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First Decade Plant Succession Following the Sundance Forest Fire, Northern Idaho

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RESEARCH SUMMARY

First 10 years of development and change in vegetation established following disturbance by a holocaustic forest fire were documented by annual sampling of permanent plots. While species composition was relatively complex (about 140 species), less than 10 percent accounted for most of the seral vegetation developed during the first decade. Four species in particular (Epilobium angustifolium, Pteridium aguilinum, Ceanothus sanguineus, Salix scouleriana) provide more than half of the vegetation produced during the decade. The composite pattern for secondary forest succession exhibited an initial herb stage of 4 years duration succeeded by a shrub-predominant stage that continued through the first decade. Succession patterns on individual sites began with either herb- or shrub-predominant initial communities. The duration of the initial herb stage was largely dependent on the composition of the shrub component and ranged from 1 to 10 or possibly more years. Treedominant communities did not develop in the first 10 years.

The pattern and rate of succession on individual sites appears to be primarily dependent on the combination of surviving and colonizing plant species comprising the initial postfire community. This study documents that sequential replacement of initial species by secondary species subsequently established has not occurred. Rather, the process of successional development that appears to be paramount in the first postfire decade is one of differential development of the species established in the initial community.

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INTRODUCTION

Prior to settlement, secondary forest succession in the Northern Rocky Mountains was initiated principally by wildfire. Fire was a frequent and recurrent element of these forest ecosystems, as noted by many investigators, including Leiberg (1899, 1900), Ayres (1900a, 1900b), Marshall (1928), Daubenmire and Daubenmire (1968), Wellner (1970), Habeck and Mutch (1973), Norum and others (1974), and Arno (1976, 1980). Forest fires varied in intensity from light ground fires to severe crown fires (Ayres 1900a; Arno 1976; Wellner 1970). Although the severity of fire characteristic for this region has been the subject of some discussion (Wellner 1970; Arno 1976, 1980), Larsen and Delavan (1922) point out that regions in the Northern Rocky Mountains with the highest total precipitation, but with dry summers that average less than 2 inches (5 cm) of precipitation per month, are more likely to experience high-intensity holocaustic fires when they do burn.

Holocaustic burns represent the severest natural fire disturbance of forest vegetation in the Northern Rocky Mountains. A holocaustic fire burns with a severity sufficient to destroy all the aboveground portion of the vegetation, as evidenced by (1) all coniferous trees killed, (2) crowns of both understory and ground-layer vegetation consumed or killed back to the ground, and (3) the organic mantle of the forest floor reduced to ash down to the mineral ground surface (fig. 1).

The Sundance Fire of 1967 was representative of this kind of fire disturbance and was comparable to the major fires that burned in this forest region during the early decades of this century (Spencer 1957; Koch n.d.). Similarly, the Sundance Fire occurred at the height of the fire season in the normally dry period of late summer. Ignited by a lightning strike on Sundance Mountain in the Selkirk Range of northern Idaho, it smouldered for 12 days before breaking out on August 23. In the next 10 days, it burned 56,000 acres (22 663 ha) of forest land. The largest portion of this area, 50,000 acres (20 235 ha), burned in a 9-hour period on September 1. During this time it became an intense, running crown fire that reached "fire storm" proportions as it burned over the study location in the Pack River Valley (Anderson 1968).

Occurring after three decades of increasingly effective fire suppression, the Sundance Fire provided a unique opportunity to examine the response of forest vegetation returned to its most elemental initial conditions for



Figure 1.—Results of disturbance by Sundance forest fire. The severity of this fire treatment destroyed the overstory and understory layers of the stand and reduced the organic mantle of the forest floor to ash down to the mineral soil surface, thereby returning the forest vegetation to its most elemental condition for initiating secondary succession.

secondary plant succession. The severity of this burn also provided an opportunity to observe features that enable forest plant species to survive extreme natural fire disturbance.

This paper describes the development of seral vegetation for the 10 years following the holocaustic Sundance Fire in the western redcedar-western hemlock forest type in northern Idaho. Successional development of seral vegetation was documented by repeated measurements on permanent plots.

PRIOR WORK

Inspectors of the then newly established Federal Forest Reserves observed forest succession in the Northern Rocky Mountains following fire as early as the late 1800's (Leiberg 1897, 1899; Ayres 1900a, 1900b). Succession was described in terms of trees, shrubs, grasses, and "weeds." The emphasis was on the tree component and its successional status.

Leiberg (1897) provides one of the earliest descriptions of forest succession in northern Idaho for the "white pine zone." He describes secondary plant succession following "first burns" in these forests as progressing through three periods of "forest recovery." The first, within a few months after the fire, showed the establishment of young plants of willow and Ceanothus and, if near a timbered edge, conifer seedlings. After 3 or 4 years, a second period was characterized by the accumulation of humus from the litter of deciduous shrubs and herbaceous plants that "appear to be essential to the germination of the seeds of conifers." Replacement of shrubby vegetation by a thriving growth of young trees marked the beginning of the third period. Leiberg also recognized a difference in the duration of the early seral stages in the case of "second burns." Under these conditions young trees were destroyed by another fire that made the site "too dry" for tree reestablishment and allowed other forms of vegetation to dominate the site for long periods.

Two years later, Leiberg (1899) expanded his description of the "reforestation process" in the white pine zone to include five phases. The first three phases were distinguished by the sequential prominence of: (1) herbaceous plants—mosses and fireweed (Epilobium angustifolium L.); (2) shrubby plants—snowbrush (Ceanothus velutinus Dougl.), redstem (C. sanguineus Pursh), Salix flavescens Nutt., western serviceberry (Amelanchier alnifolia [Nutt.] Nutt.), and quaking aspen (*Populus tremuloides* Michx.); and (3) lodgepole pine (Pinus contorta Dougl. ex Loud.). In the third phase, Leiberg characterized the influence of the density of lodgepole pine on the preceding vegetation as "soon driving out nearly all other vegetation, herbaceous and shrubby." The fourth phase followed after 25 to 35 years with thinning out of the lodgepole pine and establishment of tree "species of the original forest." The fifth phase represented the development of the original forest species toward old growth.

After the "Great Idaho Fire of 1910," Humphrey and Weaver (1915) observed that the initiation of succession on heavily burned soils in this region often began with an abundant ground layer of firemoss (Funaria hygrometrica Hedw.) and liverwort (Marchantia polymorpha L.). Somewhat later, Larsen (1929) presented a generalized description of postfire forest succession for northern Idaho in which two of three stages of "subordinate" vegetation precede the first of three tree overstory stages. Pioneer herbaceous and low shrub species characterize the first subordinate stage. After 2 or 3 years these give way to a second stage, characterized by perennial plants that produce berries or berrylike fruit. Larsen states that these plants served as a nurse crop to establishing conifer seedlings by "shading and sheltering" and contributing to the rapid accumulation of leaf mold. The third subordinate stage began in 8 to 10 years with the overtopping of the second stage by the emerging young conifer trees and the replacement of the "berry species" by "somewhat uninfluential and unassuming" species tolerant of overstory shading. As the coniferous overstory developed into a climax forest condition, the third subordinate stage was eventually replaced by climax

understory of perennial evergreen species. The process of forest succession for the climax cedar-hemlock-grand fir forest, Larsen believed, was one in which each preceding understory and/or overstory stage "improves the site and paves the way" for the succeeding successional stage.

In a more recent interpretation of forest succession in the Northern Rockies, Daubenmire and Daubenmire (1968) characterized succession following fire or timber harvest as a sequential process involving three stages keyed to tree development: (1) "invasion," (2) "stagnation," and (3) "resumption of regeneration." The "invasion" stage contains surviving sciophytic (shade plant) shrubs and herbs and heliophytic (sun plant) tree, shrub, and herb species that invade the site from outside the burned area. This stage continues for a decade or two, depending on the distance to tree seed source, and terminates when the crown closure of the young coniferous trees marks the beginning of the "stagnation" stage. In this second stage there are no further additions to species composition from outside sources. Coniferous overstory development continues, and the denser canopy intensifies shading that permits the survival of only the most.sciophytic undergrowth plants. The stagnation stage witnesses the replacement of fast-growing tree species by slower growing ones and ends with the eventual maturity of the climax tree species.

The initiation of the last, or "regeneration," stage is marked by the readmittance of light to the forest floor as a result of overmaturity and death in the climax tree stand. Seedlings of the most shade-tolerant trees, shrubs, and herbs, restricted to sun-fleck aggregations in earlier stages, diffuse across the forest floor as the shading intensity of the overstory becomes less severe.

In the process of forest succession, the Daubenmires note that all members of the various seral dominants, plus climax tree species, may become established in the first year of succession, and that it is the differential rates of development to maturity that serve to distinguish successive seral stages. They further note, in contrast to Larsen and others, that there is little evidence that the dominants of any seral stage require modification of the ground surface environment to enable their establishment.

Lyon's permanent plot studies of vegetal development following prescribed burning and wildfire represent the first work on forest succession in the Northern Rocky Mountains based on sampling actual changes in postfire vegetation. In the first of these studies, Lyon (1971) reports seral development for 7 years following a prescribed burn of a standing Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) forest on the Sawtooth National Forest in central eastern Idaho. Herbaceous plants represented the dominant life form of the initial successional stage. Community dominants during the first 5 years were three species of herbs. A biennial, Dracocephalum parviflorum Nutt. (syn. Moldavica parviflora [Nutt.] Britt.), was the predominant species in the first 2 years of succession. At its maximum development in the second year it was the most abundant species and provided 37 percent cover. Thereafter, two perennial herbs, fireweed and wild hollyhock (Iliamna

rivularis [Dougl.] Greene), were the most abundant species, collectively providing about 20 percent cover until the sixth year. Snowbrush became the dominant plant species in that year. Lyon suggests that shrubs will dominate to about the 30th year, or until overtopped by trees.

In a second study conducted on the Bitterroot National Forest in western Montana, Lyon (1976) documented early postfire vegetal development in a high-elevation lodgepole pine forest following wildfire. Aerially seeded, exotic herbaceous species formed the initial cover group for the first 3 years, after which native herb and low shrub species comprised the dominant group. Maximum cover values for introduced herbs were reached in the sixth year and for native species in the eighth year. By the 12th year, coverage for the introduced group had declined by two-thirds, but coverage for the native group remained at 90 percent of maximum values. These changes took place in the presence of the establishment of dense stands of lodgepole pine, which developed into a prominent tree component on most study sites after the eighth year. The absence of a welldeveloped shrub component in the majority of these seral communities resulted in a successional sequence that proceeded directly from an herb to a tree stage. The study covered 12 years, during which various forest management activities superimposed on most of the study sites compromised the original objective. In spite of these postfire management disturbances, a general successional trend from herb to tree prominence was still evident.

STUDY AREA

The Pack River Valley is the principal drainage traversing the Selkirk Range in northern Idaho. In this valley. 18 study areas were located at elevations between 2,900 and 4,300 feet (880 and 1 310 m) in T. 60 N., R. 2 W., B.M., 20 miles (32 km) north of Sandpoint, ID. All but three of the study sites are within a 2-mi 2 (5.18-km 2) area within sections 8 and 9, nearly a mile (1.6 km) from the nearest burn edge.

