

Dynamics of Forest Communities Used by Great Gray Owls

James R. Habeck, Division of Biological Sciences,
The University of Montana, Missoula, MT 59812

INTRODUCTION

Great gray owls (*Strix nebulosa*) inhabit forests, but not all forests possess identical characteristics. To understand the owl, we must understand the dynamics of the vegetation communities that support them. Those dynamics operate differently in the Northern Rocky Mountains and the Cascade-Sierra Nevada complex, both of which are inhabited by great gray owls.

The range of the great gray owl in western North America south of Canada extends from northern California, Oregon, and Washington eastward through Idaho, Montana, and Wyoming. The owl's actual distribution in these states is irregular or even disjunct (Sanderson *et al.* 1980, Franklin 1988, Forsman and Bull 1989, Groves and Zehntner 1990, Bull and Henjum 1990, Bergeron *et al.* 1992). The great gray owl occurs wherever forests in these states meet their life needs, which not all forests do.

Pioneer ecologists C. Hart Merriam (1889) and Rexford Daubenmire (1943) were among the first to provide detailed ecological descriptions and interpretations of western forest zonation patterns. They also provided early understanding of how forest vegetation types in this region interacted with elements of the environmental complex: mountain physiography, geology, climate, wildlife, and wild-fire.

Modern ecologists have continued to accumulate knowledge on these complex interactions (Hall 1980a, Smith 1985, Habeck 1987, Peet 1988, Despain 1990). Interpreting the current status of owls in the Rocky Mountains (Franklin 1988) is predicated on accepting the idea that animals respond directly to (1) habitat features such as vegetation structure, vegetation composition, and forest patterns, and (2) successional stages following wildfire, cyclic insect and pathogen outbreaks, and silvicultural treatments (Thomas 1979).

Hall (1980b) made clear that any vegetation management aimed at enhancing native avian populations in western North American forests must be

based on understanding a given area's presettlement vegetation condition and the historically important processes that shaped it. Application of such baseline knowledge during the development and evaluation of forest management alternatives provides greater assurance of long-term avian management success (DeGraff 1980). Timber harvesting and altered natural fire regimes in the Northern Rocky Mountains will receive special attention in this analysis of vegetation dynamics.

NORTHERN ROCKY MOUNTAINS

The geographic area often designated as the Northern Rocky Mountains (NRM) extends from the Snake River Plain in southern Idaho, northward to the Canadian border. For this discussion I expand the area to include portions of western Wyoming and southeastern Idaho, encompassing Grand Teton and Yellowstone National Parks, and portions of the Caribou and Targhee National Forests, which are often included in the northern part of the Middle Rocky Mountains. All these places are areas of recent great gray owl studies and include the southern-most distribution of this owl in the Rockies (Franklin 1988, Groves and Zehntner 1990, Levine 1992).

Phytogeographic Provinces in the Northern Rocky Mountains

The low- and mid-elevation montane forests in the NRM used by the great gray owl fall primarily into USDA Forest Service's (1977) Western Forest Type #26, lodgepole pine (*Pinus contorta*) and Type #20, Douglas-fir (*Pseudotsuga menziesii*). Within Kuchler's (1964) potential natural vegetation types, the great gray owl's range falls within Type K-12, Douglas-fir, and Type K-15, Engelmann spruce-subalpine fir (*Picea engelmannii*-*Abies lasiocarpa*). The NRM region falls within Bailey's (1978) Highland Ecoregion, Rocky Mountain Forest Province, M3110, which features Douglas-fir.

