is the most fire resistant of the four conifers discussed in this paper and lodgepole pine the most susceptible. Western larch, lodgepole pine and Douglas-fir begin to produce seed at an early age. However, Douglas-fir has intermittent seed crops whereas western larch and lodgepole pine usually produce some seed every year and heavy seed crops occur at 2- to 5-year intervals. Seed of western larch and Douglas-fir are disseminated by wind for greater distances than those of the pines. Lodgepole pine may produce serotinous cones whereby mature cones may remain on the tree for several years and retain viable seed. Fire favors the opening of such cones whether on the tree or in the litter. Both western larch and lodgepole pine are relatively intolerant to shade. Their vigorous reproductive capacity and rapid juvenile height growth permit them to compete with the more tolerant species that invade burns or denuded areas concurrently. Thus, we see many adaptations in western larch and lodgepole pine for the early, rapid, and aggressive invasion of burned areas where soil moisture is adequate for seedling establishment and competing vegetation is temporarily destroyed. Throughout the northern Rocky Mountains, the high percentage of burns regenerated to western larch and lodgepole pine have resulted in the labeling of these two conifers as "fire-regenerated" species.

In those habitat types where western larch is a frequent seral, the quality, quantity, and distribution of fuels are usually adequate to support complete and intense burning once fire is ignited. The nature and behavior of such fires are usually determined by the amount of moisture in the fuels and the wind velocity during burning. Ground, surface, or crown fires may develop. If larch is still represented in the sere when a fire occurs, many older individuals invariably escape death because of their resistance to fire. They remain as scattered residuals and produce seed to regenerate the burned area. Because they usually produce some seed annually, they enjoy a distinct advantage over most of their coniferous competitors. Thus, as the frequency of fires increases, western larch normally becomes more abundant. In those western larch infected with *Arceuthobium laricis*, the parasite also produces seed annually. The seeds are cast down upon the young regeneration, which inevitably becomes infected. Thus, we have an ideal situation for the spread and perpetuation of the parasite; through its ecological role in maintaining an extensive population of western larch, fire is a factor in maintaining and perpetuating *A. laricis*. Many areas within the northern Rocky Mountains reflect such results. An excellent example is Quartz Creek on the Kaniksu N.F. where a fire in 1930 burned a rather large area and left a scattered overstory of dwarf mistletoe-infected western larch. The regeneration is ca. 80 percent western larch. The residuals have remained alive and the 40-year-old larch understory is heavily infected.

If western larch has essentially disappeared from the sere at the time of the fire or the fire does not leave a residual overstory of western larch, the relationship between fire and dwarf mistletoes may be reversed temporarily. Under such circumstances, the percentage of western larch in the regeneration will be less and the dwarf mistletoe inoculum source will be confined to the border of the burn. Following the parasite's initial spread from the older trees on the border for 60-70 feet into the regeneration, it must spread through a somewhat uniform structure of trees. This is a rather slow process—but it will spread.

We stated earlier that *A. laricis* has a rather wide host range and is known to reproduce rather readily on hosts other than western larch. Three such hosts are *Pinus contorta*, *Abies lasiocarpa*, and *Tsuga mertensiana*. In those habitat types at higher elevations where these species and western larch occur during development of the sere, these host relations become significant in the perpetuation of *A. laricis*. Individual dwarf mistletoe-infected western larch from an earlier developmental stage of the sere may remain as relics far into the climax stage. The climax species will become infected; and, even if the relics die before a disturbance sufficient to regenerate the seral stage again, the pest can reproduce on *A. lasiocarpa* and *T. mertensiana.* Thus, a bridge is established to reinfect the seral species whenever it returns to the area because of fire or other disturbances. An example of this is the *Tsuga mertensiana-Menziesia ferruginea* habitat type in Tributary Creek on the Coeur d'Alene National Forest where both *A. lasiocarpa* and *T. mertensiana* are frequently and heavily infected by *A. laricis.* Very few infected western larch remain as relics.

Small, dense, witches'-brooms readily develop on western larch infected by *A. laricis.* Debris, mainly fallen needles, collect in these brooms and snow and ice may accumulate in them during the winter. The wood of western larch is rather brittle and branches easily break from the trees. Consequently, witches'-brooms on western larch do not attain the size of those caused by the dwarf mistletoes on other conifers. Piles of witches'-brooms are commonly found beneath older western larch infected by dwarf mistletoe. Where infection is heavy, the original crown may be completely removed and the existing narrow, conical, living crown represented by a series of small secondary or tertiary order witches'-brooms of epicormic origin. The uppermost portion of the stem usually dies, a condition called "spike-top." The accumulation of dead witches'-brooms at the base of a tree contributes to the fuel and serves to concentrate the effects of fire at that point on the individual. This often results in deep scars that may shorten the life of the tree, but seldom kills it immediately. The sparsity of the crown reduces the probability of the tree being killed by crown fires.

