Early Vegetal Succession Following Large Northern Rocky Mountain Wildfires

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INTRODUCTION

WILDFIRE is a naturally recurring phenomenon in the forests of the Northern Rockies. Historical accounts of earliest explorations contain references to areas denuded by fire, and the massive forest fires of this century have been documented. Written records before 1800 are sketchy, but charcoal in the ground, burned stumps, and fire scars in tree cross sections provide evidence of a forest-fire history predating the oldest living vegetation in the Northern Rockies. Thus, it is generally accepted that these forests have evolved in the presence of repeated fires.

Despite this evolutionary concept, recognition of the ecological significance of fire is relatively recent and not yet well defined. Much of the literature treats fire as the external disturbance of an otherwise stable system. By implication, forest succession becomes evidence of ecosystem resilience or ability to recover from outside disturbance, and predictive models tend to assume the classic concept of succession in which early seral plants modify the site to their own exclusion and thereby permit establishment of interseral and climax species. Our data suggest that this is a poor conceptual model for forest succession in the Northern Rockies.

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As an alternative, we believe that fire should be treated as an internal perturbation of a generally stable system. Forest succession can then be modeled as a sequential development of dominance, during which the forest community reverts to its prefire structure, with some random variations in composition and duration of seral stages that do not alter the general developmental sequence or eventual structure of the community.

We claim little credit for this concept, although we believe it requires continuing emphasis. Two recent papers in *Ecology*, one dealing with hardwood forest succession (Henry and Swan, 1974), the other with old-field succession (Niering and Goodwin, 1974), provide further discussion of the ecological debate including Egler's (cf. Niering and Goodwin, 1974) concept of "vegetation development" from "initial floristics" as opposed to "succession" by way of "relay floristics." As is true of many ecological debates, neither extreme can be defended as unequivocal truth. We only suggest that one approach provides a better conceptual base for modeling forest succession following fire.

FOREST COMMUNITIES AND FIRE

Mature forests of the Northern Rocky Mountains typically are composed of dominant overstory conifers with an understory of shade-tolerant shrubs and herbs. Relationships between the overstory and understory exhibit a full range of dominance patterns, but very often there appears to be an inverse relationship between understory density and overstory crown closure. Community predisposition to fire is indicated by organic accumulation in excess of decomposition (Roe et al., 1971; Beaufait, 1971), a considerable number of plant species with characteristics that enhance flammability (Mutch, 1970), and regional weather patterns that provide both adequate ignition sources (Wellner, 1970) and fuel moisture conditions favorable for burning.

Fires usually occur during a late-summer dry season, with results that are best characterized as variable in both pattern and intensity. Only in large, intense wildfires does variability approach a consistent and predictable level. Given such a fire, the crowns of both overstory and understory vegetation are destroyed and the organic mantle is reduced to mineral ash. Admittedly, this total reduction appears to be an excessive expression of internal perturbation, but it may also be perfectly normal. Wellner (1970), summarizing the reports of Lieberg (1904), Flint (1930), and others suggested that Northern Rocky Mountain fires are characteristically large and catastrophic. A full spectrum of fire intensity has, however, been recorded in the Northern Rocky Mountains. and, while large, intensely burning wildfires occur with lesser frequency, they affect larger, contiguous areas and best demonstrate the adaptability of this vegetation to fire.

Vegetal recovery from these large fires can also be characterized as variable, even though the eventual outcome is relatively consistent. Of the nearly 5 million acres burned in the Northern Rockies in the first 2 decades of this century, excluding multiple-burn areas, only a small percentage is not now forested. On a time scale of half a century, postfire forest succession throughout the Northern Rockies has a consistent and predictable pattern leading to dominant overstory conifers with an understory of shade-tolerant shrubs and herbs.

On the other hand, early vegetal succession appears to be much less consistent and predictable, although it is usually accepted that herbaceous plants, shrubs, and trees appear in a more or less orderly sequence. In this paper, we accept the sequence, but propose that expression be in terms of vegetation dominance rather than species composition. Herbaceous species dominate the earliest successional stages because their period of development to maturity is shorter. Later successional stages are dominated by trees because of their slower development, greater maximum size, and age. Thus, the orderly sequence provides a logical concept for succession modeling in terms of predominant vegetation independent of the consistency or variability of floristic composition.

STUDY AREAS

In developing the thesis presented here, we have drawn on data from three wildfires of the past 15 years. All three are representative of large and catastrophic forest fires in Northern Rocky Mountain forests.

Sleeping Child Fire

This wildfire burned 28,000 acres on the Bitterroot National Forest during August 1961. We established 12 sample transects within the burn, but rehabilitation and management activities have compromised vegetal recovery on 8 of these. Our data, then represent averages for 4 areas lying between 6,000 and 7,200 feet in the Douglas-fir and subalpine fir/Englemann spruce types. The dominant tree species at the time of the fire was lodgepole pine on all areas.

