RESEARCH ARTICLE

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# Endemic Forest Disturbances and Stand Structure of Ponderosa Pine *(Pinus ponderosa)* in the Upper Pine Creek Research Natural Area, South Dakota, USA

**John E. Lundquist**

**Jose F. Negron**

USDA Forest Service
Rocky Mountain Research Station
240 W. Prospect Road
Fort Collins, CO 80526
jIundquilrmrs@fs.fed.us

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ABSTRACT: Disturbances are natural and essential components of healthy ecosystems, but their ecological roles in the maintenance of endemic conditions for an area (that is, long-established levels of activity that are of low magnitude and relatively static intensity and cause unnoticed or relatively low amounts of tree killing, defoliation, or deformation) are poorly understood. The purpose of this study was to develop a conceptual model of stand development that links stand structure with underlying tree-killing disturbances. Transect surveys were used to identify and assess stand structure of a 60-ha study site in a ponderosa pine *(Pinus ponderosa* Douglas ex P. Laws. & C. Laws.) stand with no harvest or management history. The site was composed of a mosaic of four different stages of stand development. The conceptual model hypothesized that different disturbance agents were associated with different stand types, and that these agents played two basic ecological roles: (1) fire, wind, and epidemic populations of mountain pine beetle *(Dendroctonus ponderosae* Hopkins) killed trees over large enough areas to allow new stands to develop, and (2) suppression, competition, ice/snow buildup, western gall rust, endemic mountain pine beetle populations, wildfire, shrub competition, poor site quality, low light intensity, limb rust, wind, lightning, and armillaria root disease created small-scale canopy gaps that changed the growth environment for established trees and thereby influenced stand development and structure. The importance of single agents may be difficult to estimate because disturbances interact concurrently and sequentially in time and space.

*Index terms:* stand dynamics, disturbance, fire, forest diseases, forest insects

## INTRODUCTION

Stand structure in unmanaged forests is an expression of continuously interacting disturbance and recruitment processes (Pickett and White 1985, Oliver and Larson 1996, Smith et al. 1997). According to Reice (1994), "the normal state of communities and ecosystems its to be recovering from the last disturbance."

Much of what is known about impacts of forest diseases, forest insects, wildfire, wind, and other disturbances has been derived from studies of catastrophic events. These disturbances, however, exhibit a range of levels of activity and impact be-fore catastrophic levels are reached. The lower limit of natural variability is called endemic activity. Despite being a fundamentally intuitive concept, the term "endemic" is not well-defined (Tarr 1972). In this paper, we define the "endemic" state of a disturbance as follows: the disturbance is long-established in an area (see Zadoks and Schein 1979), is typically of low magnitude and relatively static intensity, and causes unnoticed or relatively small amounts of tree killing, defoliation, or deformation in forested stands. Stands with endemic levels of disturbance represent a baseline state in which potentially catastrophic disturbances are restricted by their interactions with other disturbance agents and with their environment. These interactions and the impacts associated with them are mostly undescribed.

"Outbreak" is a term used to describe a sudden rise in the severity of a disturbance agent, as measured by vegetation responses. The point at which an endemic condition becomes an outbreak has never been well-specified. Outbreak conditions are noticeable at the landscape level but can vary widely from one stand to the next and thus show considerable spatial heterogeneity (Schmid and Mata 1996).