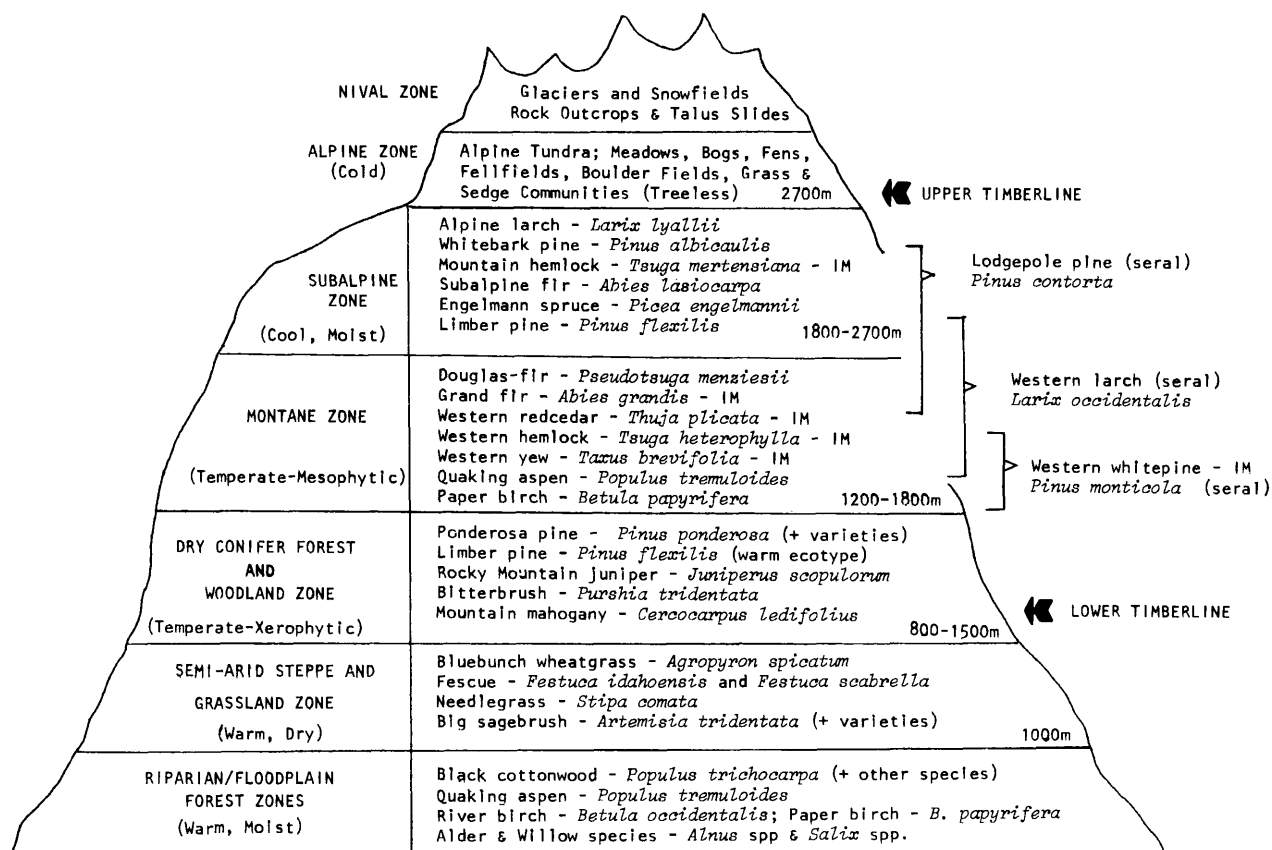


Figure 1.--Vegetation zonation in the Northern Rocky Mountains, typical of western Montana and northern Idaho. Approximate elevational limits of forest zones are given, as are average positions of upper and lower timberlines. Tree species functioning as post-fire seral dominants are shown on the right. IM = Inland Maritime Province (after Habeck 1987).

Rocky Mountain vegetation zonation has been graphically depicted in earlier reports by Habeck (1987) and are duplicated in figures 1 and 2. Peet (1988) summarized forest distribution patterns in the NRM through a series of gradient mosaic ordinations, wherein interactive elevation and moisture gradients are related to vegetation patterns (figures 3 and 4). Other graphic depictions of vegetation zonation and forest habitat type distributions for Montana, Idaho, and Wyoming are provided by Cooper *et al.* (1991), Pfister *et al.* (1977), Steele *et al.* (1981), and Steele *et al.* (1983). Despain (1990) has also provided graphic descriptions and interpretations of Yellowstone National Park (YNP) vegetation. Recent NRM vegetation reports usually include analyses of fire history and descriptions of post-disturbance forest succession.

In the northwestern NRM, south of Canada, including northeastern Washington, northern Idaho, and northwestern Montana eastward to the Continental Divide in Glacier Park, a moist inland-maritime subregion exists that features a well-developed oceanic (Pacific coastal) influence. Here the NRM exhibit nearly continuous forest cover composed of several conifers with west coast affinities. These include western red-cedar (*Thuja plicata*), western hem-

lock (*Tsuga heterophylla*), western white pine (*Pinus monticola*), and grand fir (*Abies grandis*). Forests dominated by these trees formed continuous cover before the era of logging. Before this century fires were less common in these moist forests with fire-free intervals of 100-200 years (Arno and Davis 1980). The only likely exception to the closed-canopy condition may have been natural lakes, marshes, and wet meadows occupying glacially formed depressions.

Elsewhere, away from the maritime influence, the remaining parts of the NRM experience significantly colder and drier continental climatic conditions. The latter areas display well-defined cold subalpine / timberline zones on the upper mountain slopes; these feature subalpine fir, Engelmann spruce, lodgepole pine, limber pine (*Pinus flexilis*), and white-bark pine (*P. albicaulis*). At lower elevations warmer, drier montane forests show a "lower timberline" composed of savanna, steppe, grassland, and shrubland types (Habeck 1987). The mid- to low-elevation montane forests are dominated either singularly or in mixtures of Douglas-fir, ponderosa pine (*Pinus ponderosa*), and lodgepole pine.

The several phytogeographic provinces composing the NRM (figure 5) were established by Arno