Landforms in the prominent mountain valley of the Pack River, cut into the granite of the Kaniksu Batholith, have been modified by glaciation (Alden 1953). The resulting topography at middle and low elevations is moderate in relief, with rounded interior ridges and generally uniform slopes. Moderate areas of smoothed granitic bedrock outcrop on interior ridges and spurs from midslope upwards. Study sites represent all four cardinal exposures and slopes that range from 15 to 50 percent (modal value 30 percent). Soils of the valley flank derive from granitic tills overlaid by a loess cap of yellowish-brown silt loam 6 to 30 inches (15 to 76 cm) thick (USDA Forest Service n.d.). These mountain soils are regosolic in character and contain a low volume of coarse, angular fragments of granitic rock.

The climate of the Selkirk Range in northern Idaho is unusually moist for inland mountains in the Pacific Northwest (Arno 1970). Arno, using a modified version of the Koeppen [Köppen] system (Critchfield 1966), classifies this mountain climate as a maritime influence type (Koeppen's Df'), which is characterized by high annual

precipitation and maritime, snowy winters. Although the mean annual precipitation for the adjacent valley stations at Sandpoint Experiment Station and Priest River Experiment Station is 33 and 32 inches (84 and 81 cm), respectively (Rice 1971), the annual precipitation for the general area of the study is estimated to be in the 40- to 60-inch (102- to 152-cm) range (Rice 1971). At the Priest River Experiment Station, 15 miles (24 km) southwest of the Sundance study area, about 75 percent of the precipitation falls in the dormant season (October through April), mostly as snow. The driest months are July and August, with minimum monthly precipitations at the valley stations between 0.5 and 1 inch (1.27 and 2.54 cm). Annual mean temperatures at these two stations are 44 and 45 °F (24.4 and 25.0 °C), respectively, and the coldest monthly means (January) are 6 and 8 °F (3.3 and 4.4 °C) below freezing, respectively. The mean frost-free season at Priest River Experiment Station is relatively short-88 days, from June to September. Thus, for the valleys at medium to lower elevations within the Selkirk Range, the dormant season is relatively long, cool but not cold, and moist, while the growing season is relatively short, warm, and dry, but not particularly droughty.

Under these climatic conditions, forest vegetation has been characterized by Daubenmire (1952) as belonging in the Thuja-Tsuga zone. Although it was difficult to determine after the fire, most of the study sites appeared to best fit Daubenmire's (1952) Thuja-Tsuga/Pachistima association on the basis of (1) the general prefire presence of western hemlock (Tsuga heterophylla [Raf.] Sarg.), (2) the composition of the tree component (up to 11 species) of the prefire forest, (3) the greatest proportion of surviving indicator species represented by the Pachistima union, and (4) the high presence in the general area of the most typical species of this union. As expressed in the later refinement of this classification, all but the most xeric sites would probably represent the Tsuga heterophylla/Pachistima myrsinites habitat type (Daubenmire and Daubenmire 1968).

METHODS

Shortly after control of the Sundance Fire, 20 sites in the burn were selected for study of vegetation response to a severe wildfire treatment. Criteria for site selection included (1) upland well-drained area, (2) uniform slope and exposure, (3) uniform burning treatment, (4) free of mechanical disturbance, and (5) representation of the range of prefire communities as evident from their post-fire physiognomic remains. Study sites included old forest (large trees), young forest (dense, smaller trees), clearcut old forest, and brushfield. Study plots were installed the following summer on 17 sites that remained free of disturbance from timber salvage logging and on one additional burned brushfield site.

Seral vegetation development was measured on permanent plots using nondestructive sampling techniques. (Study was designed and executed in metric; thus only metric units are reported for the methodology.) Each study area consisted of two 5- by 25-m transects. The downhill edge of each transect served as a permanently

marked baseline to which all sample plots were referenced. Each transect consisted of five contiguous 5- by 5-m blocks. Each block contained three nested square plots of 1.5, 3, and 5 m. Woody plants over 0.5 m high were stratified into three height classes and sampled in their respective size-nested plots. Height classes and associated plot sizes are given in table 1. For each transect, herbaceous and low woody plants (including shrubs and trees less than 0.5 m high) were sampled in 10 plots of 0.5- by 0.5-m regularly arrayed along the baseline.

The diameter of trees over 2.5 m high was measured at a height of 1.4 m to the nearest centimeter. Trees less than 2.5 m but more than 0.4 m high were counted by species. Those 1.5 to 2.5 m in height were assigned a diameter of 1.25 cm. The aerial crown cover of each shrub and tree over 0.5 m high and rooted within the plot was sampled, as if it were an ellipse, by measuring its long axis and one at right angles to it. The height of the aerial crown above its rooted point was also measured. All crown measurements were made to the nearest decimeter. Crown area coverage of all herbaceous and low woody species (including shrubs and trees less than 0.5 m high) was estimated to the nearest one-sixth of the 0.5- by 0.5-m plot. The representative height within the plot was measured to the nearest half decimeter. Aerial crowns of herb and low woody species covering less than one-sixth of the plot were grouped and treated as miscellaneous vascular vegetation. Ground surface not covered by vascular vegetation was classified as (1) moss and lichen, (2) litter, (3) rock, or (4) bare ground, and cover estimated in units of one-sixth of the plot. All herb and low woody species occurring within the plot were recorded for frequency. The presence of all species within the vicinity immediately adjacent to the transect was recorded.

Tree diameters were converted to basal area. Cover for shrubs and trees over 0.5 m high was calculated as the area of an ellipse. The volume of space occupied by these shrubs and trees was represented as a cylindroid and computed as the product of the crown area and the height. Cover of herbs and low woody plant species (including shrubs and trees less than 0.5 m high) was determined directly from estimated units of area. Volume of space occupied for these plants was computed as the product of the area and the measured representative height. All attributes quantifying species abundance were standardized to a 0.01-ha base.

Table 1.—Summary of permanent plots and associated vegetation sampled for a study area

		*	
Plot size	Height limits	Vegetation sampled	No./study area
Me	eters		
5 × 5	2.5 +	Shrubs and trees	10
3×3	1.5-2.45	Shrubs and trees	10
1.5×1.5	0.5-1.45	Shrubs and trees	10
0.5 × 0.5	< 0.5	Shrubs and trees and all herbaceous plants	20

Botanical nomenclature follows Hitchcock and Cronquist (1973). Identifications of plant species were made by the author with verification of most species by Frederick J. Hermann and Charles Feddema, both formerly of the USDA Forest Service Herbarium, formerly in Fort Collins, CO. Voucher specimens for most species are on file at the Forestry Sciences Laboratory Herbarium, Missoula, MT (MRC), with duplicates at the Forest Service Herbarium (USFS).

SERAL ORIGINS

In the following sections, early phases of secondary forest succession are described in terms of species' dominant life form and composition. Each section represents a less inclusive and more specific examination of the plant community and associated structural changes over time. In clarifying these relationships, it is necessary first to provide an outline of the sources of plant species involved in succession.

When defined by source and time of establishment, postfire vegetation consists of four groups: (1) survivors, (2) residual or onsite colonizers, (3) initial offsite colonizers, and (4) secondary offsite colonizers (table 2). Survivors are those species with established plants on the site at the time of the fire that were capable of regrowth after burning. Regrowth for nearly all survivors was evident by the end of the first postfire growing season. Occasionally, shade-tolerant species that normally do not survive severe burning treatments will appear above ground in the second or third year after a fire as resprouts from underground plant parts (Hutchinson and Freedman 1978). On the Sundance Burn three species have been identified with this response pattern and have been designated as accidental survivors in the appendix.

Table 2.—Composition of seral vegetation on the Sundance Burn by origin, source, and initial flora, 1968 through 1977

Compositional component	No. of species	Percent
Seral origin		
Survivors ¹	64	46
Residual colonizers	16	12
Initial offsite colonizers (SY:1) ²	28	20
Secondary offsite colonizers (SY:2-10) ² Total	31 139	$\frac{22}{100}$
Source		
Onsite (survivors, residual colonizers)	80	58
Offsite	59	42
Total	139	100
Initial postfire flora (SY:1) ²		
Survivors	59	42
Residual colonizers	16	12
Initial offsite colonizers	28	20
Total	103	74

¹Includes three secondary survivor species (plants first detected in SY:2 or 3 not of seedling origin).

²SY:1 = Succession year 1; designates the number of years (growing seasons) since the fire.

Colonizers are species that establish new plants from postfire seedlings. Residual colonizers originate from seeds or fruits present on the site at the time of the fire. Seeds of residual colonizers are adapted to withstand burning in the fuel concentrations in which they naturally occur or survive occasionally by the protective circumstances of locations in which they chance to occur. Onsite seed sources occur either in the overstory canopy or on the forest floor (ground stored). The residual colonizer group includes species with apparently both long- and short-lived seed. Offsite colonizers are species that originate in unburned areas. Characteristically, the seed or fruit of these species is capable of relatively long-distance dispersal. Their requirements for germination and seedling establishment are usually those of ruderal (pioneer or weedy) plants. Viability of their seed is typically short lived. Secondary colonizers differ from initial offsite colonizers in their later time of arrival after the initial plant community has become established. Seedlings of secondary colonizers must be capable of establishing in closed or partially closed plant communities. For this report, species derived from offsite sources that appeared after the first year were designated secondary colonizers.

Nearly half of the species comprising the postfire flora were survivors. And most of the remainder (colonizers) were also present in the first postfire year. Survivors represented the largest and residual colonizers the smallest seral origin groups of species constituting the postfire flora in the first year (table 2). Collectively, these two groups compose that element of the postfire flora derived from onsite sources. Even with the severe burning treatment effected by this fire, nearly 60 percent of the total species composition originated within the burned area. Survivors represented the principal source for species revegetating the burn in the first 10 years. By the end of the decade, survivors still represented the largest group of species on half the study sites. On the remaining half, secondary colonizers constituted the largest source of species.

Most species (90 percent) showed only one seral origin. However, 14 species displayed the capability to function both as survivors and colonizers (appendix). For example, fireweed, an important early seral perennial herb, functioned primarily as an initial offsite colonizer by means of a light, air-mobile seed capable of long-distance dispersal. But occasionally it responded as a survivor regrowing from deep-seated rhizomelike roots. Redstem, a pioneer shrub, exhibited another combination of seral origins. When present on a site prior to the fire, it functioned as a survivor by regrowing from burned root crowns. More commonly, redstem functioned as a residual colonizer by establishing seedlings from longlived seed stored in the ground. For those species with more than one seral origin, the summary in table 2 gives priority to the survivor classification.

SPECIES COMPOSITION

The flora of the seral vegetation developing over the first 10 years on 18 study areas was composed of 139 species of vascular plants (appendix). Of these species, 73 percent were detected in plot sampling. The remainder occurred in the immediate vicinity of the sampling plots. On individual sites floristic composition averaged 53 species and ranged between 43 and 70 species. The degree of uniformity in species composition between sites was relatively low. Only eight species were present on all study sites while an additional 40 species occurred on at least half of the sites. Thirteen species accounted for most of the seral vegetation produced in the first decade of succession (table 3).