Sampling transects on the Sleeping Child burn consist of 10 permanently marked 0.04-acre circular plots for trees and shrubs and ten 2x2-foot quadrats for seedlings and herbaceous plants. Trees were counted and shrubs measured in two crown dimensions and height; seedlings were counted and cover and frequency were recorded for herbaceous species. Data were taken annually for the first 6 years and in alternate years from 1967 through 1973. Available information includes frequency, density, cover, and crown volumes by species. A representative transect is illustrated in Figure 1.

Neal Canyon Fire

This prescribed fire on the Sawtooth National Forest has been reported by Lyon (1971). One hundred and twenty acres of standing Douglas-fir timber on a north aspect at 6,500 feet were burned August 1, 1963.

Sampling methods in Neal Canyon are similar to those for the Sleeping Child. A total of thirty-five 0.04-acre circular plots and fifty-five 2x2-foot quadrats were sampled annually for 7 years and in 1972. Data consist of frequency, density, cover, and crown volume by species. Representative recovery is illustrated in Figure 2.

Sundance Fire

This large wildfire burned nearly 56,000 acres of the Kaniksu National Forest, mostly on September 1, 1967. Our 18 sample areas are located in the Pack River drainage at altitudes between 3,000 and 4,200 feet. All aspects and several different age-structure combinations of the prefire cedar/hemlock forest type are represented.

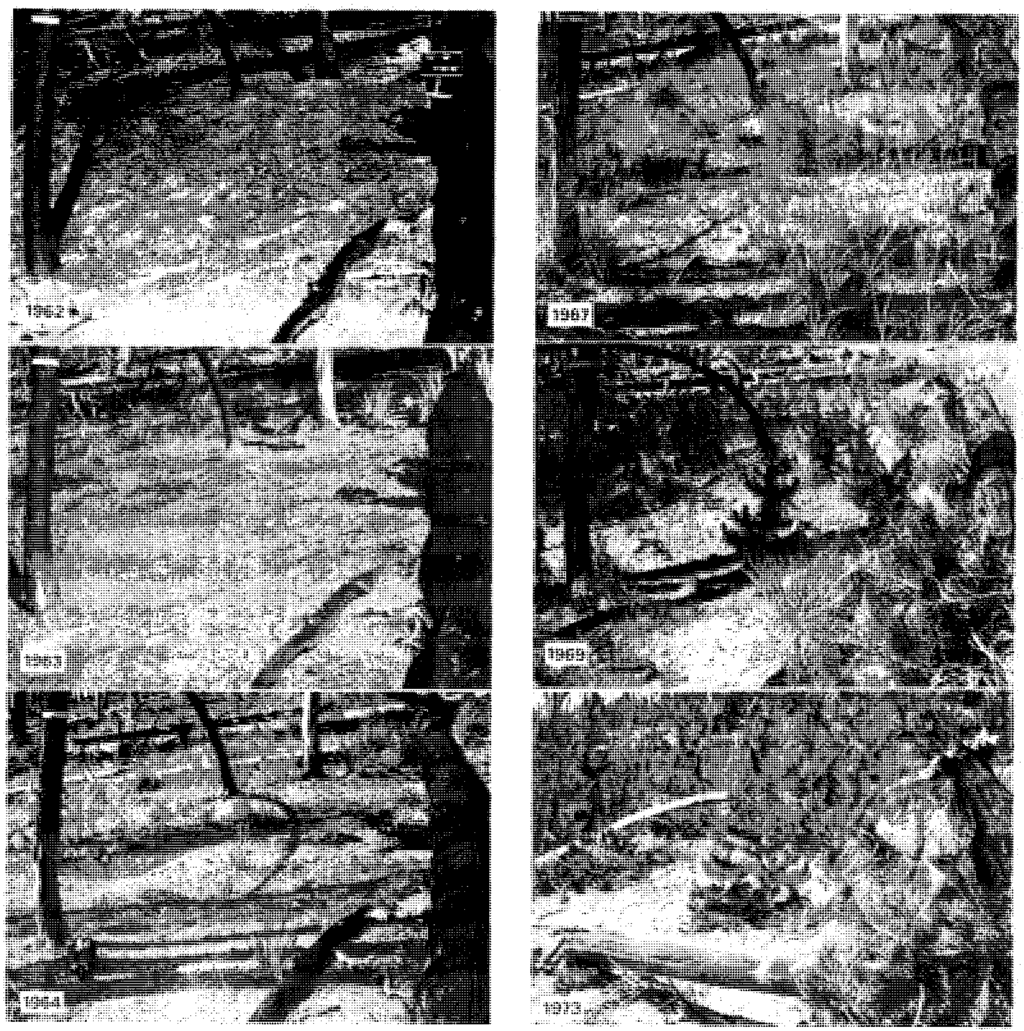

Fig. 1. Representative transect within the Sleeping Child burn.