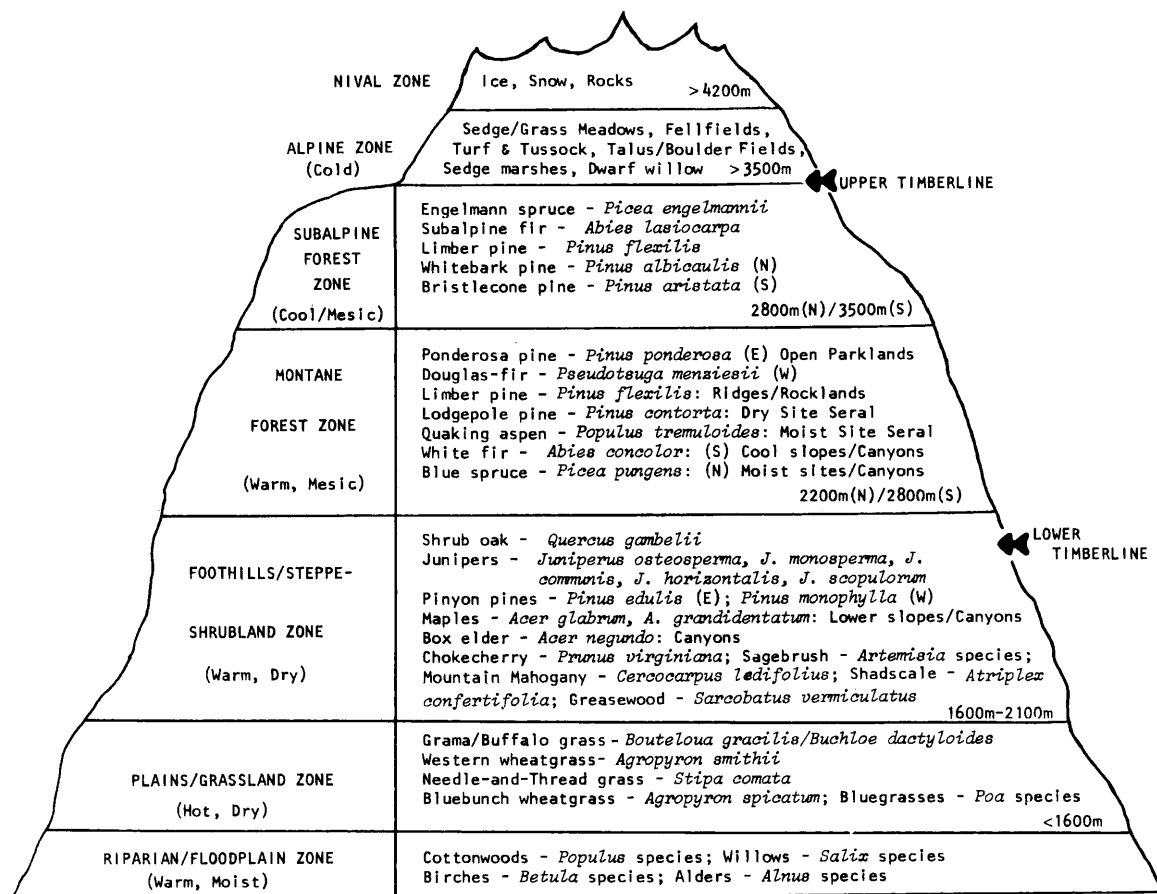


Figure 2.--Vegetation zonation in the Middle Rocky Mountains, typical of western Wyoming and central/southeastern Idaho. Positions of timberline are shown, and major dominants in each zone are listed. After Habeck (1987).

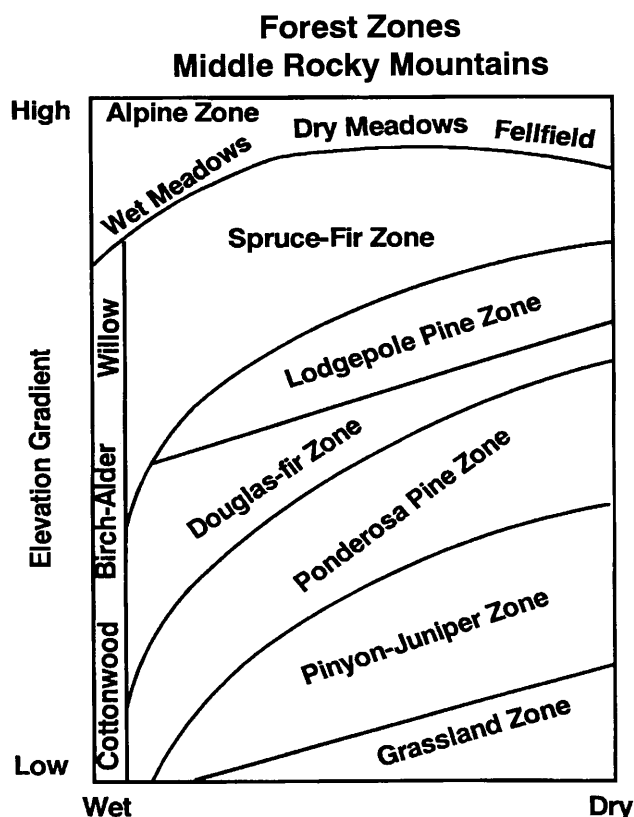


Figure 3.--Ordination diagram of Middle Rocky Mountain forest vegetation zones, including Yellowstone Ecosystem in western Wyoming and southeastern Idaho. Shown are topographic positions and limits of each forest zone employing elevation and moisture gradients as axes. Adapted after Peet (1988).

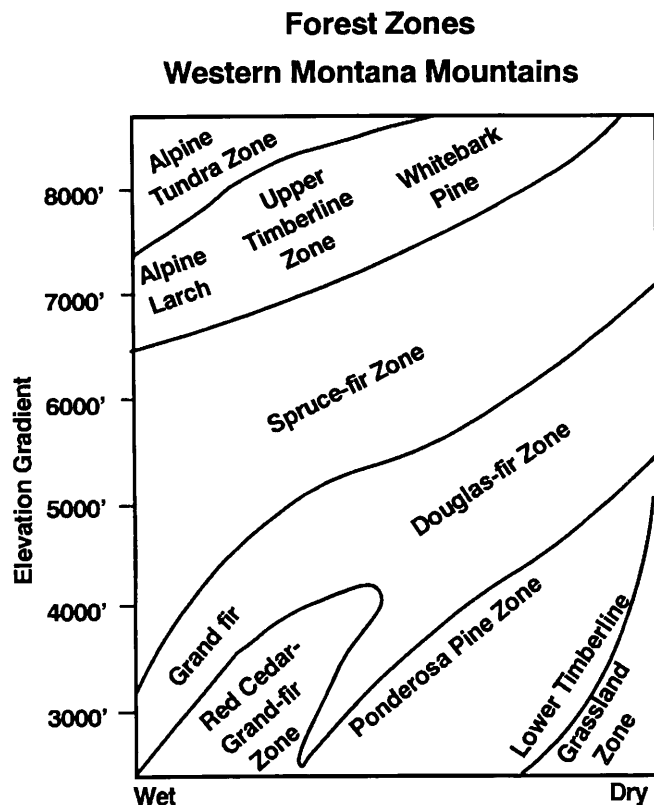


Figure 4.--Ordination diagram of western Montana forest vegetation zones, representing a major part of the Northern Rocky Mountains. Shown are topographic positions and limits of each forest zone employing elevation and moisture gradients as axes. Adapted after Peet (1988).

