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Early Development of Vegetation Following Holocaustic Fire in Northern Rocky Mountain Forests[1]

Introduction

Information about the recovery process and postfire development of forest vegetation has evolved from forest succession studies conducted in central and northern Idaho and western Montana. Permanent plots were sampled for species abundance annually for periods of 7 to 22 years. More than 60 study sites were involved. A study of the initial postfire communities establishing after the 1988 Northern Rocky Mountain holocaustic fires (including the Northfork Fire in Yellowstone National Park) indicates that the mechanism for initiating recovery and succession is the same as that displayed by the permanent plot succession studies.

Holocaustic Fire Treatment

Fire is an inherent phenomenon of Northern Rocky Mountain forests and has been the principal and most extensive initiator of forest succession in the region for at least the last several thousand years (Hemphill 1983, Mehringer *et al.* 1977, Wellner 1970). The severity of burning in these forests varies from light ground fires to severe, tree-overstory-killing crown fires (Arno 1980, Wellner 1970). Holocaustic fires (Stickney 1986) represents the severest natural burning disturbance sustained by Northern Rocky Mountain forest vegetation, and as such it provides the conditions to best assess the maximal limit of the ability of forest species to survive fire. A holocaustic fire is defined as one that incinerates all of the finer fuels on a site. Its characteristics in Northern Rocky Mountain forests are (1) destruction of the coniferous tree overstory, (2) reduction of the tree-shrub understory and herb layers to ground level, and (3) conversion of the dead organic mantle of the forest floor to ash down to the mineral ground surface. Although this fire treatment incinerates the above-ground portion of the forest community, the below-ground portion can remain intact and essentially undisturbed.

[1]From the Symposium "Environmental Disasters: The Nature of Recovery" held at the Sixty-Third Annual Meeting of the Northwest Scientific Association, March 21-23, 1990, Corvallis, Oregon. Mark V. Wilson and Nan C. Vance, editors.

Initial Community Components

As defined by their postfire or seral origin (Stickney 1986), plants that compose the initial community establishing on burned sites after a holocaustic fire belong to one of three components: survivor, residual colonizer, and offsite colonizer. Survivors derive from burned plants capable of regrowth. Colonizers are postfire plants established from seed. Residual colonizers originate from burned sources. Offsite colonizers originate from sources not subjected to burning.

The Danish ecologist C. Raunkiaer classified plant life forms according to the position of their active growing points in relation to their exposure to air temperature of the "unfavorable season" (Raunkiaer 1934). The closer the growing points were to the ground the greater the capability to survive unfavorable temperatures. The survival mechanisms of Northern Rocky Mountain forest plants to fire may be visualized by applying Raunkiaer's idea to the position of both the dormant and active growing points exposed to the lethal temperatures of a holocaustic fire. This application shows that the coniferous tree (leftmost mode in Figure 1) has no mechanism by which to survive holocaustic fire treatment. Forest herb and shrub species with root crown or underground stem life forms are capable of surviving this kind of fire (Table 1, Figure 1). Thus, survivors of holocaustic fires are preburn plants with growing points near, in, or below the mineral ground surface.

Residual colonizers, whose seed was present on the site prior to the time of the fire, represent the other onsite source for species in the initial community. The seeds of residual colonizers survive fire treatment either in cones within tree crowns or as ground-stored seed (Figure 2). Residual colonizer seeds stored for a year or more in the ground characteristically exhibit poor dispersal capability, hard seed coat, and long-term viability. Although the number of species in this group constitute a small percentage of the seral flora, they represent some of the most abundant cover species