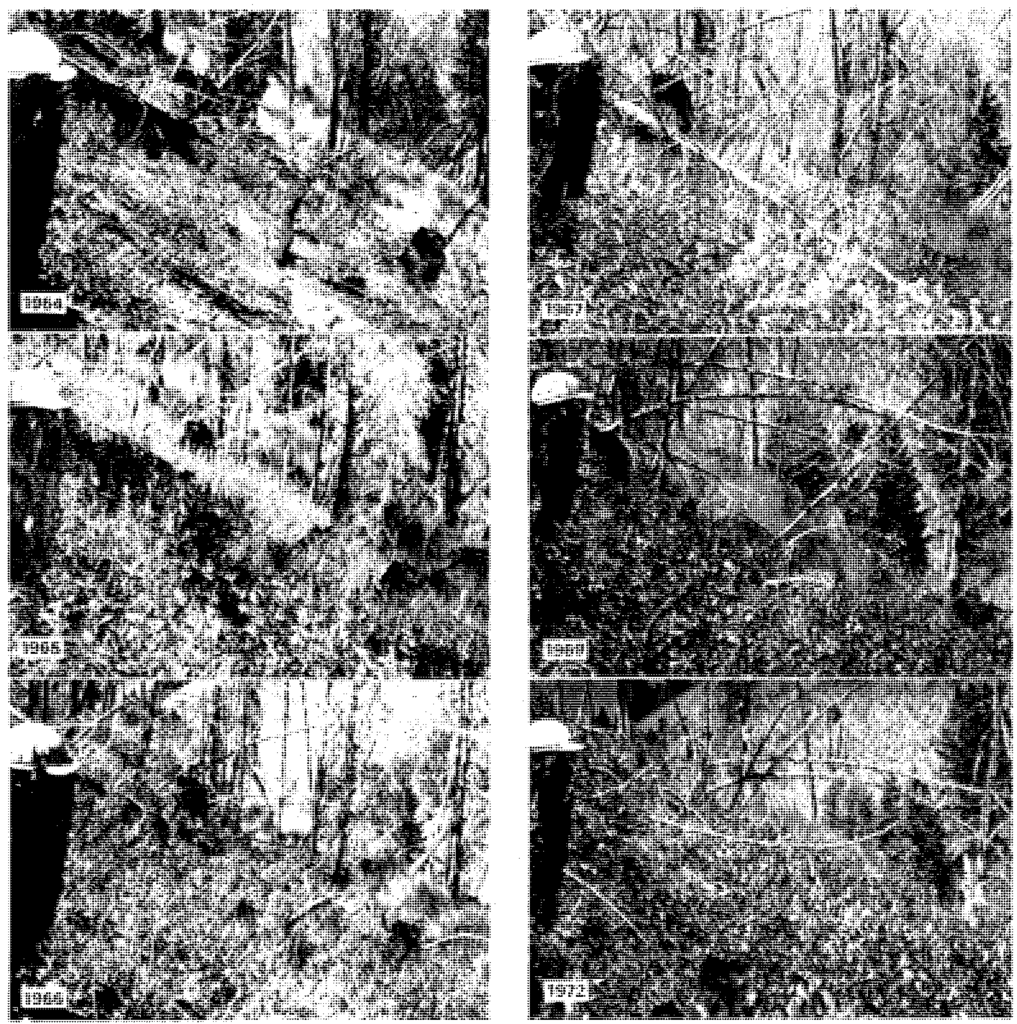

Fig. 2. Representative transect within the Neal Canyon burn.