Disturbances influence forest ecosystems mostly by killing trees within established stands (Castello et al. 1995), thereby creating openings in the forest canopy. The size, shape, abundance, and spatial distribution of these openings are determined by characteristics of the killing agents, the forest vegetation, and the environment (White 1979, Pickett and White 1985). By altering canopy characteristics, killing agents can speed up and sometimes redirect subsequent stand development (Haack and Byler 1993). Holah et al. (1997), for example, found that phellinus root disease, caused by *Phellinus weirii* (Murrill) Gilbertson, indirectly caused a relative increase in basal area of late-successional tree species in old-growth Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) forests in the lower Cascades in the Pacific Northwest, and they concluded that this disease "pushes" the successional sequence in affected stands. Some general conceptual models have been proposed that de-scribe the linkages among stand structure and underlying disturbances (Knight 1987, Rykiel et al. 1988, Castello et al. 1995, Wargo 1995). Castello et al. (1995), for example, combined gap-phase (Pickett and White 1985), disease spiral (Manion 1991), and stand development (Oliver 1981, Oliver and Larsen 1996, O'Hara et al. 1996) models to illustrate the ecological roles of diseases in stand dynamics. The model presented by Castello et al. (1995) offers a useful framework for examining the ecological roles of specific disturbance agents.

The purposes of this study were to de-scribe the structure of the ponderosa pine.. *Pinus ponderosa* Douglas ex P. Laws. &. C. Laws., forest in the Upper Pine Creek Research Natural Area located in the Black Hills of South Dakota as a case study, and to develop a hypothesis that explains how disturbance agents may have helped create this structure. Specifically, we developed a qualitative hypothetical model, using an approach similar to one used by Castello et al. (1995), to help explain the roles of endemic levels of diseases, mountain pine beetle *(Dendroctonus ponderosae* Hopkins), and other small--scale disturbances and their interactions as regulators and generators of this structure.

## MATERIALS AND METHODS

### Study Site

The Upper Pine Creek Research Natural Area (UPC; 43° 52' North, 103° 30' West) was established in 1932. The 482-ha natural area is located approximately 8 km west of Mt. Rushmore and is entirely within the Black Elk Wilderness Area (Ryan et al. 1994) in the Black Hills National Forest in South Dakota. Research Natural Areas are lands administered by the U.S. Forest Service, U.S. National Park Service, U.S. Bureau of Land Management, and U.S. Fish and Wildlife Service that represent ecosystems found on public lands. These areas have been set aside for the purposes of maintaining biological diversity, con-ducting nonmanipulative scientific re-search, conducting monitoring to deter-mine the effects of management on similar ecosystems, and fostering education (Ryan et al. 1994). The site examined in this study was a 180-ha area located in a bowl at the headwaters of the Upper Pine Creek drainages. Ponderosa pine was the dominant species, covering nearly 85% of the area (C.E. Boldt, unpubl. data). White spruce *(Picea glauca* [Moench] Voss) and aspen *(Populus tremuloides* Michx.) also occurred at the site but their incidence was limited. The remaining area not covered by these tree species was either riparian area or rock outcrop. Forests had never been harvested (although some scattered individual trees had been felled for unknown reasons) or grazed by livestock. Elevation varied between 1829 m and 2105 m.

Several different terms have been used to describe the elements composing the type of mosaic that results from small-scale disturbances. In this paper, we adopt those used by Smith et al. (1997): a single cohort is an aggregate of trees that starts as a result of a single disturbance; a stand is "a contiguous group of trees sufficiently uniform in species composition, arrangement of age classes, site quality, and condition to be a distinguishable unit" (stands may consist of single, double, or multiple cohorts). Canopy gaps were found within stands and occurred as a result of the death of at least one dominant or codominant tree.

### Transect Surveys

Six 1,000-m parallel transects were established across the 60-ha study area to characterize stand distribution (Runkle 1992) in summers of 1996, 1997, and 1998. Stands were grouped on the basis of visual similarity. The transects were generally oriented northeast–southwest at 100-m intervals, which was generally resolute enough to intersect all stand types. We noted distance along each transect where one stand terminated and a different stand began. Some transitions were distinct, but others were not. For the latter, best judgments were made. We mapped stand distribution by aligning the edges of similar stands from the transect locations, and verifying positions and adjusting by follow-up site assessments. We then subsampled five or more stands composed of the same type using variable-radius plots (three plots per stand) to develop a quantitative description of each stand type. Data from the subsampled plots were pooled for each stand type; basal area, stern density, and average stem diameter were calculated using methods described in Husch et al. (1972). In addition, stem cores were extracted from at least one codominant tree within each stand, and the number of annual rings was counted in the lab to deter-mine age.

