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INTRODUCTION

THROUGHOUT much of its range, lodgepole pine (*Pinus contorta* Dougl.) produces serotinous cones. Because of a resinous bond between the cone scales, serotinous cones do not open at maturity. When subjected to temperatures of 45 to 50 degrees C. (or even higher), the bond breaks, the cones are free to open, and stored seed is released. Wildfires cause cones to open and cones on or near the ground are opened by normal summer soil surface temperatures (Crossley, 1956; Lotan, 1964).

Critchfield (1957) classified his Rocky Mountain and Mendocino White Plains subspecies as predominantly serotinous, but with a continuous gradient between Rocky Mountain populations and the open-cone type of the Sierra Nevada. More recently, Lotan (1975) has shown considerable local variation within the Rocky Mountain form of the species.

Lodgepole pine has traditionally been regarded as a fire-maintained, subclimax type. In some areas, such as in the high elevation forests in and around Yellowstone National Park, succession occurs at such a slow rate, fire has maintained extensive areas of virtually pure lodgepole pine forests.

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The ecological significance of the serotinous cone habit is evident on the Sleeping Child Burn (Mine Fire) on the Bitterroot National Forest in Montana. A mountain pine beetle (*Dendroctonus ponderosae* Hopk.) epidemic in the 1930's created jack-strawed fuel that burned 28,000 acres of lodgepole pine forest in 1961. Since the fire, lodgepole pine has established itself over nearly all of this vast acreage, much of it with a density of tens of thousands of seedlings per acre. This occurred despite the fact that lodgepole pine does not normally disperse sufficient seed for restocking beyond about 60 meters (200 feet). Thus, most of the 28,000 acres burned was restocked primarily from seed stored in serotinous cones.

The biotic potential to regenerate from seed stored for many years in closed cones is of great importance ecologically and silviculturally. The persistence of a forest cover in many western areas is largely due to the capability of lodgepole pine to regenerate in dense stands following a disturbance, a characteristic furthered by its serotinous cone habit. Literally millions of seed per acre may be stored within closed cones in mature stands (Lotan, 1967 and 1968).

Silviculturists have long recognized the importance of serotiny and have relied upon this particular seed source when regenerating large clearcut blocks common in lodgepole pine silviculture. Nevertheless clearcuts in lodgepole pine have not always regenerated naturally. Oftentimes regeneration success was assumed and later efforts at planting were hampered by invading grasses and forbs. Selection of a system for regenerating lodgepole pine must be based on knowledge of cone serotiny and the source of seed. The silvicultural aspects of cone serotiny are discussed in the proceedings of a recent symposium on lodgepole pine (Lotan, 1975).

In the past decade, land management agencies have recognized the need for fire to play a more natural role in the dynamics of the ecosystem. The decisions concerning whether a fire is permitted to burn involve carefully prepared prescriptions based upon such variables as site, weather, vegetation, and fuels. Fire history and natural fire cycles are considered. An understanding of the role of fire and cone serotiny would be valuable in writing plans for these areas as well as understanding the complex relationships between lodgepole pine, insect, disease, and fire.

SEROTINY AS AN ECOLOGICAL INFLUENCE

The role of lodgepole pine in forest succession following a fire was well described by Clements (1910) and Mason (1915). More recently, the subject was reviewed by Brown (1975). Canadian experience has been similar to that in the United States (Horton, 1956; Smithers, 1961).

Lodgepole pine is an aggressive pioneer species. It readily establishes itself on most burned-out areas. Exceptions do occur, especially in areas with low incidence of closed cones. Without periodic fire lodgepole pine tends to be replaced by more shade tolerant species, e.g., Engelmann spruce and subalpine fire. In the Montane and subalpine zones of the Rocky Mountains, fire interrupts this succession and initiates another stand of lodgepole pine. In mixed stands, the proportion of lodgepole pine will increase with each recurring fire. Again, the serotinous cone habit is a major mechanism that enables lodgepole pine to become established at the expense of associated species. Only western larch approaches lodgepole pine in aggressively restocking burned areas.