Table 3.—Principal and secondary cover species of the first decade's seral vegetation on 18 study areas in the Sundance Burn

Cover species	Presen	nt C	S ¹ PCS	Maximum cover
	- No. 0	of stu	dy areas -	- Percent
PRINCIPAL				
Alnus sinuata	10		6 1	15
Amelanchier alnifolia	14		4 3	15-41
Anaphalis margaritacea	18	1	3 1	16
Betula papyrifera	8		2 2	16-48
Calamagrostis rubescens	10		4 2	24-33
Ceanothus sanguineus	14	1	8 0	36-183
Epilobium angustifolium	18	1	8 14	22.72
Lupinus argenteus	3		3 1	25
Pachistima myrsinites	18	1	3 2	15-20
Pinus contorta	15		5 1	47
Pteridium aquilinum	15	1	4 10	19-59
Rubus parviflorus	15	1	3 4	16-31
Salix scouleriana	18	1	8 17	16-75
SECONDARY			scs ³	3
Acer glabrum	12		4 2	5-8
Agrostis alba	12		3 1	11
Apocynum androsaemifolium	12		4 2	10-14
Arnica latifolia	2		1 1	6
Carex rossii	17	1		5-9
Ceanothus velutinus	6		4 1	13
Dactylis glomerata	9		3 1	6
Geranium bicknellii	5		3 2	6-11
Hieracium albiflorum	18		6 1	5
Holodiscus discolor	6		3 3	5-11
Prunus emarginata	5		3 1	9
Pseudotsuga menziesii	18		9 2	5
Rosa gymnocarpa	11		8 3	8-9
Rubus leucodermis	7		4 1	5
Spiraea betulifolia	8		5 3	10-13
Symphoricarpos albus	4		4 1	11
Thalictrum occidentale	7		2 1	5
Vaccinium membranaceum	17		6 1	10
Xerophyllum tenax	8		3 1	11

¹Cover species (1 + percent cover).

²Principal cover species (15+ percent cover).

³Secondary cover species (5-14 percent cover).

Herbs comprised the largest life-form group of species (table 4). Over one-fourth of the herb species were exotics (appendix), and nearly half of these were annuals or biennials. The majority of exotic annual and biennial species behaved as casual introductions. One-third of the exotics were intentional introductions associated with postfire rehabilitation seeding. Although more than half of these species have persisted throughout the first decade, none have become prominent elements in the seral vegetation. Only two exotics, both pasture grasses, redtop (Agrostis alba L.) and orchard-grass (Dactylis glomerata L.), developed sufficiently to exceed 5 percent cover.

Of all the species recorded for the decade, 74 percent were present in the first postfire year. Changes in floristic composition involved 51 species. Herbs accounted for most of these changes, with casual exotics the most characteristic of those disappearing and native perennial herbs accounting for most of the additions. Of the 23 shrub species present at the end of the decade, 21 were present in the first year. The number of tree species, however, increased from five to 11, in part because of reforestation plantings.

SPECIES DISTRIBUTION DEVELOPMENT

Eighty-one of the 101 species detected (sampled for frequency) in the half-meter herb plots showed a nearsteady-state pattern, with little expansion or reduction of their distributions within the site of a study area. Throughout the decade their occurrence (frequency) remained within a range of about 25 percent. The distribution of 74 of these species was limited (5 to 30 percent frequency). Beargrass (Xerophyllum tenax [Pursh] Nutt.), spirea (Spiraea betulifolia Pall.), and seedling lodgepole pine exhibited a somewhat wider distribution with occurrences between 35 and 65 percent frequency on at least one study area. Most widely distributed of the species showing only the steady-state distribution pattern were Ross sedge (Carex rossii Boott), lupine (Lupinus argenteus Pursh), mountain-box (Pachistima myrsinites [Pursh] Raf.), and thimbleberry (Rubus parviflorus

Nutt.). Each of these species maintained frequencies between 70 and 100 percent on at least one study area throughout the decade.

One-fifth of the species sampled for frequency exhibited changes that exceeded 30 percent during the decade, thereby demonstrating a marked expansion or reduction of their occurrence within the community. For the group showing a decrease, the only woody plant species declining in frequency were seedlings of paper birch (Betula papyrifera Marsh.), redstem, and Scouler willow (Salix scouleriana Barratt ex Hook.). Shade-intolerant herbs characterize the remainder of this group. Within 3 to 5 years geranium (Geranium bicknellii Britt.), cudweed (Gnaphalium microcephalum Nutt.), and rye (Secale cereale L.) declined in frequency from 50, 40, and 85 to 0 percent, respectively. Geranium and rye became locally extinct at all sites, but cudweed was still present on a few sites at the end of the decade. In 7 years white clover (Trifolium repens L.) declined from 45 to 0 percent in frequency, showing its widest distribution in the first year. On three of the drier sites fireweed declined in frequency between 35 and 65 percent. On nearly all other sites it maintained a frequency between 100 and 75 percent throughout the decade.

Sustained increase in frequency indicative of expanding populations resulted from either the establishment of new plants from seedlings or from vegetative ingrowth. In total, 13 species displayed increases in frequency, exceeding 30 percent within the first decade on at least one site. Seven of these increased by seeding in: Sitka alder (Alnus sinuata [Regel] Rydb.), pearly-everlasting (Anaphalis margaritacea [L.] B. & H.), paintbrush (Castilleja miniata Dougl.), cudweed, hawkweed (Hieracium albiflorum Hook.), tiger lily (Lilium columbianum Hanson), and round-leaved violet (Viola orbiculata Geyer). Three species with rhizomes but no observed seedlings increased by vegetative ingrowth: dogbane (Apocynum androsaemifolium L.), bracken fern (Pteridium aquilinum [L.] Kuhn.), and huckleberry (Vaccinium membranaceum Dougl.). Three species with rhizomes and seedlings present increased by both processes: redtop, arnica (Arnica latifolia Bong.), and pinegrass (Calamagrostis rubescens Buckl.).

Table 4.—Life form composition of seral vegetation on the Sundance Burn study areas, 1968 through 1977

	Species composition							
Life form component	Number		Percent		Number exotic ¹		Numbe introduce	
Tree	11		8				_	
Shrub	23		16		_		_	
Herb	105		76		29		7	
Perennial ³		80		58		16		6
Biennial		7		4		2		_
Annual		18		14		11		1
Totals	139		100		29		7	

¹Species not indigenous to the flora of the region.

²Intensional exotic introductions (included in exotic column).

Includes low woody plant species.

Among those species that expanded their distributions in early succession, the most prominent examples include bracken fern, pearly-everlasting, Sitka alder, and hawkweed. Maximal distribution expansion of bracken fern from rhizome elongation increased frequency from 50 to 100 percent in 8 years on one site and from 15 to 70 percent in 10 years on another. Pearly-everlasting (initial offsite colonizer) arrived on all study areas between the first and third years. With few exceptions, seedlings first appeared in the frequency plots in the second to fourth years. Over the remainder of the decade, this species expanded its distribution on nine study areas attaining frequencies of 70 to 100 percent. Hawkweed (secondary offsite colonizer) arrived later than pearly- everlasting, appearing on most study areas between the fourth and fifth years. Seedlings were first detected in frequency plots in the fifth to seventh years. Frequencies of this species on half of the study areas increased from 0 to between 40 and 95 percent by the 10th year. Sitka alder was the only shrub to expand its distribution by seeding in following the establishment of the initial seral vegetation. On one study area, alder resprouts from surviving root crowns first flowered when they were 5 years old. Seedlings first detected in the eighth year at the 5 percent frequency level increased to 75 percent 2 years later. Cudweed was the only species that exhibited both increases and decreases in its distribution that exceeded 30 percent frequency within the first decade.

SERAL VEGETATION DEVELOPMENT

Development of seral vegetation is described in terms of the successional change of its principal life-form components (herb, shrub, and tree). The life form with the greatest coverage was adopted as the basis for designating successional stages. Patterns of seral vegetation

development are characterized by the order and duration of the dominant life form.

Less than half of the seral flora became abundant members of the seral vegetation (table 5). Only one-fourth of the species attained coverages of at least 5 percent. The general character and appearance of vegetation at individual study sites was dependent on 13 principal species (table 3). However, only four species of this latter group produced the greatest part of the vegetation developed during the decade (63 to 76 percent cover annually). Two of these species were herbs (fireweed and bracken fern) and the other two were shrubs (redstem and Scouler willow).

Composite Successional Pattern

The general pattern emerging for the first decade of forest succession in the Sundance Burn derived from a composite of all study areas indicates a rapid development of vegetative cover (100 percent by the fifth year) in which the early prominence of herbs was succeeded after the fourth year by a shrub-dominant community (fig. 2-1). The rapid initial development of seral vegetation was largely due to the colonization of fireweed. Following the peak of fireweed development, usually in the second year, the regrowth of bracken fern mainly accounts for the maintaining of the coverage of the herb component (fig. 2-2) in the presence of the rapidly developing shrub stand. Averaged over all areas, the development of redstem and Scouler willow shrubs contributed about equally to the increase in vegetative cover and accounted for most of the shrub cover developed during the decade (fig. 2-3). In the absence of the development of a significant tree component, much of the vegetation of the Sundance Burn should remain in the shrub stage well into the second decade, if not longer.

Table 5.—Abundance components of Sundance Burn seral vegetation, 1968 through 1977

Component	No. of species	Percent of seral flora
Species sampled as cover:		
Principal cover species		
(15 + percent cover)	13	9
Secondary cover species		
(5-14 percent cover)	19	14
Cover species (1-4 percent cover)	27	19
Total cover composition	59	42
Species sampled as frequency	101	73
Species sampled as presence	139	100



Figure 2.—Composite development of seral vegetation on Sundance Burn for 18 study areas: (2·1) total vegetation and life-form components; (2·2) major herb component species: *Epilobium angustifolium* (EPAN) and *Pteridium aquilinum* (PTAQ); (2·3) major shrub component species: *Ceanothus sanguineus* (CESA) and *Salix scouleriana* (SASC). Shaded areas indicate the amount of cover contributed by the two principal secies of each life-form component.

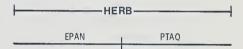
Range of Seral Development Patterns

The sequence of successional stages in the first 10 years for all but seven study areas followed the composite pattern from an herb- to shrub-dominated community. The exceptions exhibited no sequential development and maintained their initial stage throughout the decade. Four study areas in this group remained herb dominated while three study areas began and remained shrub dominated. Between these extremes in herb stage duration the remaining study areas exhibited a broad array of seral patterns. The development of vegetative cover ranged from nearly twice to less than half that for the composite. Nearly two-thirds of the sites attained maximum coverage between the seventh and ninth years. For the remaining study areas cover continued to increase throughout the decade. The extent of the cover development spectrum observed on the Sundance Burn ranged from an herb stage that lasted throughout the decade to one in which the rapid regrowth of shrubs excluded the herb stage altogether (fig. 3).