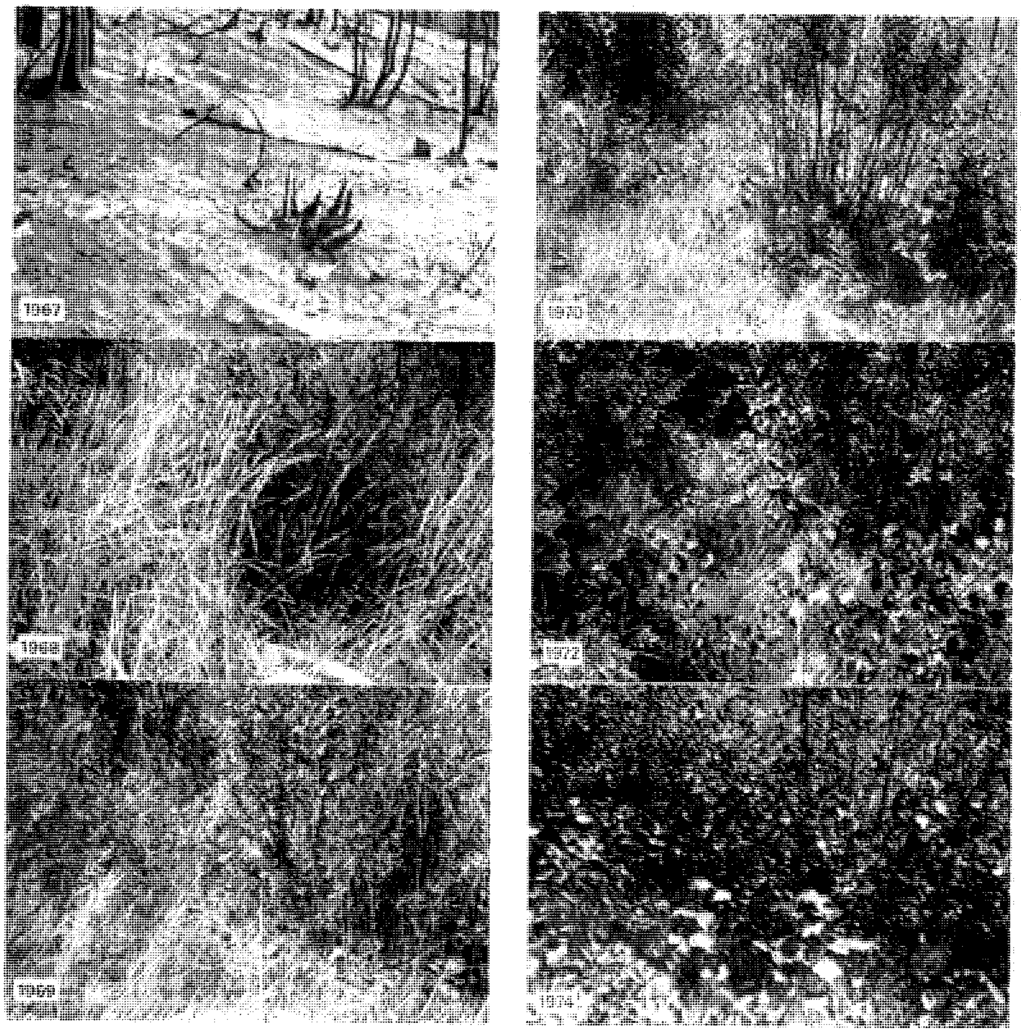

Fig. 3. Representative transect within the Sundance burn.

Vegetation samples on Sundance were taken from paired 25-m (82 feet) transects with 5 nested-block quadrat sets on each transect. Trees, shrubs, and herbaceous plants were stratified by height and recorded in one of four quadrats ranging between 0.25 m^2 (2.7 ft^2) and 25 m^2 (269.1 ft^2) in area. Data, recorded annually for 6 years, consist of frequency, density, cover, and crown volume by species. A representative transect is illustrated in Figure 3.

IMMEDIATE POSTFIRE VEGETATION

Each of these study areas represents a different forest community and habitat type, but all three burned during the peak of the dry season and all were characterized by total destruction of plant crowns and reduction of the organic layer to mineral ash. If wildfires can be modeled as internal perturbations of stable systems, as we propose, community composition should be readily predictable but recovery rates will be site-specific and unique. On-site vegetation, regardless of fire intensity, should be both a reliable source of immediate postfire flora and a major contributor to vegetation during early succession.

The alternative model, in which fire is treated as an external disturbance and succession as sequential replacement, requires a considerable latitude for revegetation from off-site recolonizing species and, in addition, should provide for continuing introduction of species that will achieve dominance at some later stage in succession.

In our three studies, prefire communities were obviously very different and the three burns have postfire recovery patterns that appear to be unique. Data in Table 1 represent averages for several sites in both the Sleeping Child and Sundance burns, but even the leveling effect of averages produces no suggestion of an underlying similarity in recovery rates. The floristic composition of these communities, however, was predominantly derived from plants or seeds already present at the time of the fire. Disregarding plants accidentally or intentionally introduced by man in the course of rehabilitation, revegetation on the Sleeping Child, Neal Canyon, and Sundance burns from surviving species accounted for 86, 71, and 84 percent of the composition of the first year community. Even more significant, of the species that combined to produce the bulk of vegetative

Table 1. General comparison of postfire development, Sleeping Child, Neal Canyon, and Sundance burns

	Postfire Succession Year											
	1	2	3	4	5	6	7	8	9	10	11	12
	Percent											
Ground layer vegetative cover												
Sleeping Child	1	6	12	17	23	30	—	32	—	35	—	34
Neal Canyon	27	69	29	47	44	51	55	—	54			
Sundance	40	60	57	55	54	45						
Shrub canopy cover												
Sleeping Child	T*	0.1	0.3	0.7	0.7	1.2	—	1.3	—	1.6	—	1.3
Neal Canyon	0.8	1.9	3.1	5.0	8.6	17.6	18.5	—	45.2			
Sundance	9.3	14.8	21.4	33.4	50.8	50.8						
	Number per acre											
Conifers (over 18 inches)												
Sleeping Child	—	—	—	—	—	191	—	1,395	—	2,719	—	3,856
Neal Canyon	—	—	—	26	30	52	105	—	736			
Sundance	—	—	10	30	50	140						

*T=trace=<0.06 percent cover

cover in the fifth postfire year, about 80 percent were present in the prefire community and all were recorded in the first year flora.