Under favorable conditions, restocking can take place without the serotinous cone habit depending upon a variety of situations. Burns in non-serotinous stands are occasionally restocked by natural seed fall, which occurs in late summer or autumn. I have also seen windblown lodgepole pine seeds "scudding" over crusted snow in midwinter suggesting that seed is dispersed over greater distance than would be expected by wind dissemination alone.

The ability of lodgepole pine to regenerate at the expense of other species is not due to cone serotiny alone. Other silvical characteristics of lodgepole pine contribute to its role in the forest ecosystems of these areas (Rafn, 1915; Haasis and Thrupp 131; Critchfield, 1957; Lotan and Perry, 1974; Illingworth 1975); seed viability, germination energy, rapidity of growth. Prolific seed production (discussed in Lotan, 1975) and ability to survive a wide variety of microsite and soil situations are other biological assets. This means that in writing prescriptions for silviculture or fire management that we must not generalize. The forest scientist must know the characteristics of lodgepole in his area and the management implications.

Fig. 1. Lodgepole pine heavy fuels 40 years after mountain pine beetle epidemic. This fuel type was responsible for the difficulty of controlling the Sleeping Child Fire of 1961. Two Bear Cr., Stevensville Dist., Bitterroot NF, Mont. 1970.

Fires vary in frequency, intensity, size, and other characteristics. All this can affect succession, longevity, stocking, and species composition. At low elevations in northern Idaho, lodgepole pine is open-coned, has black, deeply-fissured bark, and is relatively short-lived (80-100 years). At high elevations in eastern Montana, southern Idaho and Wyoming, it tends to bear serotinous cones, has a yellow-orange, thin bark, and is relatively long-lived (200-400 years).

In the Rocky Mountains, where cone serotiny appears to be the most extensive (even though local variation is present), lightning-caused fires have played an important role in lodgepole pine communities. Very likely, fire provides a natural check on insects and disease. The Sleeping Child burn will be relatively free of the mountain pine beetle and dwarf mistletoe for decades.

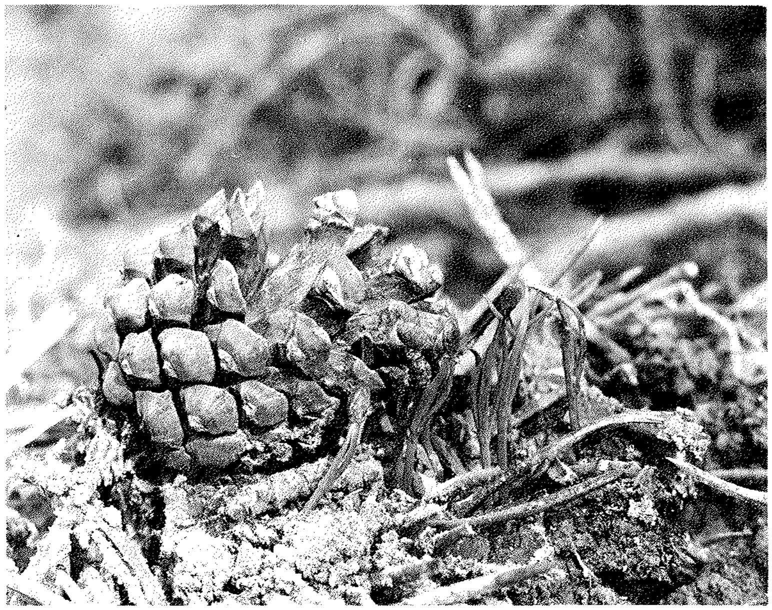

Fig. 2. Lodgepole pine seedlings beside a serotinous cone that provided the seed.

By disrupting the canopy of the mature forest, fire permits greater numbers of plant, bird, and mammal species to exist on areas that have been burned than in the mature forest (Taylor, 1969). Thirty-three vascular plants showed successional trends of establishment in a 1-year-old burn in Yellowstone National Park. The percentage frequency increased from the 1-year burn, increased through 7- and 13-year burns, reached a maximum in a 25-year-old burn, then gradually decreased in older burns up to 300 years. The greatest number of bird species and breeding pairs occurred in the youngest seral stages. Total rodent biomass was similar to the curve for vascular plant species with the greatest biomass occurring in the 13-year-old burn. Wildfire has played a major functional role in the ecology of the Rocky Mountains that we have only begun to investigate.