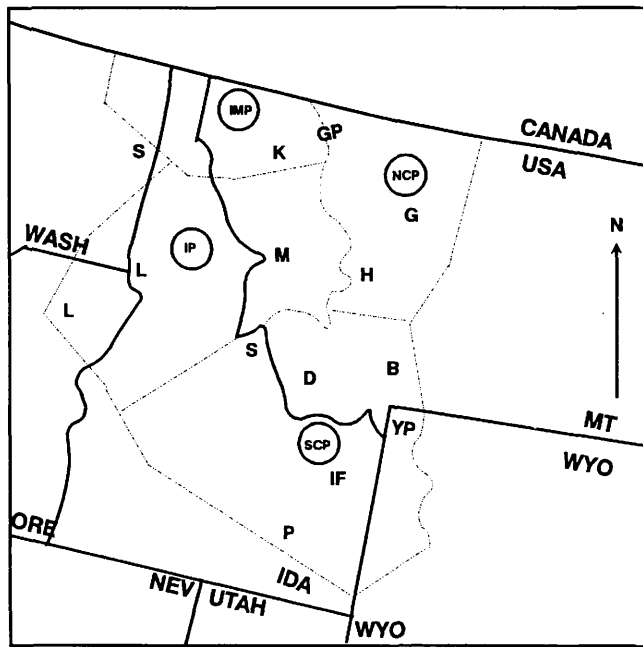


Figure 5.--Phytogeographic provinces (dot-dash lines) within the Northern Rocky Mountains. Shown are the limits of the Southern Continental Province (SCP), Northern Continental Province (NCP), Intermountain Province (IP), and Inland Maritime Province (IMP). Geographic points (letters) in Montana: M = Missoula, H = Helena, G = Great Falls, B = Butte, K = Kalispell, D = Dillon, GP = Glacier park; in Idaho: S = Salmon, L = Lewiston, P = Pocatello, IF = Idaho Falls; in Wyoming: YP = Yellowstone Park; in Oregon: L = La Grande; in Washington: S = Spokane. After Arno and Hammerly (1984) and Habeck (1987).

and Hammerly (1984). Each is differentiated by physiographic, climatic and floristic criteria. They provide a convenient outline of subregions for discussion of the NRM vegetation types that encompass the great gray owl's range. They include the Southern Continental Province (SCP), the Northern Continental Province (NCP), the Intermountain Province (IP), and the Inland Maritime Province (IMP).

Southern Continental Province

The Southern Continental Province includes those mountain ranges found in east-central Idaho and southwestern Montana: Sawtooth Mountains, Lost River Range, Lemhi Range, Beaverhead Range, Gravelly Range, and Madison Range. Contiguous to these, in west-central Wyoming and southeastern Idaho, are the Teton Range, Snake Range, Caribou Range, and Wasatch Range. The montane zones in this province are dry and cool, the low moisture (20-40 cm annually) is a result of a rainshadow partly induced by the Cascade, Blue, and Wallowa Mountains to the west in Oregon, and mountain ranges in Idaho. Forest cover in SCP ranges is generally confined to a relatively narrow zone between lower timberline at 2000 m and upper timberline at 2700 m.

Ponderosa pine is not well represented in the lower forested zones in SCP because of the cold climate and short growing season at lower timberline (Arno and Hammerly 1984). Instead, Douglas-fir is the common dominant tree adjacent to the steppe-grassland zone (*Artemisia/Agropyron-Festuca* dominated). Limber pine found in both upper and lower timberline forests joins Engelmann spruce in defining the upper timberline of dry mountain ranges. In ranges with greater moisture, Engelmann spruce typically combines with subalpine fir and white-bark pine.

Almost all forested portions of western Wyoming, Idaho, and Montana routinely burned before 1900 (Wellner 1970, Habeck and Mutch 1973, Gruell 1985a, 1985b, Bradley *et al.* 1992, Losensky 1993). As the 20th century began, lodgepole pine dominated NRM seral forest communities, covering valleys and slopes to upper timberline (figure 6). Presettlement fires occurred at various intervals. Northern Yellowstone National Park burned every 20-25 years, usually at low intensities, creeping sporadically through the forests, consuming surface litter and seedlings of climax tree species, and maintaining open forest canopies. Near Jackson Hole, south of YNP, fire-free periods lasted 80-100 years, and south and east of these areas fire frequencies may have been even less (Gruell 1980, Steele *et al.* 1983, Despain and Romme 1991).

The Yellowstone Plateau has been forested over the past century with a relatively uniform expanse of lodgepole pine, with scattered-to-dense pockets of white-bark pine. On sites protected from fire for several centuries, old forest stands of subalpine fir and Engelmann spruce prevail (Steele *et al.* 1983, Bradley *et al.* 1992). In the Jackson Hole region historic fires perpetuated lodgepole pine and quaking aspen (*Populus tremuloides*). Much of YNP falls into subalpine fir habitat types (potential climax), but fires have perpetuated lodgepole pine as a major seral dominant in the park (Despain 1990, Despain and Romme 1991). Peet (1988) describes lodgepole pine as the "archetypal post-fire species." Although many lodgepole pine become established immediately after a fire, its serotinous cones shedding abundant seeds, lodgepole pine apparently continues establishing itself over a 30-50 year period or longer. The percentage of cone serotiny among lodgepole pine populations varies in relation to the specific mode of stand establishment and whether recovery follows fire or other types of disturbance, such as blowdown or insect damage (Lotan and Perry 1983). Quaking aspen is well known for its vegetative resprouting after being burned, but the 1988 YNP fires were followed by extensive sexual reproduction of aspen (Kay 1993).