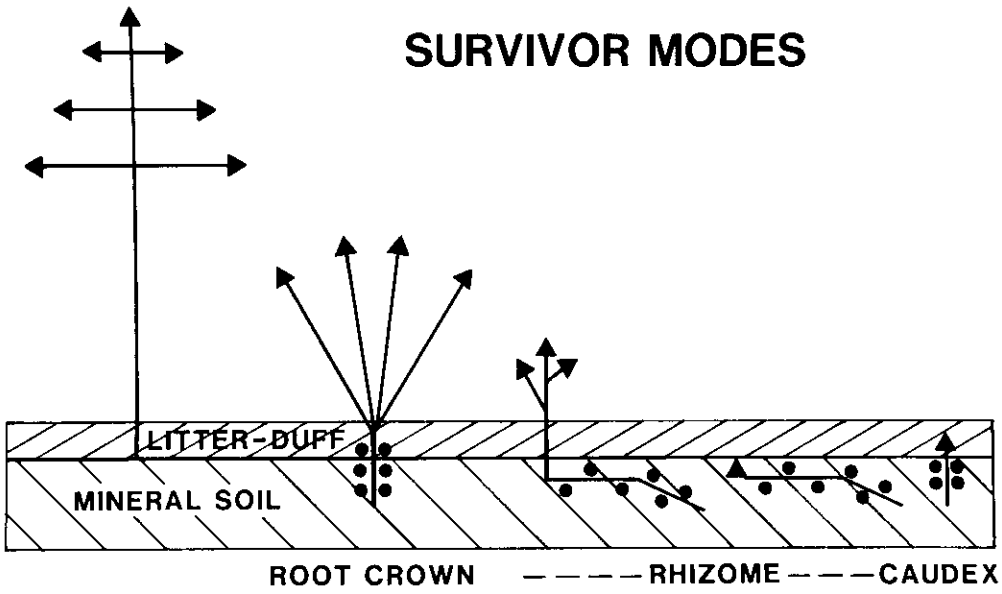

Figure 1. Raunkiaer's life forms modified to illustrate mechanisms that enable Northern Rocky Mountain forest plants to survive holocaustic forest fire. Triangles and dots represent active and dormant growing points respectively. The region from the forest canopy down to at least the mineral soil surface is subject to lethal temperatures from holocaustic fire. Active growing points within this zone are killed; protected dormant growing points are not.

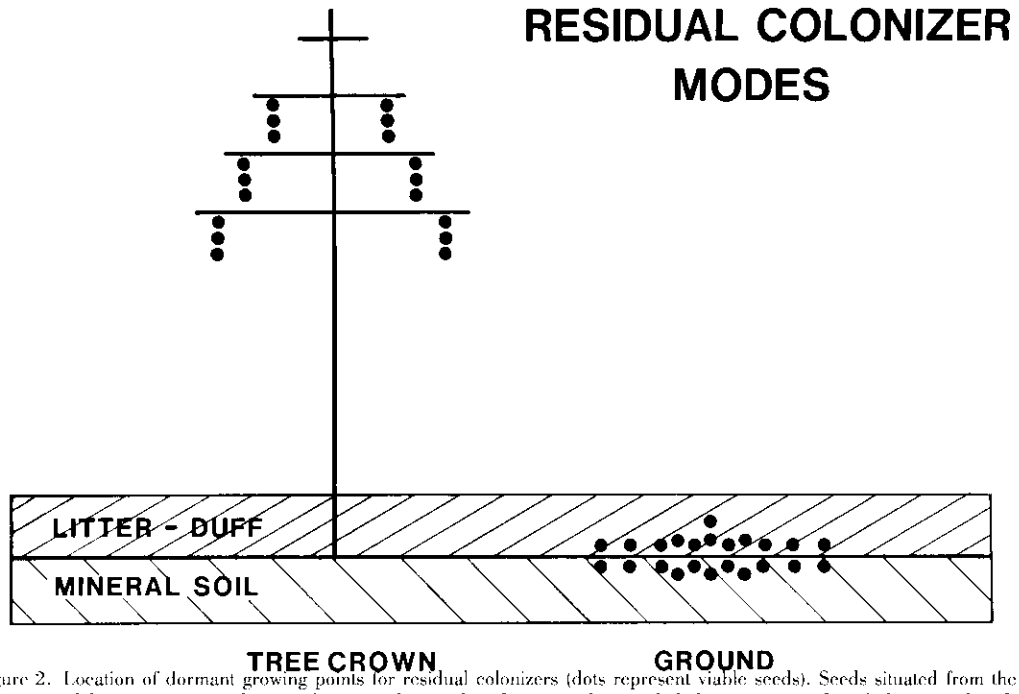

Figure 2. Location of dormant growing points for residual colonizers (dots represent viable seeds). Seeds situated from the top of the tree overstory down to the mineral ground surface are subject to lethal temperatures from holocaustic fire. Seeds in tree crowns are protected by cones; seeds in fruit in the canopy of other plants are not protected. Survival of seeds situated in the litter-duff layer depends on the characteristics of the seed coat. Seeds within the ground receive greater protection from the mineral substrate.

TABLE 1. Life forms and species from Northern Rocky Mountain forests that have demonstrated survival capabilities following holocaustic wildfires.

Life form	Species examples
Root crown shrub	*Acer glabrum, Alnus sinuata*
Rhizomatous shrub	*Spiraea betulifolia, Vaccinium globulare*
Rhizomatous herb	
Forb	*Arnica latifolia, Aster conspicuus*
Grass	*Calamagrostis rubescens*
Caudex herb	*Lupinus argenteus*
Deep-seated stem herb	*Erythronium grandiflorum, Trillium ovatum*
Rhizome-like root herb	*Epilobium angustifolium*

in the pretree stages of succession (Stickney 1986). Prominent examples of residual colonizers include the shrubs snowbrush (*Ceanothus velutinus*) and redstem (*C. sanguineus*); the herbs geranium (*Geranium bicknellii*), dragonhead (*Dracocephalum parviflorum*), and wild hollyhocks (*Iliamna rivularis*); and western larch (*Larix occidentalis*) and lodgepole pine (*Pinus contorta*).