### Determination of Mortality Agents

We visually assessed each stand for possible killing agents that had caused changes in the canopy structure. Previous studies (Lundquist 1995) had shown that the pre-dominant causes of canopy gaps in the UPC were armillaria root disease *(Armillaria ostoyae* [Romangnesi] Herink), lightning, mountain pine beetle, wildfire, ice and snow damage, weak pathogens, and strong winds. Diagnosis of these causal agents was based on a careful evaluation of obvious symptoms and signs. For ex-ample, symptoms of armillaria root disease in ponderosa pine may be red or chlorotic needles, stunted internodal growth of recent lateral and terminal shoots, a distress crop of cones, basal resinosis, and stunted needles. Obvious signs of armillaria root disease may be the presence of a mycelial fan between the inner bark and outer xylem, or the imprint of an old fan in the inner bark; fruiting bodies (mushrooms) of the pathogen growing near the base of infected trees; resin-soaked wood; or the presence of rhizomorphs under the bark at the base of the tree, or growing along infected roots. This assessment was based on presence or absence of evidence; we did not try to estimate when disturbances occurred.

**Table 1. Similarity and differences in characteristics of the four ponderosa pine stand types in the Upper Pine Creek Research Natural Area, South Dakota.**

| Stand Type | General Description | dbh (cm) | Stern Density (stems ha-$^{1}$) | Age (years) (range) | Killing Agents |
|---|---|---|---|---|---|
| 1 | single story, small trees, uniform and dense distribution; subtype la — dense regeneration; subtype lb — irregular regeneration | 18 | 486 | 72 (<1–192) | suppression, competition, ice, snow, mountain pine beetle, western gall rust |
| 2 | single story, large trees, uniform and moderately dense distribution | 27 | 157 | 171 (150–298) | low-intensity fire, shrub competition, poor site, limb rust |
| 3 | single story, large trees, large gaps; in subtype 3a: scant regeneration; in subtype 3b: dense regeneration | 36 | 117 | 173 (132–292) | in subtype 3a: armillaria, poor site in subtype 3b: mountain pine beetle, windthrow, lightning |
| 4 | two stories, overstory with large trees and understory with small trees | 33 | 180 (overstory) 381 (understory) | 179 (110–247) (overstory) 52 (31–82) (understory) | high-intensity fires |

## RESULTS

### Stand Descriptions

The survey showed that the 180-ha area was a mosaic composed of four stand types (Table 1, Figure 1), which were identified based on similarity of tree height, diameter, and spacing; canopy gap presence and characteristics; abundance and distribution of regeneration; and evidence of disturbances. Stand types showed one of the following combinations of characteristics.

*Stand Type 1:* This type was composed of a single story of relatively small trees with uniform and, initially, dense distribution (Figure 2). Eighteen of the 48 stands composing the study area were Stand Type 1. Later stages (type lb) were marked by irregular regeneration. Overall, average tree diameter was 18 cm and density was 486 stems ha-'. Average age was 72 years, ranging from <1 to 192 years. Suppression, competition, ice/snow, mountain pine beetle, and western gall rust (caused by *Peridermium harknessii* J.P. Moore = *Endocronartium harknessii [J.P.* Moore] Y. Hirat.) associated with canopy gaps were evident in this stand type.

*Stand Type 2:* This type (9 stands) was composed primarily of a single-story structure of large trees with uniform and moderately dense distribution (Figure 2). The average age of trees in Type 2 was 171 years, but age ranged from 150 to 298 years. Average tree diameter was 27 cm and average density was 157 stems ha-', with an average basal area of 22.5 m$^{2}$ ha-'. Low-intensity fire, shrub competition, site quality, and limb rust (caused by *Peridermium filamentosum* Peck) were commonly evident in this type.