Our studies indicate that practically all plants that survived the fire reestablished within the first year. Data also suggest that virtually all species that contributed significantly to early vegetal cover were established in the first year. Since the species recorded at this very early stage of succession provide the major contribution to early vegetal recovery, it seems worthwhile to examine adaptations that enable them to survive fire.

ADAPTATIONS TO FIRE

Plant species in the forest communities of the Northern Rocky Mountains exhibit a variety of adaptations and strategies for fire survival. A majority of the shrubs and herbs, for example, resprout following crown destruction by fire. In addition, seeds of some species require heat treatment before germination while other species have wind-dispersed seeds. The conifers do not resprout, but many species exhibit such fire-adaptive characteristics as serotinous cones; seeds that ripen within burned cones; lightweight, winged seeds; or thick, and fire-resistant bark. Most require mineral seedbeds for seedling establishment. All of these adaptations can be classified as functional "on-site," in the area actually burned, or functional "off-site" from unburned areas outside the fire. It is significant that the majority of survival strategies are functional on-site adaptations and, moreover, that those species with off-site strategy that achieve more than accidental status in early succession also exhibit an on-site strategy.

ON-SITE ADAPTATIONS

Fire adaptations of on-site species take two general forms: (1) surviving plant parts and (2) seeds or fruit. On large burns, surviving plant parts represent the most important adaptive forms for fire survival. On our three burns, they account respectively for 75, 40, and 60 percent of species present in the first year after fire (Table 2). The remaining on-site species, originating from seed or fruit, represented 11, 31, and 24 percent of community composition, respectively.

Table 2. Percentage composition first-year vegetation by source and survival strategy, Sleeping Child, Neal Canyon, and Sundance burns.

Item	Sleeping Child	Neal Canyon	Sundance
Composition			
On-site sources	86	71	84
Off-site sources	14	29	16
Survival strategies			
All species			
Plant parts, on-site:	75	40	60
rhizomes	33	18	33
root crowns	36	22	23
underground stems	6	0	4
Seed or fruit, on-site	11	31	24
Seed or fruit, off-site	14	29	16
Shrubs (only)			
root crowns	79	53	55
rhizomes	21	0	15
seed	0	47	30

In fires intense enough to burn the tree overstory, those portions of existing plants that survive are usually at or below ground level. These include (1) root crowns of tall and medium-sized shrubs, broadleaf trees, and caudaceous herbs; (2) rhizomes of low shrubs and herbaceous plants; and (3) deep underground stems (bulbs and corms) of some herbaceous species.

Root crowns represent the most important fire-survival adaptation for Northern Rocky Mountain shrubs (Fig. 4a). In the first year of succession, over 50 percent of all shrub species on our three burns regenerated from root crowns. Tall shrubs most prominent in early succession from root crown resprouts were *Salix scouleriana, Acer glabrum*, and *Amelanchier alnifolia.* Few species of broadleaf trees occur in the upland forests of the Northern Rockies, but when *Betula papyrifera* or *Populus tremuloides* are present, they also resprout. In addition, some species of upland forest herbaceous plants survive by regrowth from a caudex. Species of *Lupinus* illustrating this adaptive form were locally abundant on both the Sleeping Child and Sundance burns.

The rhizomatous growth form represents the most important fire-survival adaptation for low shrubs and herbaceous plants (Fig. 4b