We cannot discuss the role of cone serotiny and its ecological sig-

Fig. 3. Lodgepole pine cones in lodgepole pine slash, a major seed source in lodgepole pine ecosystems.

nificance without reference to non-serotinous cone. Patten (1969) studied the succession from sagebrush to conifers in southwestern Montana. Lodgepole pine invaded sagebrush areas on patches of bare mineral soil as a result of an annual dispersion of seed from open cones. Once lodgepole pine became established and a forest canopy developed, shade-tolerant species are established. The annual, persistent seedfall from non-serotinous cones plays a role in conversion of sagebrush to mixed conifers in the absence of fire.

On some sites lodgepole pine is the climax species or remains in a prolonged seral stage. Moir (1969) found lodgepole pine stands where climax species had not invaded in 100 years. The unevenaged stand that I studied near West Yellowstone (Lotan, 1967) did not contain shade-tolerant species in the understory. In these stands, the annual seedfall from non-serotinous cones is important in maintaining lodgepole pine in the absence of fire. Lodgepole pine is therefore likely to prevail whether disturbances in the stand are large or small.

VARIATION OF CONE SEROTINY

Of all the traits contributing to the aggression of lodgepole pine, cone serotiny remains the key factor in regenerating burned areas because of the large number of seeds that can be stored over the years then released all at one time.

Intense crown fires do not destroy all stored seed. Wildfires move swiftly from crown to crown. Beaufait (1960) studied the effects of high temperatures on cones and seed of jack pine. Cones opened in a few seconds at temperatures of 200 to 1300 degrees F. Seed in cones that ignited were harmed, but seed in cones that did not ignite were affected but very little. Thus, if the heat quickly passes and does not ignite the cones, cone serotiny is broken and seed are released unharmed.

Many theories have been considered regarding variability of cone habit in lodgepole pine. Tower (1909) was one of the earliest workers to hypothesize the variability found in the species. He felt that cone habit varied because of varying amounts of lime in the soil. Lime-rich soils contributed to serotinous cones and lime-deficient soils led to open cones. However, Clements (1910) found differences in cone opening among individual trees in the same stand in Colorado. Mason (1915) questioned Tower's thesis and reiterated Clement's findings. Mason further declared that closed cones were more common in old stands than young stands. Bates (1930) backed Tower by hypothesizing that poor soils and crowding resulted in closed cones. The soils theory was not substantiated in Crossley's work (1956), but a recent study has not been made involving soils.

There is some evidence that age of trees influences serotiny (Crossley, 1956; Lotan, 1975). Young stands tend to bear all open cones. Toward age 20 to 30 years the closed cone trait begins to express itself. Old, overmature stands may decline in cone serotiny. It is my feeling that size of tree, vigor, and crown physiology affect the relationship of age to serotiny.

Shaw (1914) considered cone serotiny and associated morphological traits (some contributing to preservation of the seed) to be an advanced state of evolution in *Pinus* (an exception is *Pinus albicaulis,* which has not evolved the capability of flexing cone scales). Shaw considered an asymmetrical, oblique, hard, persistent, serotinous cone to be relatively advanced.

Critchfield (1957) pointed out that variation in lodgepole pine cones follows Shaw's evolutionary sequence. Cones of the Sierra Nevadas are fragile, symmetrical, open, and deciduous—Shaw's early stages. Some of the northern Rocky Mountain populations and the Mendocino group are hard, asymmetrical, serotinous, and persistent—Shaw's later stages. Middle stages are represented by lodgepole pine in the Blue Mountains in Oregon, in the Cascades, and some Rocky Mountain areas.

Critchfield also suggested the existence of elevational clines and that high elevations produce open-coned trees. Local variation suggests that the situation is more complicated than a simple elevational cline (Lotan, 1975). Although variation within a stand can be and often is quite low, stands in adjacent drainages may be quite different. Serotiny seems to vary among "swarms" of different sizes that have sharp and distinct boundaries. The question is: Does fire select for serotiny and associated traits? Fire-controlled genetic selection is logical because stands originating from fire are probably largely established from serotinous cones.