Offsite colonizers are derived from seed originating from unburned sites usually outside the fire. Seeds of species characterizing this group of the initial community typically are small, light weight, and air dispersible with short-term viability. The number of species constituting the offsite component typically is large (including numerous members of the composite family) and greater than that for the residual colonizer component. Usually, a relative few become important cover species in the subsequent succession. Two of the more important offsite colonizers successionally in the Northern Rocky Mountains are the herb fireweed (*Epilobium angustifolium*) and the shrub Scouler's willow (*Salix scouleriana*).

Initial Community

Floristic composition of the initial community, the group of species that initiates the course of succession, derives from onsite (burned) and offsite (unburned) sources (Lyon and Stickney 1976, Stickney 1985). The interaction of the fire and onsite sources determines their presence in the initial community. The floristic contributions to succession from onsite sources, i.e., survivors and colonizers, are limited to those species present in the preburn forest (including its seedbank). The survivor component results from the effect of fire severity on prefire species composition. Generally, the more severe the burning treatment the higher the mortality and the less the survivor component in both species and plants. A sparse survivor component can also result from forests with little or no undergrowth vegetation that serves as a source for survivors. Similarly, the extent of a residual colonizer component is dependent on the seed already "in place" on the site. The contribution of plant species from onsite sources to the seral flora is a singular event in the succession cycle. On the basis of our permanent plot studies this event manifests itself, almost exclusively, in the first postfire year of succession.

Further additions to the floristic composition must come from offsite colonization. Unlike the onsite components, the potential for offsite species contributions to the initial community is limited only to the extent of the available flora. Species from offsite sources require no capacity to survive fire. Rather, in contrast to onsite species, they do require both a seed crop and a dispersal event that coincides with the availability of a burned site.

Thus, the floristic composition of the initial community established by the species of the survivor component and the residual and offsite colonizer components set the course of succession. Changes in the seral flora result only from the loss of initial community species (local extinction) or the addition of species from offsite colonization. Our permanent plot studies reveal that offsite colonization occurs but for a majority of sites does not alter the course of successional development established by the initial community (Stickney 1986). For those few cases where secondary colonization has had a significant influence on the course of succession, it was from postfire onsite rather than offsite seed sources.

Seral Spectrum

Various combinations of floristic composition and species abundance of survivor and colonizer species give rise to a spectrum of initial communities. Thus, the course or pattern of early forest succession for a given site can range from a survivor-dominated to a colonizer-dominated process. Brushfields occupying forest sites at the time of burning provide one example of a survivor-dominated succession. At Sundance Burn Study Site 17 the initial community consisted of survivor *Salix scouleriana, Ceanothus sanguineus*, and six

other species of shrubs, and the herbs pinegrass (*Calamagrostis rubescens*) and lupine (*Lupinus argenteus*) (Stickney 1985). All these species regrew profusely following a holocaustic wildfire. Recovery was rapid, and 20 years later survivor-origin *Salix*, *Ceanothus*, and *Calamagrostis* were still the most abundant species and made up most of the vegetation.

Illustrative of the other end of the spectrum is Miller Creek Study Site 22 where the forest overstory was killed and shrubs and herbs subjected to high mortality (Stickney 1980). The resulting small survivor component, with its slow recovery rate, provided a highly favorable site for the establishment of colonizers. In this instance large populations of both offsite (*Epilobium angustifolium*) and residual (*Ceanothus velutinus*, *Pinus contorta*, and *Larix occidentalis*) colonizers became established in succession year 1. Rapid development of *Epilobium* dominated the herb stage through year 6. This was followed by a shrub stage in which the development of seedling *Ceanothus* constituted the predominant shrub to year 20 and beyond. Concomitant with the establishment of *Ceanothus* seedlings were seedlings of *Pinus* and *Larix* trees. Their height growth was such that they overtopped the shrub canopy by the beginning of the shrub stage. As shrub coverage, principally *Ceanothus*, increased, *Epilobium* declined. By the 20th year the beginning of the decline of *Ceanothus* was associated with the continual development of the tree canopy. All the prominent colonizer species thus far constituting the succession were present in the initial community. After 20 years of recovery and development, secondary colonization from offsite sources has yet to make an influential contribution. With further development of tree overstory canopy, the recovering survivor understory species should again constitute a prominent element of this forest vegetation.

In 1989 a study of the fires of 1988 in the Northern Rocky Mountains revealed the same spectrum of initial communities found in the permanent plot successional studies. Examples illustrating predominant survivor component (*Calamagrostis rubescens*, aster (*Aster conspicuus*)) and residual colonizer component (*Dracocephalum parviflorum*, *Geranium bicknellii*) were observed within the Northfork Burn in Yellowstone National Park. The occurrence of these types of initial communities suggests that recovery and seral development of these burned forest communities should follow patterns similar to those documented elsewhere in the Northern Rockies.

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