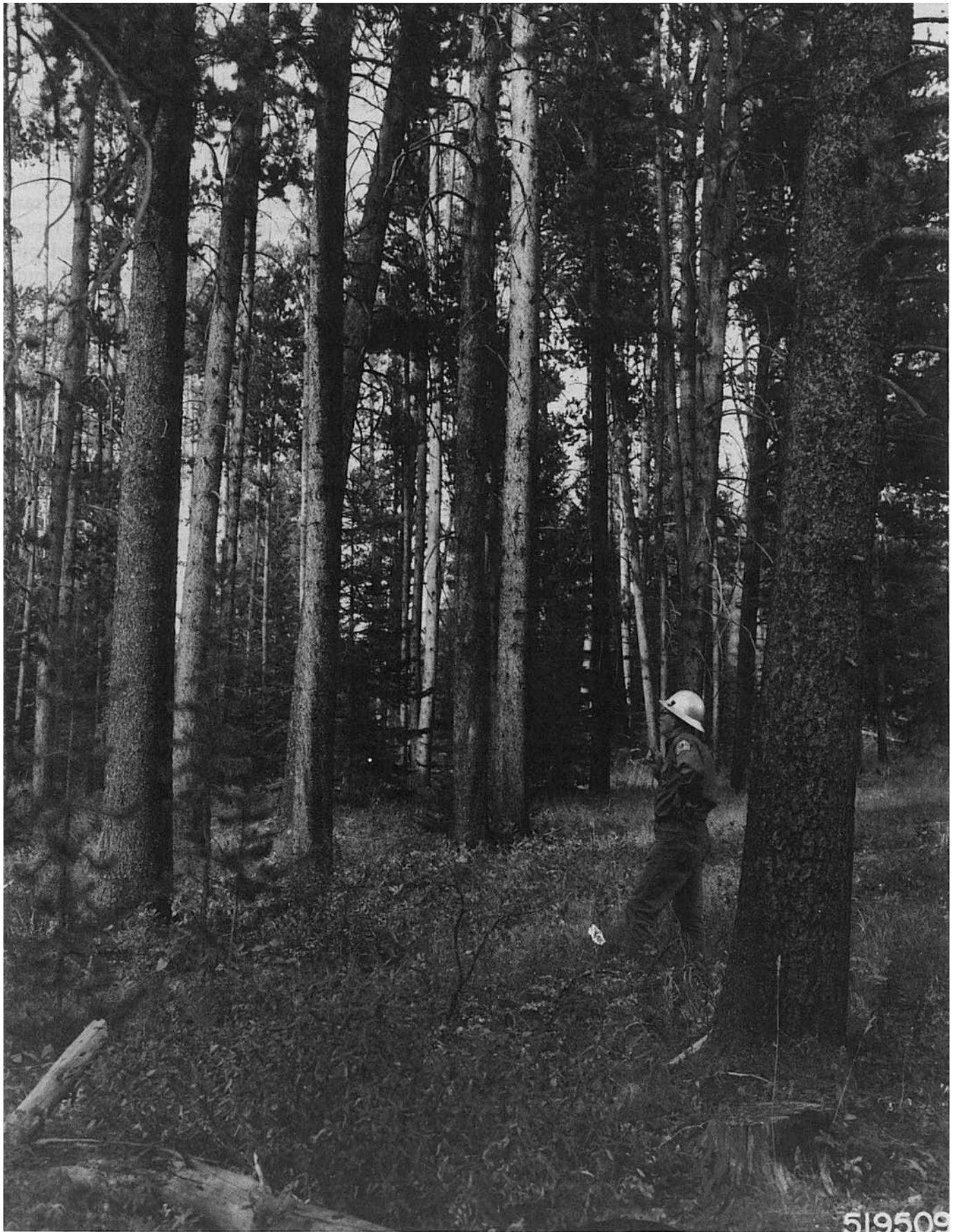


Figure 6.--Old lodgepole pine forest, with *Pinus contorta* and subalpine fir reproduction in understory. Stand located on Main Bear Creek, Gardner District, Gallatin National Forest, Montana, Southern Continental Province (see text). This type of mature lodgepole pine forest community is widespread throughout the Yellowstone Ecosystem in Montana, Wyoming, and Idaho. Photo by Danny On, September 1966, USDA Forest Service photo.

Fire exclusion policies implemented after 1900, climatic changes (cyclic drought), and livestock grazing have all been identified as factors contributing to the successional invasion of conifers into lodgepole pine/steppe grassland community types occupying the montane zones of SCP mountain ranges (Gruell 1980, Arno and Gruell 1983, Habeck 1987, Bradley *et al.* 1992). In 1886, a total of 22 million cattle grazed western North American ranges, and sheep numbered over 15 million in Montana, Idaho and Wyoming at the turn of the century (Stewart 1936).

Before 1900 wildfires regularly killed invading conifer seedlings and saplings. Extensive and intensive livestock grazing reduced fine fuel loadings and altered grass-conifer competition (Bradley *et al.* 1992). After many decades of fire exclusion, upper elevation seral lodgepole pine and Douglas-fir stands usually become invaded by shade-tolerant subalpine fir, or sometimes by Engelmann spruce (Peet 1988). Higher fuel loadings now exist, leading to a greater potential for high intensity fires over much of the Northern Rockies.

The Greater Yellowstone Area (GYA), including parts of SCP in Idaho, harbor several native (endemic) insect species that periodically reach epidemic population levels (Despain 1990, Ammon and Ryan 1991). Western spruce budworm (*Choristoneura occidentalis*) had killed numerous Douglas-fir in YNP stands, and mountain pine beetle (*Dendroctonus ponderosae*) has a long history of widespread killing of white-bark pine and lodgepole pine in this part of the Rockies. Cyclical insect outbreaks, spanning a decade or more, are closely correlated with episodes of drought, and have led to extensive conifer mortality in GYA and elsewhere in the Rocky Mountains. Despain (1990) discusses the possible interactions between mountain pine beetles, mature-sized lodgepole pine, and fire. Insect-killed timber does provide increased fuel, but insect-killed mature pines may be less capable, according to Despain, of supporting rapid-spreading crown fires than are smaller living trees. Without fire the insect-killed forests undergo succession involving the potential climax subalpine fir and/or Engelmann spruce.