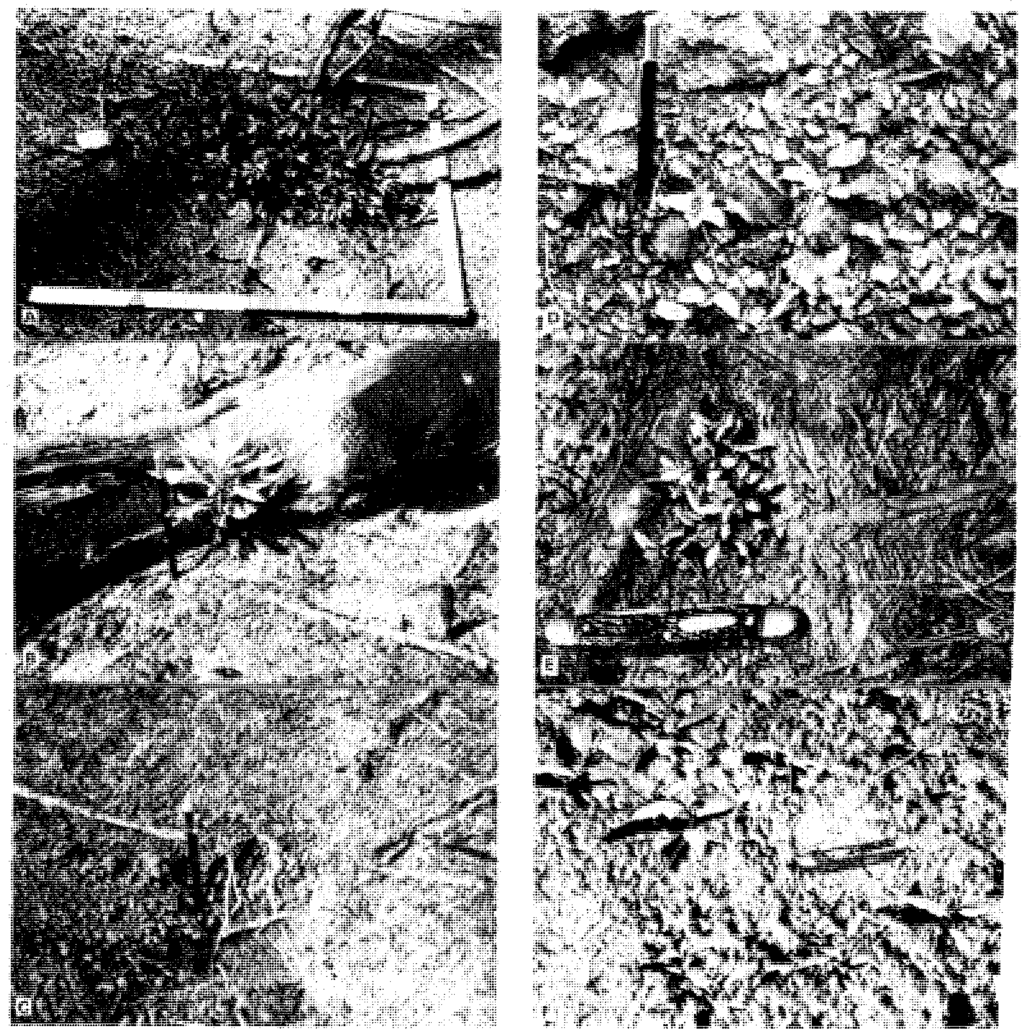

Fig. 4. Fire survival adaptations: (a) root crown resprout (*Salix scouleriana*), (b and c) rhizomes (*Epilobium angustifolium*), (d) fire-activated seed (*Ceanothus velutinus*), (e) chance occurrence (*Pachistima myrsinites*), and (f) wind-blown seed (*Salix scouleriana*).

and c). Regrowth from surviving rhizomes represented 33 percent of *all* species present in the first year after the fire on both the Sleeping Child and Sundance burns. Low shrubs characterized by survival from rhizomes and often dominant in early succession including *Spiraea betulifolia, Symphoricarpos albus,* and *Rubus parviflora.* Examples of similarly adapted herbaceous species include *Calamagrostis rubescens* (grass), *Arnica latifolia* (forb), and *Pteridium aquilinum* (fern). Herbaceous plants with deep-seated underground stems represent only a small proportion (up to 6 percent) of successional flora of the first year. Even though their perennial structure is relatively deep in the ground and, therefore, unaffected by fire, their preburn abundance constitutes such a small portion of the vegetation that they do not achieve any successional prominence.

Seeds present prior to the fire represent a second general adaptation to on-site survival. As a group, such seeds account for 10 to 30 percent of successional species of the first year. Seed survival, however, appears to include a broad spectrum of strategies ranging from fortuitous circumstance to extreme adaptation. At one end of this scale, we recorded a number of species with no recognizable adaptation to fire. These species appear to survive in lighter fuels or in such protected situations as rodent caches (Fig. 4e) or overlying rocks. In the absence of evidence that these seeds are heat resistant, their survival may simply depend on chance occurrence. Some of the climax understory species and native annuals are characteristic examples.

At a slightly higher level of adaptation, the seed crop developing or developed at the time of the fire may be protected by location or by seed covering. Some of the large-cone conifers, for example, may provide protection from fire. Haig, et al. (1941) reported that a burned forest of *Pinus monticola* established dense stands of seedlings following a large wildfire on the Kaniksu National Forest. They also cite evidence suggesting that seed maturation continues on fire-killed trees.

At the level of extreme adaptation, there are a number of plant species with seeds that retain their viability while stored on site for long periods (up to a complete forest successional cycle). These species are so highly adapted to fire that their seeds require heat in some form to initiate germination. Although the proportion of species in this category is small (about 10 percent of first-year species), some of the important early dominants of succession originate by this means. Long-term seed storage occurs at two locations in the forest stand: (1) in the forest floor near the mineral surface and (2) in serotinous cones attached to the tree crown.

Pinus contorta is the only Northern Rocky Mountain conifer known to demonstrate cone serotiny. This fire adaptation permits immediate, on-site reestablishment after fire. On the Sleeping Child burn, where the lodgepole pine overstory had an abundant supply of serotinous cones, seedling density in the first year of succession averaged over 8,500 per acre. In contrast to this, our sample areas in the Sundance burn had only a small proportion of lodgepole pine in the overstory and first-year seedling density averaged only 300 per acre.