*Stand Type 3:* This type was composed of a single story of relatively large trees and was marked by relatively large canopy gaps (Figure 2). Average age of trees was 173 (132-292). Average tree diameter was 36 cm and average density was 117 stems ha$^{-i}$, with an average basal area of 29.1 m$^{2}$ ha$^{-l}$. Because much variation occurred within this stand type, it was further sub-divided into two subtypes that differed in abundance and distribution of regenera-

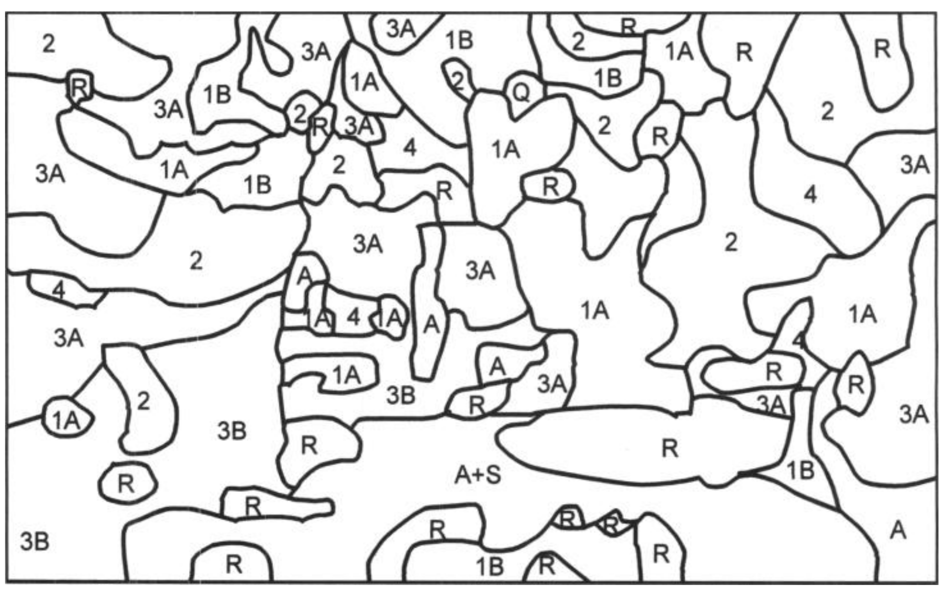


**Figure 1. Spatial distribution of stand types within the study site at Upper Pine Creek Research Natural Area. Numbers refer to stand types, which are described in the text. R = rock outcrop, A = aspen stand,** AtS = **aspen and spruce stand, Q = oak stand.**

**Figure 2. Scenes representative of the four stand types described in this study. Top to bottom: stand initiation (Type lb), stem exclusion (Type 2), understory reinitiation (Type 3b), and understory reinitiation (Type 4).**

tion. The first subtype (Type 3a, 14 stands) was single story with gaps that lacked or had scant re-generation. Type 3b (one stand) was single story with gaps that had dense regeneration. Armillaria root disease and poor site quality were associated with Type 3a, and mountain pine beetles, wind-throw, and lightning were associated with Type 3b.

*Stand Type 4:* This stand type (6 stands) was two-storied and composed of an overstory of relatively large dominant and codominant trees and an understory of intermediate and overtopped smaller trees (Figure 2). Crown classes distinguished here are those defined by Smith et al. 1997. Average tree age was 179 years (range 110–247) in the overstory and 52 years (range 31–82) in the understory. Overall average tree diameter was 33 cm. Average density was 180 stems ha-' for the overstory and 381 stems ha-' for the understory. We frequently found burnt stems of large trees in this stand type, indicating previous occurrences of wildfires.

## MODEL DEVELOPMENT

Using Oliver and Larsen's (1996) model as a framework, we pro-pose the following conceptual model to describe the interactions among ponderosa pine stand types described above and endemic tree-killing disturbances found during this survey (Figure 3).