ROLE OF FIRE IN THE SELECTION OF SEROTINOUS CONES

Critchfield thought that cone characteristics centered around serotiny were probably brought about by atmospheric moisture and fire. (I feel that fire is the direct influence because moisture would affect fire frequency and intensity.) Critchfield's evolutionary sequence is supported by the fact that in the Rocky Mountains, where conflagrations remove forest cover over vast areas, the serotinous, persistent cones commonly found are a biological advantage. The Sierra Nevadas burn mostly by low-intensity fires that creep and smolder through the forest floor and surface fuels. The open, deciduous, cones found here need not be triggered by fire to release seed.

That fire is a selection agent appears to be substantiated by my comparison near West Yellowstone of an even-aged stand of recent fire origin with a contiguous uneven-aged stand (Lotan, 1967). In the even-aged stand, primarily established from seed released from cones opened by fire, 58 percent of the trees were of the serotinous-coned type. In the nearby uneven-aged stand, developed mainly from an annual seedfall from open-coned trees, only 38 percent of the trees were of the serotinous-coned type. Are we witnessing the process of selection? A high degree of cone serotiny would be expected where repeated, high-intensity fires occur. Where forest canopies are disrupted by factors other than fire, open cones annually supply seedfall for restocking disturbances such as windfalls.

Correlating variations of cone serotiny with fire characteristics poses two problems: (1) quantifying and measuring fire influences (except in the general sense as discussed above) and (2) correlating long-term evolution with short-term fire records. Fire frequency, intensity, and size vary even in the Rocky Mountains. As pointed out by Brown (1975) factors such as slope, aspect, elevation, landforms, fuels, lightning incidence, and fire season severity all influence frequency and size of fires. A hypothetical model of fire selection in lodgepole pine being formulated by David A. Perry and Lotan indicates that fire frequency can influence the alteration of gene frequencies for cone serotiny.

Teich (1970) hypothesized that cone serotiny in *Pinus contorta* and *P. banksiana* (=*P. divaracata*) is governed by a single gene and two alleles. Analysis of gene frequency did not disprove this hypothesis. Teich's hypothesis attributes trees with a preponderance of either open or serotinous cones to the homozygotes, but the phenotype of the heterozygote would bear both types of cones. An earlier hypothesis proposed by Rudolph and others (1959) for *P. banksiana* involved more than one pair of genes.

Perry and Lotan's model assumed Teich's hypothesis and showed changes in frequency for the serotinous allele for different competitive situations and for a major fire every generation. In all cases there was strong selection for the serotinous-coned trees in just a few generations. This result did not agree with my observations of variation of cone serotiny in the northern Rocky Mountains (Lotan, 1975) where even-aged presumably fire-established stands often have less than 50 percent (often nil) serotinous trees. This discrepancy has led us to reconsider our concepts of the role of fire in lodgepole pine stands and concepts of the genetics of cone serotiny. Both Dr. Perry and I feel that the latter probably is in error.

Critchfield did not decide whether cone serotiny is the derived or remnant condition, but in either case, fire appears to be an agent favoring closed cones. In fact, the relationship may not be unilateral. A recent hypothesis (Mutch, 1970) is that fire-dependent plant communities do not burn by accident or at random, they burn because they are ecologically structured to do so. Ecosystem properties make fire dependent communities more flammable than non fire-dependent communities. Brown pointed out that once fire-killed, lodgepole pine can be expected to undergo another fire 40 to 60 years hence from fuels created by the first fire therefore, the proportion of closed-coned trees would be steadily increased. The cycle of fast-growing lodgepole pine—beetle epidemics—fire are perhaps the most often cited example.

There is considerable pay-off in trying to relate cone serotiny to fire history. If cone serotiny could be linked to fire history, then cone serotiny would serve as a biometric gage or index to fire history, We are only beginning to explore the relationships of fire and cone serotiny and its ecological ramifications. An understanding of these relationships will greatly aid in predicting responses of stands to insects, diseases, and wildfires not only in areas dedicated to growing timber but also in reserve areas, such as national parks and wilderness areas where fire is now being permitted to resume some of its natural role as an ecological force.

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