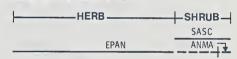
Figure 3.—Patterns of successional stages representing the spectrum of early seral development, Sundance Burn, and duration of dominant cover species associated with the development of each life-form component. Solid species line: overstory cover species; dashed species line: understory cover species. ANMA = Anaphalis margaritacea, CARU = Calamagrostis rubescens, CESA = Ceanothus sanguineus, EPAN = Epilobium angustifolium, LUAR = Lupinus argenteus, PTAQ = Pteridium aquilinum, SASC = Salix scouleriana.

Extended Herb Stage Sequence.—For study areas exhibiting this pattern, herbs constitute the most abundant cover group throughout the first decade (fig. 4). This pattern of development was associated with a prominent herb component composed of both survivor and colonizer species, a minimal shrub component represented by few survivor plants or slowly developing species, and a nearly absent to latent tree component. Of the four study areas characterizing this pattern, SD-05 exemplifies the maximal development of the herb component (fig. 5-1). Rapid initial development of the herb component resulted from the abundant establishment of fireweed (100 percent frequency in the first year). Regrowth from an extensive survivor stand of bracken fern (first-year frequency 65 percent) was largely responsible for maintaining high herb coverage following the early peak of fireweed development (fig. 5-2). Few survivor shrubs were present. The shrub component was composed mainly of Scouler willow seedlings. Consequently, shrub coverage was slow in development and remained low for most of the first decade (fig. 5-3).

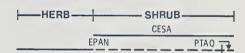
EXTENDED HERB STAGE SEQUENCE (SD-05)



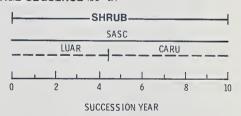
MEDIUM DURATION HERB STAGE SEQUENCE (SD-07)



SHORT DURATION HERB STAGE SEQUENCE (SD- 14)



INITIAL SHRUB STAGE SEQUENCE (SD- 17)



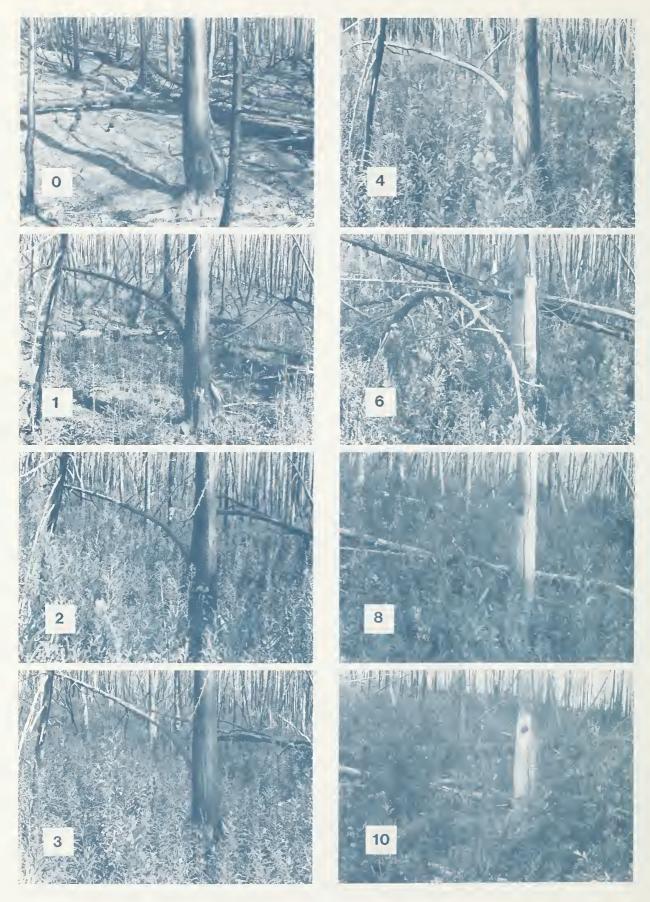


Figure 4.—Vegetation development for the extended herb stage sequence, 1967-77 (study area SD-05). Numerals designate the number of growing seasons since burning.

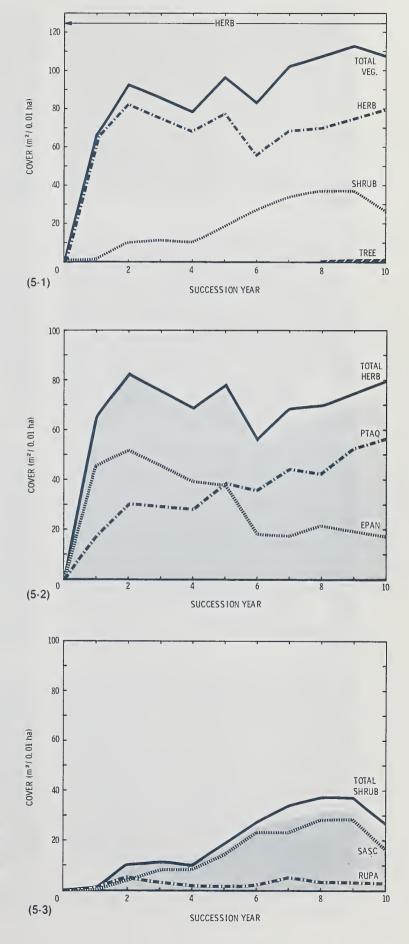


Figure 5.—Extended herb stage succession sequence (Study area SD-05): (5-1) development of plant cover and life-form components; (5-2) major herb component species: *Epilobium angustifolium* (EPAN) and *Pteridium aquilinum* (PTAQ); (5-3) major shrub component species: *Rubus parviflorus* (RUPA) and *Salix scouleriana* (SASC). Shaded areas denote the amount of cover contributed by the two principal species of each life-form component.

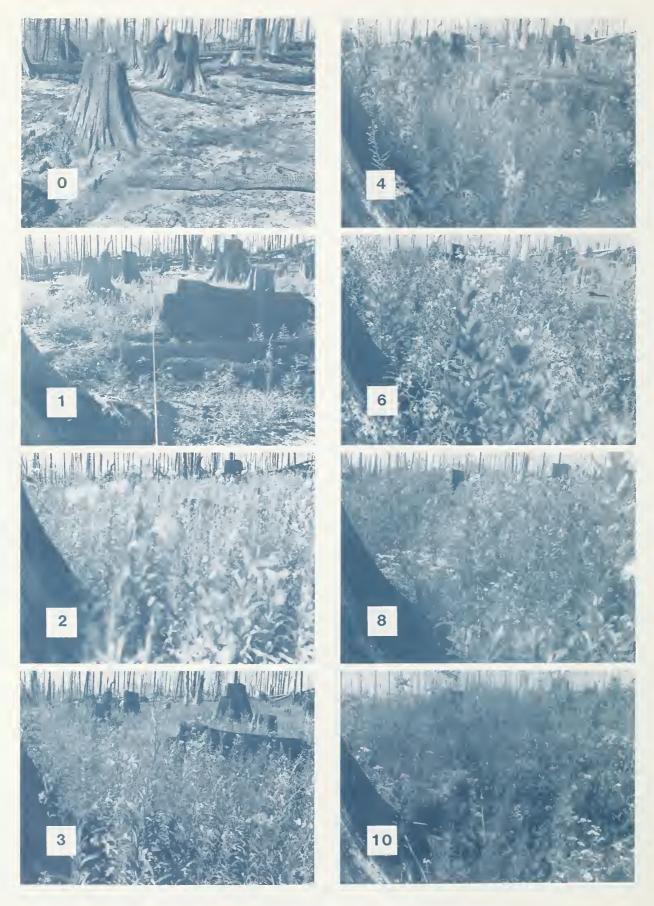
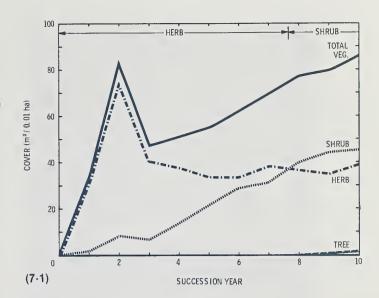
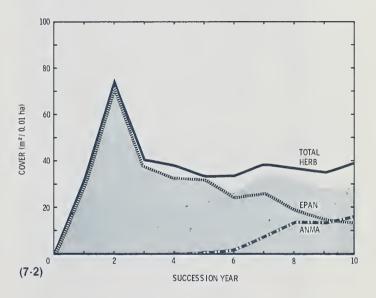


Figure 6.—Vegetation development for the medium-duration herb stage sequence, 1967-77 (Study area SD-07). Numerals designate the number of growing seasons since burning.

Medium-Duration Herb Stage Sequence.—A succession pattern with the herb stage of intermediate duration occurred on six study areas where shrub development surpassed herbs in the latter half of the decade (fig. 6). Major herb and shrub components were similar to those represented in the extended herb sequence except for the abundant presence of bracken fern. As with extended herb sequence, a tree component was poorly represented. Study area SD-07 characterized this pattern (fig. 7-1). Fireweed was responsible for the rapid initial development of the seral vegetation. Absence of associated abundant herb species following the early peak of fireweed's cover development in the second year resulted in a substantial decline in vegetative coverage (figs. 7-1, 7-2). The establishment and development of pearlyeverlasting, a secondary offsite colonizer, was insufficient to compensate for the decline in fireweed in maintaining herb cover as bracken fern had done in the extended herb stage (fig. 7-2). The development of Scouler willow seedlings was primarily responsible for the increase in vegetative cover and succession to the shrub stage by the eighth year (figs. 7-1, 7-3). The shrub components for the extended and medium-duration herb stage patterns were quite similar in their composition and development.





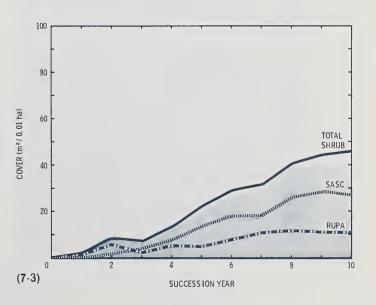


Figure 7.—Medium-duration herb stage sequence (Study area SD-07): (7-1) development of plant cover and life-form components; (7-2) major herb component species: Anaphalis margaritacea (ANMA) and Epilobium angustifolium (EPAN); (7-3) major shrub component species: Rubus parviflorus (RUPA) and Salix scouleriana (SASC). Shaded area denotes the cover contributed by the two principal species of each life-form component.