### Stand Initiation Stage

Stand initiation begins after a major disturbance caused by in-tense crown fires, catastrophic wind events, or mountain pine bark beetle outbreaks creates growing space for new trees to become established or preexisting trees to expand; this can hap-pen at any stage of stand development. As the new stand develops, density and spatial patterns of re-generation are moderated by suppression, competition, ice/snow damage, and western gall rust (Stand Type 1 a). Stand initiation proceeds until tree crowns close, which in the UPC occurs about 70 years after disturbance.

### Stem Exclusion Stage

Ponderosa pine stands then enter the stem exclusion stage, in which average stem and crown diameter gradually increase, with a corresponding reduction in number of trees per hectare as a result of self-thinning and scattered mountain pine beetle-caused mortality (Stand Type lb). This stand type can be maintained over time by the spatially uniform occurrence of low-intensity fires, undergrowth shrub competition, poor site quality, low light intensity, and limb rust—disturbances that are not intense enough to destroy large numbers of trees and encourage the establishment of many new trees (Stand Type 2).

### Stand Reinitiation Stage

Alternatively, scattered dominant and codominant trees can be killed in various patterns by a variety of agents, opening the canopy enough to allow new plants to become established. Such stands enter the stand reinitiation stage, in which either (1) mountain pine beetles, windstorms, or lightning can kill groups of trees, thus creating canopy gaps large enough for clumps of abundant regenerated trees to become established (Stand Type 3b), or (2) relatively high intensity wildfires burn uniformly, causing enough mortality of overstory trees to create conditions for a uniform distribution of new regeneration, and thus a two-story structure (Stand Type 4). A different pattern results when unfavorable microsite conditions or armillaria root disease resident in soil prevent the establishment of pine regeneration, even though other conditions would be other-wise favorable (Stand Type 3a). Mountain pine beetles can infest trees at the edges of armillaria root disease pockets in this stand type and enlarge canopy gaps.

### *Old-Growth Stage*

No stands were found that could fit the definition of old growth in Oliver and Larson's (1996) stand development mod-el. Stand replacement disturbances (fire, windstorms, and mountain pine beetles) occurred between about 170 and 200 years ago (ranging up to around 300 years ago), killing enough trees over a large enough area to allow new stands to be established.

## DISCUSSION

Historic disturbances and the magnitude of their activity are reflected in the current structure of forest stands (White 1979). Our model is an attempt to interpret how the nature, magnitude, and intensity of disturbances lead to the development of stand structure in the ponderosa pine forest of Upper Pine Creek. The interplay between endemic disturbances that cause canopy gaps, and those that replace stands, has created the patch mosaic of the Upper Pine Creek watershed. The model suggests that many disturbance agents can cause canopy gaps, but only a few can cause stand replacement. The nature of the impact of these few is determined by their intensity. Interactions between cause and intensity are linked to stand dynamics.

### Scale Effects

Disturbance is a common feature in the endemic forest of the UPC (Lundquist 1995). Thirteen disturbance agents were evident in the UPC: three diseases, one insect, six abiotic stresses, and three stresses induced by competition among individual plants/trees. Disturbances can interact con-currently and sequentially in time and space. The ecological role of a tree-killing agent depends on its relative position in time and space in the hierarchical structure of an ecosystem (Allen and Hoekstra 1992).

According to Wiens (1989), "if we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale." For example, a large-scale catastrophic wildfire that occurred 200 years or more ago may have destroyed trees over the entire UPC watershed. Such a catastrophic disturbance occurs over much larger intervals of time than the killing agents examined in this study. The current stand structure in the unharvested ponderosa pine forest of this study is spatially distributed as a patchwork of small stands. Gaps, stands, and the watershed appear to be the fundamental scales in the ponderosa pine wilderness in this area of the Black Hills. An examination of the functional roles of diseases and insects in this ecosystem should take this hierarchical scale into account. Gaps are relatively small because the disturbance agents that cause them act over a limited area. Stands can be relatively large because sometimes the activities of these disturbance agents approach the upper limit of their range of natural variability, that is, they are outside the "endemic state." Gaps and stands occur at two different spatial scales, even though both of them can arise from the same tree-killing events.