Lodgepole pine is a frequent seral invader of the habitat types of the *Abies lasiocarpa* series. It reaches its highest frequency in the *Abies lasiocarpa-Vaccinium scoparium* habitat type where it is essentially unchallenged by competing serals such as *P. menziesii, L. occidentalis, P. monticola,* and *P. albicaulis.* It often forms pure stands in this habitat type where continental climates prevail and natural fires frequently occur.

In the northern Rocky Mountains, fires frequently occur in the *A. lasiocarpa* series of habitat types, particularly in western and central Montana and Wyoming and in eastern Idaho where the *Abies* *lasiocarpa-Vaccinium scoparium* habitat type is abundant. About 70 percent of these fires are caused by lightning. Moderately high temperatures, low atmospheric moisture, fuel conditions, and frequent lightning during the summer favor frequent catastrophic fires that destroy entire stands. Consequently, over much of this area, fires have prevented succession of the sere to the climax stage and maintained vast areas of the seral lodgepole pine. Lodgepole pine is relatively susceptible to fire because of its thin bark and most trees are readily killed. Some may escape, but the predominant population structure is a mosaic of irregular-shaped, even-aged, pure lodgepole pine stands. The distribution pattern of *A. americanum* on these forests is invariably "patchy or spotty" and infection centers are readily identified. A scattering of lodgepole pine residuals may remain, at least for a few years, after burning. If these residuals harbor the parasite, a uniform distribution of the pest will develop in the young forest throughout the burned area.

In older lodgepole pines, large, pendant witches'-brooms may develop from dwarf mistletoe infections. Such brooms increase the potential for crown fires or "torching" of individual crowns during burning. These brooms are not as readily broken from the tree crowns as are those of western larch and Douglas-fir; so their contribution to fuels for surface fires is not nearly so great. In general, brooms on lodgepole pine play much the same insignificant ecological role in fire behavior as brooms do on ponderosa pine.

In those habitat types where Douglas-fir and ponderosa pine are major seral species, one seldom finds optimum conditions for the spread and perpetuation of their respective dwarf mistletoes. Several conifers compete as serals in the succession of the sere and seldom do pure stands of Douglas-fir or ponderosa pine develop over vast areas. The stand structure is relatively uniform. Usually Douglas-fir or ponderosa pine comprise less than 50 percent of the stocking, and the distribution of infected hosts is randomly scattered through the forest. Fires are less frequent in these habitat types than in the *A. lasiocarpa* series. Although they are generally catastrophic, they do not exhibit as strong an influence on succession of the sere to the climax stage. The Douglas-fir and ponderosa pine serals in these types are not resistant to the parasite, however. We find them invaded by the parasite where these habitat types border on those where Douglas-fir and ponderosa pine are climax. The distribution of the parasite is spotty and usually definite infection centers exist, reflecting the original inoculum source.

CONCLUSIONS

We have discussed several relationships between fire and dwarf mistletoes in the northern Rocky Mountain forest ecosystems. The most significant relationships are indirect; they involve not only the dwarf mistletoes and fire, but the coniferous host of the parasite. Such relationships suggest many ways in which fire can be used as a practical and applicable tool in the management of the forest ecosystems of the northern Rocky Mountains. Until this century, fire was an integral ecological factor in the development of these forest ecosystems.

We believe that management of the northern Rocky Mountain forest ecosystems must be guided by ecological principles rather than solely by economic motivation. We do not subscribe to cessation of fire protection and suppression activities in these ecosystems that would permit wildfires to burn at random. We subscribe to the use of fire as a management tool because it is doubtful that these forest ecosystems can be managed for the greatest good of mankind without fire. The highly interactive environmental complex must be considered, and fire is an integral factor of the complex, particularly, in the northern Rocky Mountains.

The habitat type system, a valid system for classifying the landscape on an ecological basis, is available. This system permits prediction concerning productivity, response of vegetation to disturbances, and trends in vegetation succession. It also permits predictions about the distribution and perpetuation of certain pests. Until a better system is developed, the habitat type should form the basic unit for our forest management activities.

Fire control is an integral part of current management planning for the forest ecosystems of the northern Rocky Mountains. Although prescribed burning often has been advocated, it is rarely practiced. Pest control is commonly spoken of in connection with management planning. In actual practice, the term "control" is relegated to synonomy with the term "eradication"; from the highly relative to the absolute.

It seems reasonable to suggest that fire should be managed, pests should be managed, plants should be managed. Man should strive to manage the total forest ecosystem and not to control or to eradicate certain segments of it. What better place to start than by planning management activities on a habitat type basis?

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