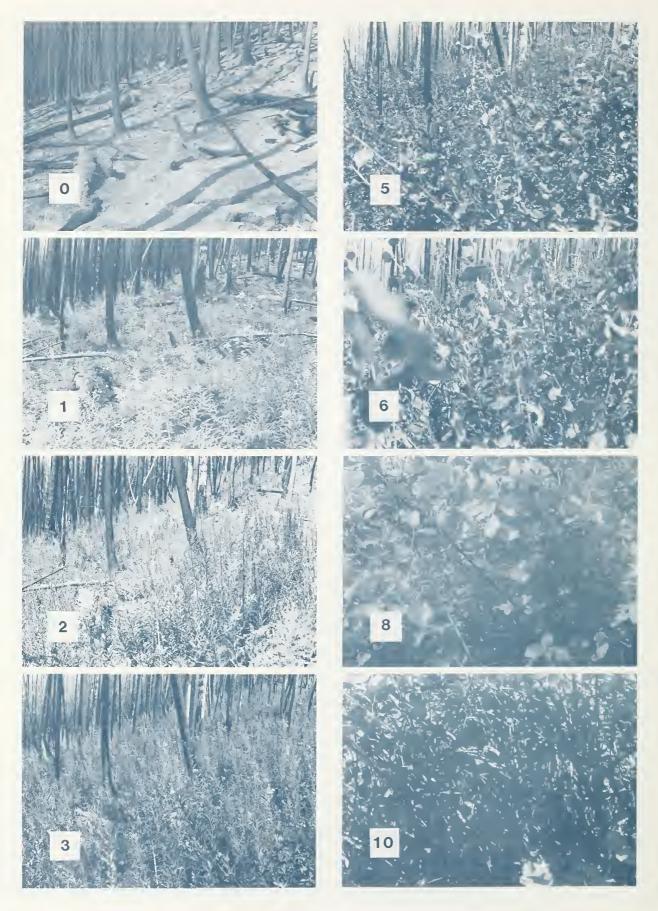
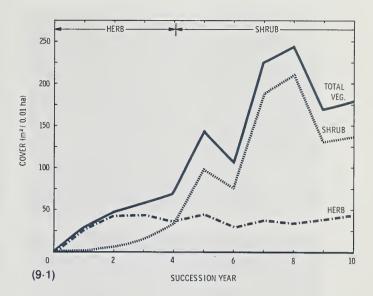
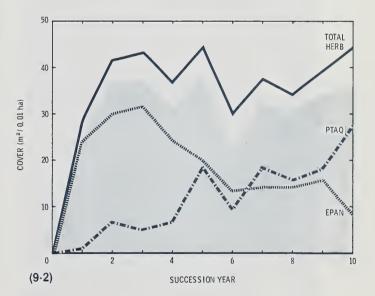


Figure 8.—Vegetation development for the short-duration herb stage sequence, 1967-77 (Study area SD·14). Numerals designate the number of growing seasons since burning.

Short-Duration Herb Stage Sequence.—Herb stage duration is shortened when the initial community contains an abundant shrub component of rapid-growing colonizer species. Five study areas showed a development sequence where shrub coverage exceeded that for herbs by mid-decade (fig. 8). Study area SD-14 provided the best example of the successional sequence associated with the development of a rapid-growing colonizer shrub species (fig. 9-1). Composition and relative development of the abundant species of the herb component were similar to those of the extended herb stage (fig. 9-2), as were the absence of a tree component and the presence of Scouler willow seedlings. However, composition of the shrub component differed markedly with the abundant presence of redstem seedlings. Relative to Scouler willow, development of redstem shrubs from seedlings was quite rapid. Following a short period of establishment, redstem rapidly increased its coverage through the eighth year and remained the dominant shrub through the end of the decade (fig. 9-3). Primarily as the result of redstem's development, the duration of the herb stage was reduced to 4 years. On several other study areas in this group the presence of minor components of survivor shrubs in addition to the seedling redstem served to shorten herb stage duration still further.





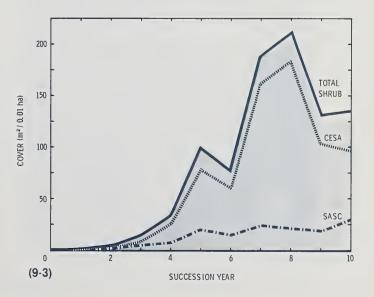


Figure 9.—Short-duration herb stage sequence (Study area SD-14): (9-1) development of plant cover and life-form components; (9-2) major herb component species: *Epilobium angustifolium* (EPAN) and *Pteridium aquilinum* (PTAQ); (9-3) major shrub component species: *Ceanothus sanguineus* (CESA) and *Salix scouleriana* (SASC). Shaded area denotes the amount of cover contributed by the two principal species of each life-form component.

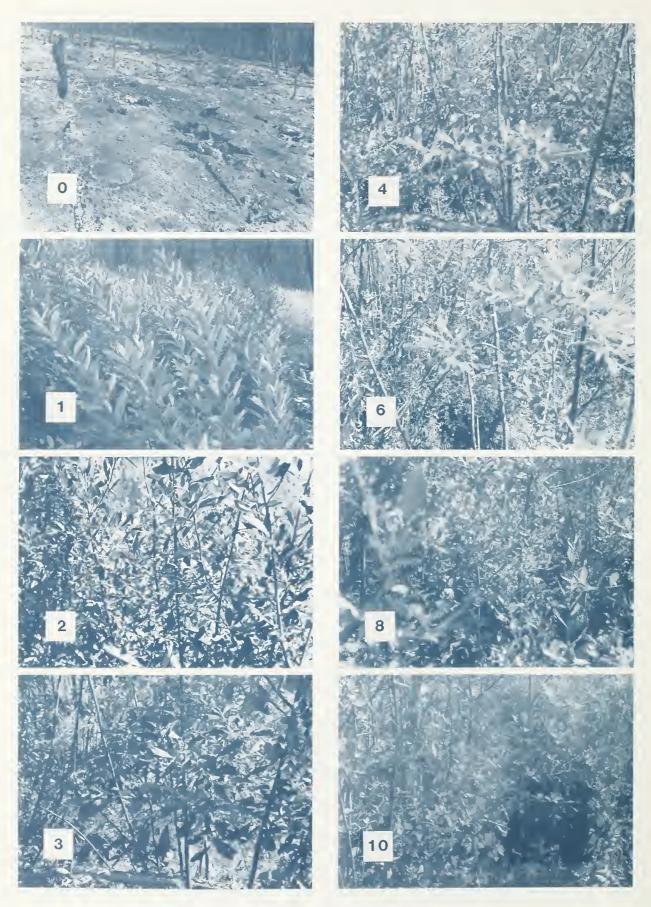
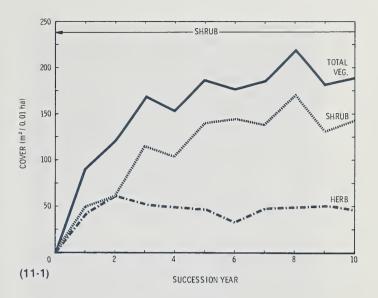
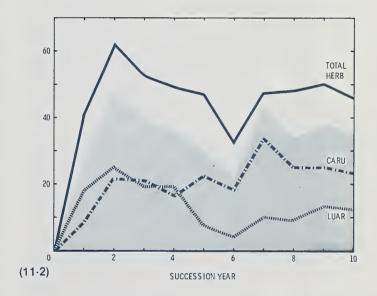


Figure 10.—Vegetation development for the initial shrub stage sequence, 1967-77 (Study area SD-17). Numerals designate the number of growing seasons since burning.

Initial Shrub Stage Sequence.—The initial herb stage can be eliminated when an abundant survivor component of shade-intolerant shrubs is present; with their rapid resprouting forest succession, in effect, begins at the shrub stage. Three study areas that were brushfields prior to the Sundance Fire developed shrub coverages that exceeded the herb component in the first year and remained so throughout the decade (fig. 10). This pattern was associated with an abundant presence of survivor herb and shrub components and a poorly represented or absent tree component. Postfire composition remained essentially that of the prefire community. Study area SD-17 represents this type of succession pattern (fig. 11-1). Rapid initial development of the herb component was due to the regrowth of pinegrass and lupine, both well-distributed survivor species (fig. 11-2). Regrowth from well-developed surviving Scouler willow root crowns largely accounted for the initial rapid increase in shrub cover during the first 3 years (fig. 11-3). Further development of shrub and vegetative cover resulted mainly from the slower regrowth of eight associated survivor shrub species, among which redstem was the most abundant. The cover development of redstem illustrated in figure 11-3 represents a combination of survivor resprouts and colonizer seedlings.





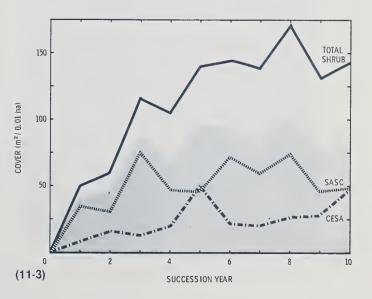


Figure 11.—Initial shrub stage sequence (Study area SD-17): (11-1) development of plant cover and life-form components; (11-2) major herb component species: Calamagrostis rubescens (CARU) and Lupinus argenteus (LUAR); (11-3) major shrub component species: Ceanothus sanguineus (CESA) and Salix scouleriana (SASC). Shaded area denotes the amount of cover contributed by the two principal species of each life-form component.

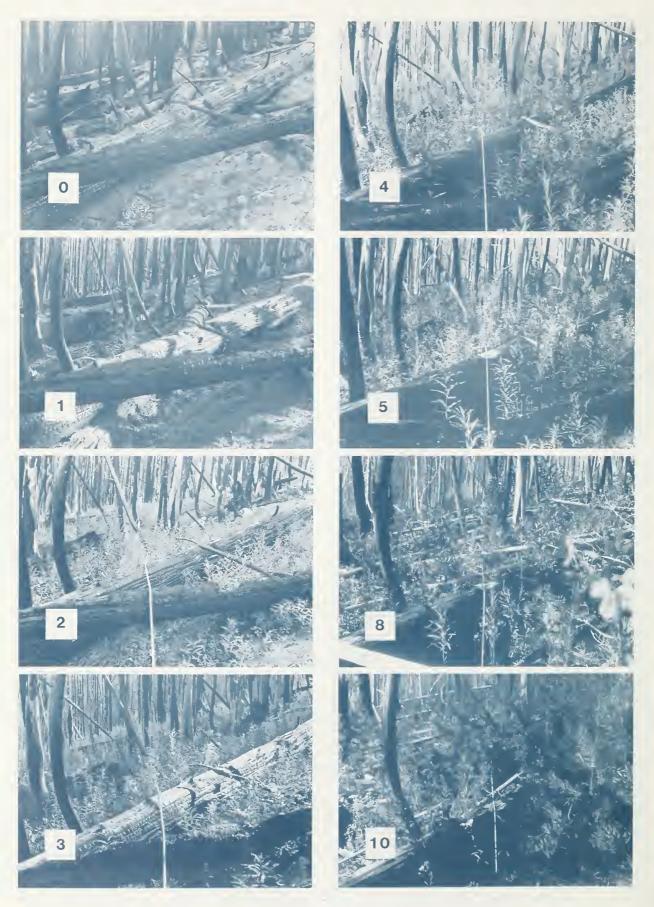
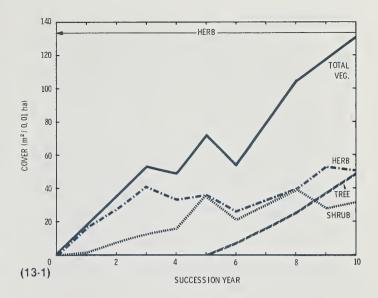
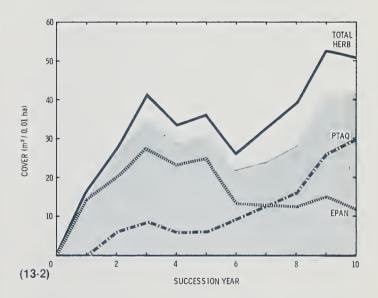


Figure 12.—Vegetation development for the herb-tree stage sequence, 1967-77 (Study area SD-19). Numerals designate the number of growing seasons since burning.