### What Inhibits Outbreaks?

Outbreaks are prevented by interactions of disturbance agents and their environment during the endemic state. According to Reice (1994), "interaction between distur-bance and patchiness in virtually all systems is the underlying basis for the control of community structure." In UPC, patchiness is associated with different stand types that seem to have different susceptibilities to disturbance agents. Across the landscape, patterns of fire spread and mountain pine beetle-caused mortality probably

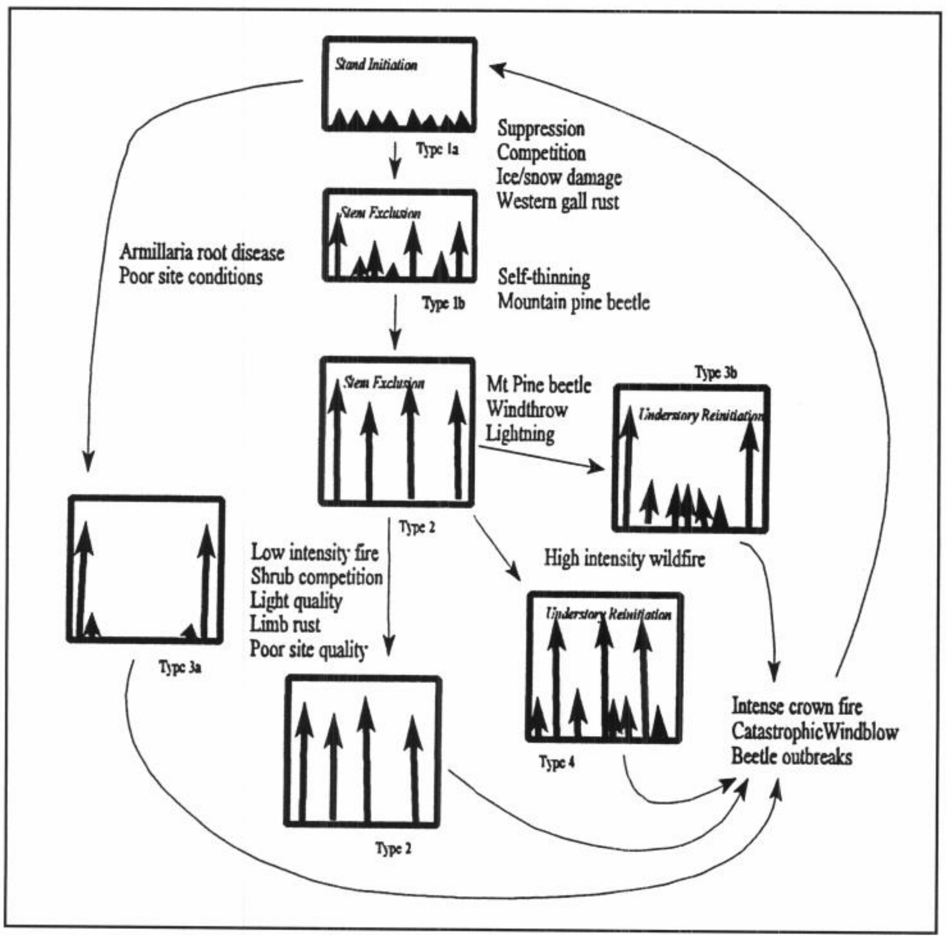


**Figure 3. A conceptual model of the relationship between disturbances and developmental stages of a previously unharvested ponderosa pine stand in the Black Hills, South Dakota.**

depend partly on the spatial placement of different stand types. The mosaic nature of stands in the landscape might prevent fires or mountain pine beetle outbreaks from spreading widely, because some stand types may temper the probability of catastrophic fires or mountain pine beetle outbreaks. The spatial arrangement of gaps and stands characterizes this forest community. When catastrophic mountain pine beetle out-breaks or large-scale fires occur, however, the disturbance can spread despite the patchy condition of the landscape. Forest managers may bebetter able to predict or perhaps act to restrict the impacts of disturbances by understanding how various agents interact with other components of the ecosystem during the endemic state. A greater understanding of the natural endemic condition of many important diseases, insects, and other agents is necessary before managers can do this, however.