Dwarf mistletoe (*Arceuthobium* spp.) infestations also cause a significant build-up of dead, woody fuel on the forest floor and witches'-brooms in the tree canopies, setting the stage for intense wildfires (Crane and Fischer 1986). These latter authors have established a series of "fire groups" for central Idaho that have application elsewhere in the SCP. They have generated a series of post-fire forest successional pathway models for forest habitat types common in central Idaho. Wildlife responses to fire treat-

ments in each "fire group" are also documented by Crane and Fischer (1986) and Bradley *et al.* (1992).

Wind and snow breakage are less common, but nevertheless influential forces acting on SCP forest communities. Tornado-level winds or severe thunderstorm down drafts ("microbursts") can cause extensive areas (100-300 ha) of broken stems and blowdowns of criss-crossed tree stems. If fire does not intervene, post-wind succession is usually rapid, involving only a minimum of compositional change.

According to Steele *et al.* (1983), the eastern Idaho-western Wyoming portion of the SCP experienced intensive early-day logging at lower elevations where timber was most accessible to town sites, homesteads, and mining developments. Usually only high quality timber was selectively taken. Transcontinental railroad construction created a demand for track ties which were taken from tie-sized members of Douglas-fir and lodgepole pine populations occupying lower elevations (Steele *et al.* 1983). This latter type of "tie-hacking" selection left size/age class gaps in forest tree populations which Steele *et al.* (1983) found detectable in their modern forest surveys. Steele *et al.* (1981), discussing central Idaho forests, state that recovery from logging disturbance is very slow, and the "clearcut and burn" techniques used in northern Idaho and western Montana failed as tree regeneration techniques in the more droughty and nutrient-stressed sites found in central Idaho. Modern logging still focuses on the most accessible forest stands. Only the steep, rugged mountain terrain prevents the removal of remnant old forests remaining in SCP mountain ranges. National parks and designated wildernesses in this subregion of the Rockies still support a reasonably complete size and age array of forest types, but even collectively they represent only a restricted acreage (Steele *et al.* 1981).

Unregulated cattle grazing during 1860-1900 (Stewart 1936) impacted substantial portions of SCP. Livestock damage was greatest in parts of the forest where grasslands and meadows interrupt the forest cover. New clearcuts cause localized congregations of cattle, and conifer seedlings are killed by trampling. More importantly, exotic plants are now replacing native grasses and forbs. Since 1900 regulation of livestock grazing has increased, but recovery from past disturbance is slow and of variable success. Wildfires, logging, insect and disease outbreaks, as well as other factors appear to have maintained much of SCP's forest cover in various stages of successional recovery. Very little of the landscape supports mature seral or climax old growth forest (Steele *et al.* 1981, 1983).

Few current studies from SCP specifically cite old-



Figure 7.--Old-growth *Pinus contorta* forest with scattered snags (background), adjacent to "temporary meadow" (foreground) created by clear cutting. This landscape combination of old-growth lodgepole pine forest and contiguous clearcut sites provides suitable nesting and foraging habitats for *Strix nebulosa*. Area located on the Bozeman District, Gallatin National Forest, Montana W. E. Steuerwald, August 1964, USDA Forest Service photo.

growth, perhaps because of the reduced amounts of these forest types. Mehl (1992) provides old-growth descriptions for the Middle Rocky Mountains, including Wyoming. He makes clear that older forests dominated by fire-dependent species, such as mature seral lodgepole pine, or by shade tolerant climax species, such as subalpine fir, are encompassed within current old-growth classifications. Mehl summarizes stand characteristics and attributes that have been used to develop old-growth definitions in the Rocky Mountains, and these definitions are currently being used to inventory remaining old-growth. Of further significance, in relation to the great gray owl's habitat requirements, Mehl points out that as old-growth stands continue to mature in the absence of stand-altering disturbances, canopy gaps are formed following tree death and downfall. Such canopy openings enhance the great gray owl's flight movements through stands where nest sites exist.

Levine's (1992) great gray owl surveys were concentrated in the Wasatch Range in southeastern Idaho, the southern reaches of the Rockies considered within the SCP. This region closely coincides

with the great gray owl's southern distributional limits. The Wasatch Range is exceptionally steep and rugged and represents the western edge of the Rockies (Arno and Hammerly 1984); its peaks reach up to 3600 m. Upper timberline consists of Engelmann spruce, subalpine fir and limber pine, with all of these exhibiting krummholz life forms. Pacific storms bring considerable winter and spring snowfall, which produces frequent snow avalanches that cut through subalpine and montane forest zones.

Gruell (1980) summarized the influence of reduced fire frequency on wildlife habitat in Bridger-Teton N.F., Wyoming, adjacent to Caribou N.F. where lodgepole pine stands now lie between valley floor and 2700 m. He stated that lodgepole pine stands have changed considerably over the past century. Subalpine fir has become a principal component in the understories of lodgepole forests. Subalpine fir has also been invading mature fire-generated Douglas-fir in this part of the SCP.

Levine (1992) noted that the average elevation where great gray owls were found was at 2276 m (range 2194-2378 m on lower to middle north-slope aspects). Forests at this elevation are late seral or

mature mixed stands dominated by lodgepole pine, either unlogged or only partially cut, with 70-90% canopy closure. Owls were not noted in other forest types in this part of the Wasatch Range. All owl locations were adjacent to riparian meadows, other wetlands, or clearcut sites. Figure 7 illustrates the combination of old lodgepole pine forest and a contiguous clearcut site at the northern end of the GYA.