Herb-Tree Stage Sequence.—Trees generally were poorly represented, and their development on all but two sites did not exceed 10 percent cover. In the first decade no site developed a tree stage. However, the two sites with a well-distributed tree component have the potential of progressing to a tree stage in the second decade (fig. 12). Study area SD-19 had a well-represented coniferous tree component of an abundant population of seedling lodgepole pine. As an onsite colonizer, lodgepole pine seedlings established in the first year of succession along with seedlings of fireweed and Scouler willow, both from offsite sources, to form a major colonizer component in the initial community. The development of this combination of seral herb, shrub, and tree species is presented in figure 13-1. In addition to fireweed, bracken fern was well represented as a survivor in the herb component. The general pattern of development for these two herb species is similar to that for the extended and short-duration herb stages (figs. 13-2, 5-2). Development of the shrub component largely resulted from the growth of Scouler willow seedlings and the regrowth from several surviving root crowns of Sitka alder (fig. 13-3). The development of seedling willow in association with a dense stand of lodgepole pine and continued increase in bracken fern appears to preclude the occurrence of an intervening shrub stage between the herb and eventual tree stages (fig. 13-1).





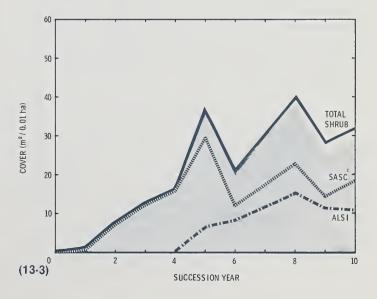


Figure 13.—Herb-tree stage sequence (Study area SD-19): (13-1) development of plant cover and life-form components; (13-2) major herb component species: *Epilobium angustifolium* (EPAN) and *Pteridium aquilinum* (PTAQ); (13-3) major shrub component species: *Alnus sinuata* (ALSI) and *Salix scouleriana* (SASC). Shaded areas denote the amount of cover contributed by the two principal species of each life-form component.

DISCUSSION

The term succession, applied to the development of forest vegetation, implies change. Both compositional change and structural change were evident in the secondary forest succession of Sundance Burn communities.

Compositional Change

Changes in vegetation over the first decade of succession involved amount more than kind of species. Compositional changes included about 40 percent of the seral flora. Of the 103 species recorded in the first year, 84 were still present in the 10th year. The addition of 36 species and the loss of 19 brought the seral floristic composition in the 10th year to 120 species. The average net increase was nearly two species per year.

However, the addition and loss of 55 species scarcely affected the character and abundance of seral vegetation. By the end of the first decade, only two of the herb species added to the initial flora, paintbrush and hawkweed, exhibited the development pattern of a potentially important secondary offsite colonizer. Both species displayed continuous increases in distributional occurrence (at least 30 percent frequency) and abundance (cover exceeded 1 percent) (table 6). Their low stature would appear to preclude the potential to dominate later phases of the herb stage. Nearly half of the additions to the seral flora have the potential to increase abundance in later seral stages, but present levels of occurrence for most of these species (including the climaxlike tree species western redcedar [Thuja plicata Donn ex D. Don] and western hemlock) are so infrequent as to remain undetected by any sample parameter other than presence. Thus, changes in floristic composition resulting from secondary offsite colonization have not affected the overall character of the seral vegetation of the first decade and appear to offer little potential for altering it in the second.

The principal changes in early seral vegetation largely reflect the development of the more important members of the initial postfire community. Most prominent among these over the burn generally were the perennial herbs fireweed and bracken fern and the shrubs redstem and Scouler willow. In addition, the perennial herbs pinegrass and lupine, the shrubs western serviceberry, pachistima, and thimbleberry, and the pioneer tree species paper birch and lodgepole pine constituted important local elements of the seral vegetation on one to several study areas.

The trend for these species has been increasing abundance, with many attaining a maximum or more or less stable level of cover development during the first 10 years of succession. Fireweed was the only major seral species to show a marked, continuous decline after attaining peak coverages early in the decade. This decline occurred in both the absence and the presence of other major seral species such as bracken fern and redstem. Bracken fern appears to be the exception among the important early seral herb species by continuing to increase its coverage throughout the decade even as an understory species in dense shrub stands. As would be expected from their slower development rate and longer maturation time, both paper birch and lodgepole pine continued to increase their coverage through the end of the decade.

Structural Change

Early accounts of forest succession in the Northern Rocky Mountains used elements of both composition and structure in describing developmental changes. However, differences in structural characteristics were readily perceived and have been more extensively employed in identifying stages of sequential development. The structural changes used for the early stages most often reflected changes in the dominant life form. In later stages, changes in size and height of the tree component were used.

In characterizing the succession perceived for the forests of northern Idaho, both Leiberg (1897, 1899) and Larsen (1929) included several stages that preceded the overtopping of the subordinate vegetation by trees. Their initial period was represented by establishment of pioneer plants, followed by maturation of perennial herbs and shrubs. Results from the Sundance Burn study support this general representation of forest succession but differ in that (1) the initial postfire community contained both pioneer and climaxlike species derived from survivor and colonizer origins, and (2) the differential development of the herb and shrub life forms was the defining feature of the pretree stages.

Prior to the development of vascular vegetation, an early seral stage noted by Leiberg (1899) and Humphrey and Weaver (1915) included ground surface bryophytes such as firemoss or liverwort. A well-developed ground surface bryophyte layer occurred extensively on the Sundance Burn. However, it did not appear as a distinct initial stage but developed concurrently with the herb

Table 6.—Development of secondary colonizer species exhibiting progressive increases in frequency and cover throughout the first decade

	Initial appearance	Maximum increase in frequency		Maximum increase in cover		
Species	SY ¹	SY ¹	%	SY ¹	%	
Castilleja miniata	3-10	6-10	5-35	10	2	
Hieracium albiflorum	2-7	6-10	5-95	9-10	1-5	

¹Succession year; designates the number of years (growing seasons) since the fire.

stage. The bryophyte surface layer, composed of ground mosses such as firemoss or similar pioneer species but without liverworts, occurred on all study areas. Patches of a ground moss layer were evident in the first year and increased rapidly in coverage over the next several years. Because vascular vegetation was given priority over bryophytes in making coverage estimates, actual cover values for moss are not available. But by the third year on most of the mesic sites, the moss layer covered all of the available ground surface not physically occupied by vascular plants or woody debris. Throughout the decade it has continued to maintain high coverages even under the shade of dense stands of pioneer herbs and shrubs. In shaded microsites beginning about the third or fourth year, larger mosses such as Polytrichum juniperinum Hedw. became evident and more abundant, locally replacing the smaller mosses. In sunny, exposed sites, however, this replacement did not take place. These apparent changes suggest that a successional process is operating at the bryophyte level on the ground surface and in conjunction with development of the vascular vegetation. Later in the decade, some deterioration of the ground bryophyte layer has been observed. This situation was restricted to accumulations of slower decomposing litter debris, notably from bracken fern and large, charred bark flakes from firekilled trees and occasionally from local concentrations of redstem litter sufficient to completely bury the moss. The litter produced by most of the early seral vegetation did not produce a sufficiently persistent accumulation to eliminate the ground bryophyte layer. It appears that the destruction of this layer will be related to the buildup of coniferous foliage and twig litter sufficient to exclude light from the ground surface.

Leiberg's (1897, 1899) observations on the establishment of fireweed and the pioneer species of willow and Ceanothus in the initial stage that became prominent in early succession are substantiated by the results of Lyon's (1971) work and the present study. No evidence was found, however, to support Leiberg's contention that the accumulation of humus derived from the litter of early pioneer deciduous shrubs and herbaceous plants was essential for the germination of coniferous tree seed. On the study area that developed a dense stand of pioneer conifers, newly germinated tree seedlings were observed only in the first year. These trees became established on an exposed, ash-bed surface in the year following the fire. The relative absence of conifer seedlings in the first and subsequent years for many of the Sundance Burn study areas represents a successional situation Leiberg (1897) described as "second burns." This was attributed to the lack of onsite seed sources for tree species that resulted from the reburning of coniferous forest stands prior to the time trees had reached abundant cone-bearing size.

Larsen's (1929) descriptive sequence for subordinate vegetation included a second stage that preceded the first tree stage. The second stage was characterized by perennial plants, mostly shrubs, with berries or berrylike fruit. For the Sundance Burn the berry-fruited species represented 16 percent of the seral flora. The majority of

these species derived from survivor origins and were slow to develop (less than 5 percent cover during the first decade). Collectively, berry-fruited plants contributed little to the seral vegetative cover of the Sundance Burn, but two shrub species, western serviceberry and thimbleberry, did constitute substantial amounts of cover on a few study areas. In these instances their relative contribution to shrub cover was greater during the initial herb stage. Though coverages of these two species continued to increase in the shrub stage, their proportionate representation generally declined. Of all of the berry species present, thimbleberry—with its broad leaves, relatively wide distribution among study areas, and potential for local expansion by rhizome growthoffers the greatest potential to fit Larsen's descriptive stage, but such an occurrence has yet to develop on the areas under study.

Of the earlier representations of succession in northern Idaho, Daubenmire and Daubenmire (1968) most closely agree with the results of this study. With about 40 percent of the total floristic composition for the decade originating from offsite sources and a significant part of the seral vegetation attributable to fireweed and Scouler willow, the successional development indeed fits the Daubenmires' (1968) initial or "invasion" stage. But because most of the important offsite-origin seral species became established on sites unoccupied by surviving vegetation, the term "colonization" more appropriately describes the process involved. Rather than an invasion, with aggressive displacement of established species, the process appears to be passive in that initial colonizers use unoccupied sites created by fire disturbance. Secondary colonizers differ in this respect, for they must be tolerant of site modification and competition from established seral vegetation.

Sequence and Duration of Early Stages

For the first decade of secondary forest succession, the 18 Sundance Burn study areas provide examples of both two-stage (initial herb to shrub stage) and one-stage patterns. One-stage patterns were evident on sites where the lack or abundance of shrubs resulted in either an initial herb stage or an initial shrub stage that remained dominant throughout the decade. On 15 study areas, the successional sequence began with the herb stage. By the end of the first decade, 11 study areas had developed to a shrub stage but none had reached a tree stage. The sequential relationship between the development of the three life-form groups is most apparent when pioneer colonizer species of each life-form group establish in the first year. For the early phases of secondary succession on the Sundance Burn, the concurrent development of the three life-form components proceeding at different rates appears to be the principal successional process operating.

For most study areas where succession began with an herb stage, the rapid development of the herb component was due to the abundant presence of fireweed. Results from the Sundance Burn indicate that the duration of each stage was dependent largely on the composition and abundance of the species already established for

the next higher order life form. For example, the slower rate of cover development for bracken fern was responsible for extending the duration of a dominant herb stage into the latter half of the first decade on sites where shrub development was minimal or slow. For most study areas durations for the herb stage were directly related to the composition and growth form of the principal members of the shrub component.