Plants with dormant, ground-stored, fire-activated seed are found only in the shrub and herbaceous life forms of Northern Rocky Mountain vegetation. These species often dominate early successional phases. Their seeds are characteristically small, rounded to spherical, smooth textured, and are without obvious means of dispersal much beyond the limits of the parent plant. Shrubs of the genus *Ceanothus* have received considerable attention in this regard and are one of the best examples of this adaptive strategy (Fig. 4d). Gratkowski (1962) working with *Ceanothus velutinus* conclusively demonstrated that the seeds of this species require heat to germinate and further that after 200 to 300 years of dormancy enough seeds are viable to produce a complete cover of *Ceanothus* after burning. The stands of *Ceanothus* that now dominate the successional vegetation of the Neal Canyon and Sundance Burns originated in this manner.

Quick (1954, 1962) showed that similar fire-adaptive properties exist for some *Ribes* species. In several native herbaceous species, we have observed that successional occurrence and development closely parallel *Ceanothus* and *Ribes.* We believe that the seeds of these species exhibit the same adaptation to fire. Prominent examples include the annual, *Geranium bicknellii;* a biennial, *Dracocephalum parviflorum* (formerly *Moldavica parviflora*); and the perennial, *Iliamna rivularis.*

OFF-SITE ADAPTATIONS

Functional off-site species demonstrate adaptation to fire by their ability to introduce disseminules from areas well removed from the burn. Characteristically, these are lightweight airborne seeds or fruit, but some are dispersed by animals or water. Off-site introductions are subject to a variety of such uncertainties as the occurrence of seed crops, burns, and transport agents. As a consequence, their appearance in the postfire vegetation is generally unpredictable.

Off-site species did constitute up to 30 percent of the species composition immediately after the fire, and on all three areas, we have recorded continuing introductions of plants not found in prefire or first-year communities. However, the vegetation originating from native species of off-site origin generally contributed only minimally to vegetal cover by the fifth postfire year. Moreover, we have identified very few species, other than trees, that have a potential for demonstrating vegetal dominance when not present in the initial flora.

The general exception is demonstrated by a small group of species that also exhibit on-site fire-survival adaptations. On the Sundance burn, reestablishment of *Epilobium angustifolium* by rhizomes and *Salix scouleriana* from root crowns was predictable, but an overwhelming saturation of airborne seed from these species (Fig. 4f) has raised reestablishment percentages of both far above on-site expectation in early successional dominance.

A CONCEPTUAL MODEL FOR EARLY SUCCESSION

Integration of the hypothesis and data presented here into a preliminary model (Fig. 5) for predicting early forest succession required the following assumptions:

1. The majority of plant *species* on site prior to the burn will survive or reestablish on the burn;
2. The plant species that can be expected to dominate early succession will become established in the initial postfire year.

Thus, the basic information required to predict early postburn community composition is a preburn species inventory. Such an inventory should provide at least 75 percent accuracy, and this can be im-

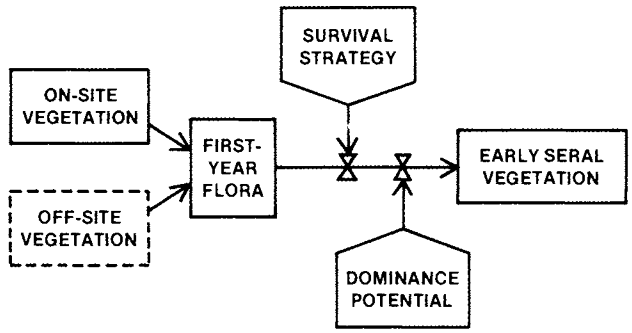

Fig. 5. Preliminary model of early forest succession.

proved with a species inventory of the first postfire growing season flora.

Early seral vegetation is predicted from either of these estimates, but the latter offers somewhat greater precision. Basically, the estimate is an attempt to recognize those species that will achieve an easily detectable level of community dominance during early succession. To this end, we assume that the initial computational control determining species contribution to community vegetation is the survival strategy peculiar to the species (Table 3). Any scale of measurement can be applied in this table. For example, it can be predicted that a species with 10 percent cover and a root crown strategy will contribute slightly less than 10 percent cover in the early seral community and a species at 5 percent frequency with underground stems will remain at about 5 percent.

However, this prediction is subject to a further computational control based on a species-by-species assessment of dominance potential and shade tolerance. For example, *Pyrola secunda* grows poorly in direct sunlight and is a small plant with little dominance potential. Even if a high frequency is predicted, pyrola will have little vegetal

; 3. Predicted contribution to early seral vegetation of plant species with various survival egies (See appendix I for adaptations of some species.).

survival strategy	Early seral contribution
ırecognizable	Accidental only
site surviving parts	
Root crowns	Minor decrease
Rhizome	Large increase
Underground stems	No change
ı-site seed	
Long viability	Large increase
Short viability	Some increase[1]
Fortuitous survival	Minor decrease
)ff-site seed	
Airborne	Large increase (potential)[2]
Other transport	Accidental only

[1]Potentially large for some conifer tree species.