Northern Continental Province

The Northern Continental Province (NCP) includes mountain ranges in central Montana, east of the Continental Divide ("Rocky Mountain Front"): Lewis Range, Big Belt Mountains, Crazy Mountains, Little Belt Mountains, Bear Paw Mountains, and Sweetgrass Hills (figure 5). Great gray owl sightings, including evidence of successful breeding, have been made in the Lewis and Clark N.F. and Deerlodge N.F., both located in NCP. Mature lodgepole pine forests surrounding, or adjacent to natural meadows compose the landscapes where these sightings occurred (Montana Natural Heritage 1993 Database, Bergeron *et al.* 1992). Circumstantial evidence of breeding owls as well as simple observations are recorded over a broad range of NCP.

Valley elevations in NCP are lower than within SCP, and somewhat less arid than SCP. Lower timberline is 1200-1500 m, and continuous forest cover occupies a broader elevational range than in SCP. Ponderosa pine forms the lower timberline in this part of the Montana Rockies. However, ponderosa

pine does not tolerate fluctuating winter temperatures, so, north of Great Falls, it is replaced by combinations of quaking aspen, Douglas-fir, limber pine, and lodgepole pine (Arno and Hammerly 1984).

USDA Forest Service Forest Type #20, Douglas-fir, Type #21, ponderosa pine; and Type #26, lodgepole pine, compose much of the conifer forest cover in NCP (1977). Kuchler's (1964) potential natural vegetation forest types for the same province include K-11 and K-16, ponderosa pine; K-12, *Pseudotsuga*; K-15, *Picea-Abies*; and K-98, *Populus-Salix*. The latter floodplain forest type occupies riparian sites on the Missouri and Yellowstone Rivers. Large expanses of NCP are covered with K-63, *Agropyron-Festuca-Stipa* (Foothills Prairie) and K-64, *Bouteloua-Stipa-Agropyron* (Grama-Needlegrass-Wheatgrass). The montane zones (1500-1800 m) of NCP mountain ranges are dominated by varying mixtures of Douglas-fir and lodgepole pine. The upper zones are codominated by subalpine fir, Engelmann spruce and white-bark pine. Upper timberline occurs between 2300 and 2600 m.

As a part of the effort to implement ecosystem management in the northern Rockies, Losensky (1993) analyzed early forest inventory records and used these records to describe the historic forest vegetation throughout the Forest Service's Northern Region, including NCP. Timber resources came under heavy use soon after gold discovery in the 1860s. Ranching and agricultural development between 1880 and 1900 further reduced forest cover. Else-

Table 1.—Percent of acres, by age classes and forest cover types for Northern Region (R1) National Forest lands, including northern Idaho and western Montana, circa 1900. Data are projections from a historic vegetation map and early-day timber inventories compiled and analyzed by Losensky (1993).

Forest type	Non-stocked acres	Seedlings & saplings 1-40 yr	Pole stands 41-60 yr	Immature stands 61-101 yr	Mature stands 101+ yrs	Potential old forest 121+ yrs
White pine	21%	23%	4%	10%	17%	25%
Ponderosa pine	10	9	4	5	24	48
Larch/	19	24	6	9	17	25
Douglas-fir						
Hemlock/	3	10	13	4	26	44
Grand fir						
Douglas-fir	22	20	7	18	26	7
Engelmann spruce	7	8	2	10	32	41
Lodgepole pine	25	41	9	15	7	3
Redcedar	7	7	1	8	6	71
Cedar/	15	16	17	10	18	24
Grand fir						
Average for all types	17%	23%	6%	12%	17%	25%

where on the Rocky Mountain Front, construction of the Great Northern Railway in 1892 led to the harvesting of significant amounts of timber. Railway construction also triggered a period of increased fires within forests adjacent to the rights-of-way. Losensky's summary of historic forest inventory data (age class per cover type for 1900 data, and volume per cover type for 1930's data; national forest lands only) for northern Idaho and western Montana, are presented in tables 1-2. These data are being used as reference points to assess shifts and alterations that have taken place in the Northern Rocky Mountains over the past 60-100 years (table 3).

Fire played a major role in forest dynamics throughout the East Front of the Montana Rockies; an in-depth analysis of fire ecology east of the Continental Divide is provided by Fischer and Clayton (1983). They established a series of "fire groups" to organize and discuss the ecological role of fire within forest habitat types found in an area that closely matches the geographic extent of the NCP. Some of these groups feature ponderosa pine occupying warm-dry sites as well as warm-moist sites. Similar treatment is given to Douglas-fir habitats on a range of sites. One fire group is assigned to lodgepole pine stands that were historically perpetuated by periodic fires.

Ponderosa pine resists fire well. Even seedlings and saplings of this species can withstand high temperatures generated by surface fires or from the thermal stress associated with hot, dry exposures. On

Table 2.—Percentage area by cover type for USDA Forest Service Northern Region (R1) federal forest lands in northern Idaho and western Montana, based on timber inventories conducted in 1933; data compiled by Losensky (1993).

Forest cover type	Northern Idaho forests	Western Montana Forests
Western white pine	22.4	2.0
Ponderosa pine	13.0	13.7
Larch/Douglas-fir	9.1	17.3
Hemlock/grand fir	1.7	0.1
Douglas-fir	5.9	5.1
Engelmann spruce	2.1	2.3
Lodgepole pine	8.1	13.4
Western redcedar	0.4	0.1
Redcedar/grand fir	1.8	Trace
Spruce/subalpine fir	10.7	12.9
Noncommercial forests	7.3	15.5
Nonforest	17.5	17.6
Totals	100.0	100.0

Table 3.—Changes in historic land cover and vegetation type groups in USDA Forest Service's Northern Region (R1) occupying all federal lands in Idaho, Montana, and portions of the Dakotas, based on a draft assessment of data originating from a 1933 historic vegetation map (Losensky 1993) and a 1993 NDVI (Normalized Difference Vegetation Index) vegetation index map displaying existing vegetation cover classes (Hann *et al.* 1993). Vegetation types created by agricultural tilling and woodlots added as new 1993 categories. MM = millions of acres.