For those study sites exhibiting a two-stage sequence in which the shrub stage began in the first half of the decade, the seedling form of redstem was the major shrub component. Where the shrub stage began in the latter half of the decade, the seedling form of Scouler willow was the major shrub component. On sites where survivor shrubs made up an increasingly larger proportion of the shrub component, the duration of the herb stage was correspondingly shortened. When mature Scouler willow constituted a major portion of the survivor shrub component, its rapid regrowth was largely responsible for the exclusion of an initial herb stage. Thus, the spectrum of succession patterns identified from the Sundance Burn varied in the duration of the dominant life-form stage rather than in sequential order. The sequence of dominant life-form stages was consistent with the modal pattern (herb-shrub-tree) historically used for representing secondary succession of Northern Rocky Mountain coniferous forests.

CONCLUSIONS

All of the species important to the early development of seral vegetation on the Sundance Burn were present in the first year of succession. Species composing the initial postfire vegetation derived from three origins: survivor, residual colonizer, and initial offsite colonizer. Survivors constituted the largest group of first-year species and represented more important seral species than any other group. Major survivor species included bracken fern, Scouler willow, thimbleberry, pinegrass, lupine, western serviceberry, and paper birch. Residual colonizers constituted the smallest group of first-year species but included two of the most important early seral species, redstem and lodgepole pine. Initial offsite colonizers of major importance were fireweed and Scouler willow. During the first decade no major seral species originated from the secondary offsite colonizer

Most of the prominent early seral species exhibited a cover development pattern during the first decade that tends to level off following the initial period of increase. Fireweed was the only prominent seral species with an unequivocal peaking out (increase-decrease) pattern within the first decade. Redstem may have similarly peaked in development in the first decade, but with maximum coverages occurring later in the decade the permanancy of this trend is not clear. The development pattern for bracken fern and lodgepole pine, in contrast to the other major seral species, continued to increase in cover throughout the decade.

In this study, examples of colonizer-dominated seral vegetation were most often associated with formerly

well-developed forested sites. On such sites the survivor component was usually poorly represented or absent. At the other end of the seral development spectrum, seral vegetation developing on prefire brushfields and formerly open (lightly shaded) forest sites was usually dominated by survivors. Thus, even with the severe fire treatment of the Sundance Fire, the composition of the prefire vegetation directly influenced the presence and composition of the postfire survivor component, and this in turn influences the suitability of the site for colonizers. Given the knowledge of the prefire composition, the species composition of the postfire survivor component is largely predictable. Probable composition of onsite colonizers may also determine if past seral and current stand history are known, or if adjacent seral examples are available. Composition of the postfire offsite colonizer component is the most uncertain element due to the chance nature of the immigration event. But even here a knowledge of the regularity of seed or fruit production and the regional suitability of burned sites for seedling establishment could do much to reduce the uncertainty of the presence of prominent seral species such as fireweed.

Changes in floristic composition (species gained and lost) over the first 10 years demonstrated little effect on the course or development of seral vegetation. No evidence supported the "relay floristics" concept of vegetation development (Egler 1954; Drury and Nisbet 1973) whereby initial or preceding dominant species modify the site to their own exclusion, thereby preparing it for replacement by succeeding species. Rather, results from this study suggest that the preponderant successional process operating during the first decade of the Sundance Burn succession was one of differential development of species forming the initial community. Supporting this view is the sequential development of herb and shrub stages dominated by pioneer colonizer species established at the start of succession (such as fireweedredstem succession on SD-14 or fireweed-Scouler willow succession on SD-07).

A degree of autogenic modification of the ground surface has occurred from shading and litter deposition by the developing seral vegetation. In the first decade, the influence of these modifications appears to be reflected more in the tolerance of established species to changes in the near-surface environment than to preparing the site to accommodate the establishment of more climaxlike species. Up to this time, short-lived obligate pioneer and exotic ruderal species (such as geranium, cudweed, and rye) appear to have been the most affected. The establishment and dispersal of paintbrush between the third and ninth years may be an example of the effect of the autogenic modification process in facilitating the establishment of a secondary colonizer species. As succession proceeds to later stages, with development of the coniferous component and its associated formation of a coniferous organic mantle, this process should become more pronounced and important.

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APPENDIX: SERAL CHARACTERISTICS OF THE FLORISTIC COMPOSITION OF THE FIRST DECADE'S SECONDARY SUCCESSION ON SUNDANCE BURN STUDY AREAS.

	Physiognomic		Fire survival	First/last S.Y.	_ 0	ccurre	nce
Species	life form	Seral origin	adaptation	record	Pres	Freq	Cove
Abies grandis	Tree	Introduced		2	6	4	3
Acer glabrum	T-Shrub	Survivor	Root crown	1	12	2	4
Achillea millefolium	Herb	Survivor	Rhizome	1	11	2	1
Adenocaulon bicolor	Herb	Survivor	Caudex	1	3	1	
Agoseris grandiflora ^a	Herb	2d O-S colonizer		9	4	1	
Agrostis alba ^b	Herb	Introduced		1	12	7	3
Agrostis exarata	Herb	2d O-S colonizer		5	2	1	
Agrostis scabra	Herb	I O-S colonizer(?)		1	9	1	
ALNUS SINUATA	T-Shrub	Survivor	Root crown	1	10	8	6
Alopecurus pratensis ^b	Herb	2d O-S colonizer		9	1		
AMELANCHIER ALNIFOLIA°	T-Shrub	Survivor	Root crown	1	14	12	4
ANAPHALIS MARGARITACEA	Herb	I O-S colonizer		1	18	17	13
Antennaria microphylla	Herb	2d O-S colonizer		3	3		
Antennaria neglecta	Herb	2d O-S colonizer		9	1	1	
Apocynum androsaemifolium ^a	Herb	Survivor	Rhizome	1	12	9	4
Arabis holboellii	B-Herb	R-colonizer	GSS-1	1	3	1	
Aralia nudicaulis ^c	Herb	Survivor	Rhizome	1	2	2	2
Arnica cordifolia	Herb	Survivor	Rhizome	1	2	1	
Arnica latifolia	Herb	Survivor	Rhizome	1	2	2	1
Asarum caudatum	Herb	R-colonizer	GSS-1	1	2	1	'
Aster conspicuus	Herb	Survivor	Rhizome	1	6	'	
Aster engelmannii	Herb	Survivor	Caudex	1	4	1	
Aster laevis	Herb	2d O-S colonizer	Oaddex	3/4	1	'	
Athyrium filix-femina	Herb	Survivor(A)		2	2		
Berberis repens ^c	LWP	Survivor	Rhizome	1	6	3	1
BETULA PAPYRIFERA	Tree	Survivor	Root crown	1	0	3	'
BLIOLA FAFINITENA	rree	R-colonizer	CSS-1	1	8	5	2
Bromus inermis ^b	Herb	2d O-S colonizer	C33-1	10	-1		
CALAMAGROSTIS RUBESCENS			Dhizoma		1	7	
	Herb	Survivor	Rhizome	1	10	7	4
Calochortus apiculatus	Herb	Survivor	Bulb	1	1	1	
Campanula rotundifolia	Herb	2d O-S colonizer	0.00(0)	7	1		
Carex deweyana	Herb	R-colonizer	GSS(?)	1	1		
Carex geyeri	Herb	Survivor	Rhizome	1	2	2	1
Carex pachystachya	Herb	R-colonizer	GSS(?)	1	1	1	
Carex rossii	Herb	R-colonizer	GSS-2	1	17	12	10
Castilleja miniata	Herb	2d O-S colonizer	_	3	12	5	1
CEANOTHUS SANGUINEUS	T-Shrub	Survivor	Root crown	1	14	12	10
		R-colonizer	GSS-2	1			
Ceanothus velutinus	Shrub	Survivor	Root crown	1	6	3	4
		R-colonizer	GSS-2	1	Ü	0	7
Chenopodium album ^b	A-Herb	Introduced(A)		1/1	1		
Chimaphila umbellata	Herb	Survivor(A)		3	2		
Cirsium arvense ^{b.a}	Herb	Survivor	Rhizome	1	4	1	1
Cirsium vulgare ^{b.a}	B-Herb	I O-S colonizer		1	12	7	
Clintonia uniflora ^c	Herb	Survivor	Rhizome	1	17	8	3
Collinsia parviflora	A-Herb	R-colonizer	GSS-1	1	3	3	
Conyza canadensis	A-Herb	I O-S colonizer		1	17	10	
Cryptantha affinis	A-Herb	R-colonizer	GSS-1	1	2	2	1
Dactylis glomerata ^b	Herb	Introduced		1	9	4	3
Deschampsia elongata	Herb	2d O-S colonizer		6	3		
Disporum hookeri ^c	Herb	Survivor	Rhizome	1	17	12	3
Dracocephalum parviflorum	B-Herb	R-colonizer	GSS-2	1/1	2		
EPILOBIUM ANGUSTIFOLIUM ^a	Herb	I O-S colonizer		1		40	10
		Survivor	Rhizomelike root	1	18	18	18
Epilcbium paniculatum ^a	A-Herb	I O-S colonizer		1	13	8	
Epilobium watsonii ^a	Herb	I O-S colonizer		1/6	16	9	
Equisetum arvense	Herb	Survivor	Rhizome	1	1	,	
Erigeron acris	B-Herb	2d O-S colonizer	· IIIIZOIIIIO	6	6	4	
Engeron achs Erucastrum gallicum ^b	A-Herb	Introduced(A)		1/1	1	7	
= rocastrain gameum	7,11610	minouaceu(A)		171			