Little is known about the set of circum-stances that triggers outbreaks associated with stand-replacement disturbances in forests (Schowalter and Filip 1993). Eck-berg et al. (1994) showed that the various predisposing factors associated with epidemic outbreaks of mountain pine beetle populations in the Black Hills are the same factors traditionally associated with the maintenance of endemic mountain pine beetle populations. These include lightning strikes, previous unsuccessful attacks by mountain pine beetles (pitchouts) in which trees are stressed but do not die, armillaria root disease, and physical or mechanical damage to trees. These disturbances originate in all stages of stand development except stand initiation. The later part of the stem exclusion stage would have the highest risk of mountain pine beetle infestation because basal area is high, and average stem diameters are above the threshold size for mountain pine beetle attack (Schmid and Mata 1996). In contrast, mountain pine beetles would avoid the stand initiation stage because trees are generally small in diameter. Eventually, reduced mountain pine beetle-caused mortality is observed in understory reinitiation stages because fire-caused mortality reduces the basal area.

## The Role of Fire

Although Parrish et al. (1996) stated that wildfire is the dominant disturbance in the Black Hills, their statement almost certainly refers to catastrophic fires. It is much more difficult to assess relative importance of single agents such as fire under endemic conditions. Fire is certainly a component, but it is not the dominant disturbance agent in noncatastrophic situations.

Fire history data from the Black Hills and surrounding areas are rather limited. Stud-ies by Brown and Sieg (1996) in the Black Hills, and by Fisher et al. (1987) in Devils Tower National Monument (west of the Black Hills in eastern Wyoming) reported similar patterns in mean fire-return inter-vals. Both Brown and Sieg (1996) and Fisher et al. (1987) indicated that longer fire-return intervals prevailed after Euro-pean settlement, and suggested that these longer intervals were associated with fire-suppression activities. The most common fires in the Devil's Tower study sites were spot fires caused by lightning that affected one or a few trees before being extinguished by rain or lack of fuel. These are the kinds of low-intensity fires that con-tribute to the maintenance of Stand Type 2. Stand establishment events evidently occurred in the Black Hills study sites, perhaps as a result of high-intensity, stand-destroying fires. Such stand-replacing high-intensity fires are responsible for decimating all stand types and causing stand reinitiation.

Pathogens, insects, and other small-scale disturbance agents change woody debris distribution within stands (Maser et al. 1979), which certainly influences the prob-ability of wildfire. Self-thinning during the early part of the stem exclusion stage results in large accumulations of dead and down woody material, but fire hazard is probably relatively low because this debris is small and decays relatively quickly. Fire hazard probably reaches a maximum during later parts of the stem exclusion stage, when debris decays less quickly because it is larger and bark is not thick enough to make living trees resistant to fire damage. Fire hazard is high during the understory reinitiation stages, when mor-tality adds larger debris that decays less quickly. However, stand replacing fires are less likely to occur in Stand Type 4 in the understory reinitiation stage because the frequency of less intense fires keeps hazard for intense fires low.


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*John Lundquist is a Research Plant Pa-thologist with the Rocky Mountain Re-search Station of the U.S. Forest Service in Fort Collins, Colorado. His research interests include assessment of disease im-pact on timber and nontimber resources, and the ecology of diseases in forest eco-systems.*

*Jose Negron is a Research Entomologist with the Rocky Mountain Research Sta-tion. His research interests include the bi-ology and ecology of western bark beetles.*


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