[2]Actually limited to a few species. The majority of airborne seed species are expected to be accidental contributors.

significance. In all three of our studies, we found that no more than 25 percent of the species recorded were likely to produce a measurable contribution to community vegetation by the fifth postfire year.

The final step, from early seral vegetation to early vegetal succession, requires some prediction of succession rate. At this point, our model tends to predict vegetation at about the time herbaceous cover begins to stabilize, and we have arbitrarily implied that the fifth postfire growing season is somehow significant. A more logical modeling procedure might compare the canopy coverage of shrub and tree layers with the ground layer and terminate early succession when dominance shifts from the herbaceous level. Our first approximation of vegetation does not necessarily meet this need, but we suspect that there are several possible approaches to the required function. We have begun a site-by-site analysis, in which succession rate is predicted by habitat type (Daubenmire, 1968), but this is incomplete at this time.

SUMMARY AND CONCLUSIONS

Forest succession in the Northern Rocky Mountains is not an autogenic process in which initial seral plants modify the site to their own exclusion and permit the establishment of interseral and eventually climax species. Rather, succession is a sequential development of vegetation in which the more rapidly maturing and often shade-intolerant plants assume initial dominance and in turn are dominated by taller, slower growing, and often more shade-tolerant species.

Data from three large wildfire burns show that a high percentage of plant species on site at the time of the fire survive and reestablish on the burned area. The majority of recognizable survival adaptations are on-site plant parts and seeds or fruits, and these are the major source of early seral vegetation. The exception to this rule is supplied by a few species that have both an on-site survival strategy and airborne seeds.

Whether plant community components are derived from on-site or off-site sources, however, it seems apparent that all dominants of early succession will become established in the initial postfire growing season.

Thus, on the basis of either prefire or first-year community composition, it is possible to derive reliable estimates of probable composition during early succession. Further predictions, based on survival strategies and dominance potentials of various plant species in the community, make it possible to estimate probable structural configurations of the vegetation for the early successional period.

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APPENDIX I

Survival strategies of some Northern Rocky Mountain plant species

SURVIVING PLANT PARTS

Root Crown/Caudex:

Trees: *Betula papyrifera, Populus tremuloides, Populus trichocarpa.*

Shrubs: *Acer glabrum, Alnus sinuata, Amelanchier alnifolia, Ceanothus sanguineus, Ceanothus velutinus, Holodiscus discolor, Lonicera utahensis, Menziesia ferruginea, Pachistima myrsinites, Penstemon fruticosus, Prunus emarginata, Ribes lacustre, Ribes viscosissimum, Rosa gymnocarpa, Rubus leucodermis, Salix scouleriana, Sambucus racemosa, Shepherdia canadensis, Sorbus scopulina, Symphoricarpos oreophilus.*

Herbaceous plants: *Aster engelmannii, Clematis columbiana, Lonicera ciliosa, Lupinus (argenteus* and *sulphureus), Pedicularis contorta, Phacelia hastata.*

Rhizomes:

Shrubs: *Rubus parviflorus, Spiraea betulifolia, Symphoricarpos albus, Vaccinium globulare, Vaccinium membranaceum, Vaccinium scoparium.*

Herbaceous plants: *Achillea millefolium, Agrostis alba, Anaphalis margaritaceae, Apocynum androsaemifolium, Aralia nudicaulis, Arnica cordifolia, Arnica latifolia, Asarum caudatum, Aster conspicuus, Berberis repens, Calamagrostis rubescens, Carex concinnoides, Carex geyeri, Clintonia uniflora, Disporum hookeri, Epilobium angustifolium, Galium triflorum, Luzula hitchcockii, Pteridium aquilinum, Pyrola asarifolia, Pyrola secunda, Silene menziesii, Smilacina racemosa, Smilacina stellata, Solidago canadensis, Thalictrum occidentale, Tiarella trifoliata, Trautvetteria caroliniensis, Viola adunca, Xerophyllum tenax.*

Deep, Underground Stems:

Herbaceous plants: *Calochortus apiculatus, Claytonia lanceolata, Erythronium grandiflorum, Habenaria elegans, Lilium columbianum, Trillium ovatum.*

SEED/FRUIT

Short Viability (cones in the tree):

Trees: *Abies lasiocarpa, Pinus contorta* (non-serotinous), *Pinus monticola, Pseudotsuga menziesii.*

Long Viability (heat treatment required, tree or ground stored):

Trees: *Pinus contorta* (serotinous).

Shrubs: *Ceanothus sanguineus, Ceanothus velutinus, Ribes lacustre, Ribes viscosissimum, Sambucus racemosa**.

Herbaceous plants: *Carex rossii**, *Dracocephalum parviflorum**, *Iliamna rivularis**, *Geranium bicknellii**.

*Provisional