	Physiognomic		Fire survival	First/last S.Y.	0	ccurr	ence
Species	life form	Seral origin	adaptation	record	Pres Freq Co		
Festuca arundinacea ^b	Herb	Introduced		1	16	12	4
Festuca occidentalis	Herb	2d O-S colonizer		3	3	1	
Filago arvensis ^b	A-Herb	I O-S colonizer		1	9	2	
Fragaria vesca ^c	Herb	Survivor	Caudex	1	4	1	1
Galium triflorum ^d	Herb	R-colonizer	GSS-1	1	5	2	
Geranium bicknellii	A-Herb	R-colonizer	GSS-2	1/9	5	4	3
Gnaphalium microcephalum	B-Herb	I O-S colonizer		1	18	12	1
Gnaphalium palustre	A-Herb	I O-S colonizer		1/5	7		
Gnaphalium viscosum	B-Herb	2d O-S colonizer		3	13	9	
Gymnocarpium dryopteris	Herb	Survivor(A)		3	2		
Habenaria elegans	Herb	Survivor	Tuber	1	15	4	
Heuchera cylindrica	Herb	Survivor(?)		4	1		
Hieracium albiflorum	Herb	2d O-S colonizer		2	18	15	6
Hieracium umbellatum	Herb	2d O-S colonizer		9	1		_
Holodiscus discolor	Shrub	Survivor	Root crown	1	6	3	3
Hypericum perforatum ^b	Herb	2d O-S colonizer		4/9	1	Ŭ	J
liamna rivularis	Herb	Survivor	Caudex	1			
namna medans	TICID	R-colonizer	GSS-2	1	12	8	5
luniperus communis ^c	Shrub	2d O-S colonizer	033-2	5	1	1	
Lactuca serriola ^{b.a}	A-Herb	l O-S colonizer		1/1	5	'	
Larix occidentalis	Tree	R-/I O-S colonizer(?)		10	4		
Lilium columbianum	Herb	Survivor	Bulb			8	4
Lonicera utahensis ^c	Shrub	Survivor		1	10	1	1
			Root crown	1	11		3
LUPINUS ARGENTEUS	Herb	Survivor	Caudex	1	3	3	3
Luzula parviflora	Herb	2d O-S colonizer		4	1		
Luzula piperi	Herb	Survivor(?)	D (0)	1	1	1	
Oplopanax horridum ^c	Shrub	Survivor	Root crown(?)	1	1		
Osmorhiza chilensis ^d	Herb	2d O-S colonizer	.	5	1	1	
PACHISTIMA MYRSINITES	Shrub	Survivor	Root crown	1	18	17	13
D		R-colonizer	GSS-1	1			
Phleum pratense ^b	Herb	Introduced		1	13	5	2
Picea engelmannii	Tree	Introduced		2	6	3	3
PINUS CONTORTA	Tree	R-colonizer	CSS-1 or 2	1	15	4	5
Pinus monticola	Tree	R-colonizer	CSS-1	1	13	2	1
Plantago major ^b	Herb	Introduced(A)		1	2		
Poa compressa ^b	Herb	2d O-S colonizer		9	1	1	
Poa palustris ^b	Herb	I O-S colonizer		1	3	1	
Polygonum douglasii	A-Herb	R-colonizer	GSS-1	1	2	2	
Polygonum lapathifolium ^b	A-Herb	Introduced(A)		1/1	1		
Populus tremuloides ^a	Tree	Survivor	Root crown	1	13	7	3
		I O-S colonizer		1	13	'	3
Populus trichocarpa ^a	Tree	Survivor	Root crown	1	2	1	
		I O-S colonizer		1	2	'	
Prunus emarginata ^c	T-Shrub	Survivor	Root crown	1	5	3	3
Pseudotsuga menziesii	Tree	Introduced		1	18	12	9
PTERIDIUM AQUILINUM	Herb	Survivor	Rhizome	1	15	15	14
Pyrola asarifolia	Herb	Survivor	Rhizome	1	6	1	
Pyrola picta	Herb	Survivor	Rhizome	1	5	3	1
Pyrola secunda	Herb	Survivor	Rhizome	2	12	7	
Ribes lacustre ^c	Shrub	R-colonizer	GSS-2	1	4		
Ribes viscosissimum ^c	Shrub	R-colonizer	GSS-2	1	2	1	2
Rosa gymnocarpa ^c	Shrub	Survivor	Root crown	1	11	8	8
Rubus idaeus ^c	Shrub	2d O-S colonizer		4	5	1	1
Rubus leucodermis ^c	Shrub	Survivor	Root crown	1			
		R-colonizer	GSS-2 (?)	1	7	6	4
RUBUS PARVIFLORUS ^c	Shrub	Survivor	Rhizome	1			
	222	R-colonizer	GSS-2	1	15	11	13
Rumex acetosella ^b	Herb	Survivor	Rhizome	1/5	1		
SALIX SCOULERIANA ^a	T-Shrub	Survivor	Root crown	1/5			
	1 Official	I O-S colonizer	TIOUT CIOWII	1	18	18	18
Sambucus racemosa ^c	Shrub	Survivor	Root crown				
	JIIIUD	Julylydl	HOOL CIOWII	1	-	4	0
		R-colonizer	GSS-2	1	5	4	3

APPENDIX. (Con.)

	Physiognomic		Fire survival	First/last S.Y.	00	curren	ICO.	
Species	life form	Seral origin	adaptation	record	Pres Freq Cove			
Secale cereale ^b	A-Herb	Introduced		1/4	10	7		
Senecio vulgaris ^b	A-Herb	Introduced(A)		1/5	9	2		
Silene noctiflorab	A-Herb	Introduced(A)		1/3	2			
Smilacina racemosa ^c	Herb	Survivor	Rhizome	1	4	2		
Smilacina stellata ^c	Herb	Survivor	Rhizome	1	8	4	2	
Solidago canadensis	Herb	Survivor	Rhizome	1	18	11		
Sorbus scopulina ^c	T-Shrub	Survivor	Root crown	1	4			
Spergularia rubra ^b	A-Herb	I O-S colonizer		1/2	6	1		
Spiraea betulifolia	Shrub	Survivor	Rhizome	1	8	7	5	
Spiranthes romanzoffiana	Herb	2d O-S colonizer		3	1			
Stellaria media ^b	A-Herb	Introduced(A)		1/5	3	1		
Stellaria obtusa	Herb	R-/I O-S colonizer(?)		1/1	1			
Symphoricarpos albus ^c	Shrub	Survivor	Rhizome	1	4	3	4	
Taraxacum laevigatum ^{b.a}	Herb	2d O-S colonizer		5/6	2			
Taraxacum officinale ^{b.a}	Herb	I O-S colonizer		1	13	9		
Thalictrum occidentale	Herb	Survivor	Rhizome	1	7	2	2	
Thuja plicata	Tree	2d O-S colonizer		6	2			
Tiarella trifoliata	Herb	Survivor	Caudex	1	2	2		
Tragopogon dubius ^{b.a}	B-Herb	2d O-S colonizer		8	1			
Trautvetteria caroliniensis	Herb	Survivor	Rhizome	1	4	1		
Trifolium agrarium ^b	A-Herb	2d O-S colonizer(?)		2/6?	1			
Trifolium hybridum ^b	Herb	Introduced		1	10	4	2	
Trifolium repens ^b	Herb	Introduced		1	12	7	2	
Trillium ovatum	Herb	Survivor	Corm	1	2			
Trisetum cernuum	Herb	2d O-S colonizer		10	2			
Tsuga heterophylla	Tree	2d O-S colonizer		6	4			
Vaccinium membranaceum ^c	Shrub	Survivor	Rhizome	1	17	9	6	
Viola glabella	Herb	Survivor	Rhiz/Caud	1		_		
		R-colonizer	GSS-1	1	6	3		
Viola orbiculata	Herb	Survivor	Rhizome	1				
		R-colonizer	GSS-1	1	16	16		
Xerophyllum tenax	Herb	Survivor	Rhizome	1	8	3	3	

(TOTAL: 139 species)

LEGEND:

Species:

Names in capital letters denote principal cover species; (15+ percent cover)

aseed or fruit capable of long-range wind dispersal

bexotic species

berry or berrylike fruit, bird and/or animal dispersed

'armed fruit, animal dispersed

Physiognomic life form:

 \dot{T} -Shrub = tall shrub (maximum height > 2 m)

LWP = low woody plant (maximum height < 0.5 m)

A-Herb = annual herb B-Herb = biennial or short-lived perennial herb

Introduced denotes planted or seeded by man

R-colonizer denotes residual colonizer (onsite source)

I O-S colonizer denotes initial offsite colonizer (immigration in succession year 1)

2d O-S colonizer denotes secondary offsite colonizer (immigration after succession year 1)

Double entry in the species listing indicates those 14 species that exhibited more than one seral origin (A) = accidental; denotes very infrequently surviving species or introduced as a "weed" seed in seeding mixture

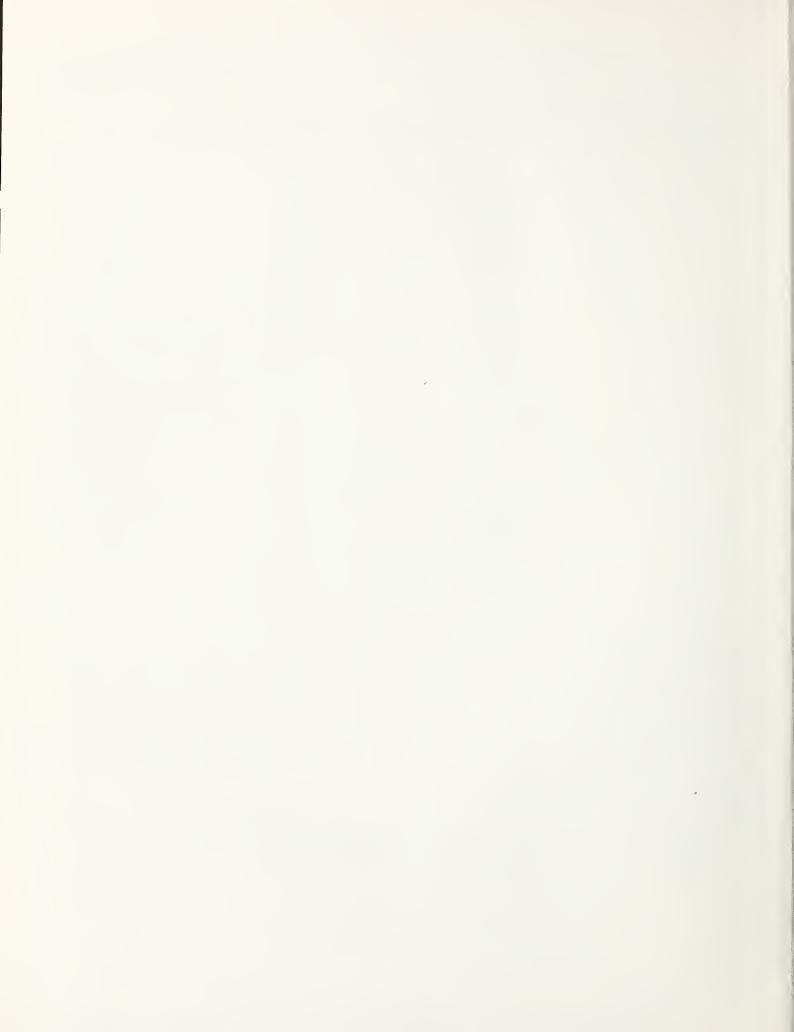
Fire survival adaptation:

CSS Tree crown source seed (onsite); -1 short-term viability, -2 long-term viability GSS - Ground source seed (onsite); -1 short-term viability, -2 long-term viability

First/last succession year (S.Y.) record: First and last year of recorded occurrence

Occurrence: Numerals denote the number of study areas on which the species occurred as presence, frequency, and cover, respectively





Stickney, Peter F. First decade plant succession following the Sundance Forest Fire, northern Idaho. General Technical Report INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 26 p.

Describes the first 10 years of vegetation development following disturbance by a holocaustic forest fire in a western redcedar-western hemlock type in the Selkirk Range. Postfire development of vegetation is represented as life-form stages and predominant cover species. Differential development of plant species established in the first postfire year appears to be the principal process operating in the early seral phase of this secondary forest succession.

KEYWORDS: postfire succession, forest succession, early seral stages, wildfire succession, western redcedar type, western hemlock type, initial vegetation

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

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