Land cover/ vegetation type groups	Historic vegetation acres (MM) (1933)	NDVI vegetation acres (MM) (1993)
Lodgepole pine	8.5	11.5
Spruce/subalpine fir	2.3	1.7
Douglas fir	7.7	9.3
Western larch/Douglas-fir	3.2	1.1
Western whitepine	3.0	0.2
Ponderosa pine forest	6.5	12.5
Ponderosa pine savanna	2.8	0.3
Douglas-fir savanna	0.6	1.5
Wheatgrass/fescue	22.2	1.1
Sagebrush/grassland	3.4	10.1
Mixed-grass prairie	83.7	53.6
Tall-grass prairie	22.7	0.6
Hardwood riparian	7.0	2.1
Oak savanna	0.9	0.1
Alpine zone	0.1	0.4
Woodlots	0.0	2.1
Agriculture crops	0.0	69.8
Water	0.6	1.0

dry sites historic fires maintained open canopies with grassland understories; crown fires were rare. On more moist sites, however, ponderosa pine formed two-storied canopies which were susceptible to higher intensity crown fires. Douglas-fir is only moderately fire-resistant, and Douglas-fir reproduction is very vulnerable to even low-intensity surface fires. When individual Douglas-firs achieve larger sizes, they develop thick, protective bark which allows them to survive underburning. During the past half century, dense sapling thickets have developed, forming ladder fuels that now endanger the crowns of old-growth Douglas-fir (Habeck 1990).

Generally lodgepole pine's relatively thin bark makes this species susceptible to lethal cambium heating. Individual, mature lodgepole pines, however, do display moderate resistance to surface fires. Throughout NCP lodgepole pine displays cone serotiny (resin-sealed scales), which assures a continued population even in the presence of frequent wildfires. Some lodgepole stands that became established after fires are so dense they are susceptible to

stagnation, snow breakage, windthrow, disease and insect infestations, all of which combine to set the stage for a high-intensity, stand-replacing fire (Lotan and Perry 1983).

Up to the mid-1970s about 50% of forested lands in Montana had been logged (Pfister *et al.* 1977). The percentage may be even higher in the NCP because of extensive historic use of timber for mining operations and railway construction between 1870 and 1920. Some forested tracts in the vicinity of Butte (Highland Mountains mining district), for example, were logged nearly to alpine timberline. Furthermore, modern fire suppression (post-1900) led to extensive forest encroachment into mountain grasslands (Arno and Gruell 1983, 1986).

Studies of the historic importance of fire on forest vegetation in the Deerlodge National Forest (Habeck 1992) have shown how the conifer invasion sequence progresses. Fire-maintained, open-canopied old Douglas-fir communities have become densely stocked and grassland species have declined from the forest understories. The 400+ year-old Douglas-firs, completely surrounded by the invading conifer reproduction, are now in danger of being killed in the next wildfire. As a consequence, loss of remaining old Douglas-fir forest is possible. A pilot landscape analysis was recently completed in a portion of NCP, aimed at integrated resource planning (O'Hara *et al.* 1993). The report discussed the historical importance of fire in the mixed conifer forests (subalpine fir, lodgepole pine and Douglas-fir) located in the NCP (Elkhorns Landscape Analysis Area, Helena N.F.) This analysis further confirmed the declining extent of mountain meadow grasslands in NCP as a result of modern fire control. The potential loss of old coniferous forests as well as reduced grasslands has direct implication to the maintenance of great gray owl's nesting and foraging habitats in this Rocky Mountain subregion.

Intermountain Province

The Intermountain Province (IP) includes northeastern Oregon, central Idaho and west-central Montana (figure 5). The Blue and Wallowa Mountains are found in northeastern Oregon; the Clearwater Mountains, Salmon River Mountains, and the western edge of the Bitterroot Mountains occur in Idaho; the Sapphire Range, Anaconda-Pintler Range, Flint Creek Range, and the southern extensions of the Mission and Swan Ranges are located in westcentral Montana.

Bull and Henjum (1990) documented numerous great gray owl breeding sites in northeastern Oregon conifer forests. In this region great gray owls com-

monly use abandoned raptor stick nests in mature western larch (*Larix occidentalis*), with some located in Douglas-fir. Mature ponderosa pine and Douglas-fir are often used as perch trees within nearby meadows and clearcuts serving as foraging sites. Atkinson (1989) reported breeding great gray owls on the Payette N.F. in central Idaho. His studies showed that mature, mixed conifer forests, dominated by Douglas-fir and/or grand fir, exhibiting high snag densities, and bordering natural meadows or small clearcuts, were commonly associated with his great gray owl sightings.

Great gray owl sightings, plus direct and indirect evidence of breeding great gray owls have been reported for an assortment of low to mid-elevation montane forests in western and northwestern Montana (Montana Natural Heritage Program Database 1993). In western Montana mature lodgepole pine and old-growth western larch forests (figure 8) are commonly associated with great gray owl occurrences. The presence of late seral stands dominated by fire-dependent lodgepole pine and western larch in montane forests (1200-1800 m) in the IP is closely correlated with historic wildfire (Arno 1980, Habeck 1987, 1990). Repeated (50-100 year intervals) fires maintained a landscape fire mosaic wherein the disturbance-dependent lodgepole pine and western larch were major components. Modern fire suppression and logging throughout IP shifted the fire mosaic from presettlement conditions and changed the environment of the great gray owl.

Intermountain Ranges are partially influenced by moist maritime air masses that pass nearby, but they receive less total moisture than does the Inland Maritime Province (IMP) to the north; summer months are typically dry. The more severe continental climate that features temperature extremes, plus cold, dry winters, and stressful chinook winds is not commonly expressed in the IP subregion (Arno and Hammerly 1984, Habeck 1987).

The montane forests of IP serving as owl habitat fall within Forest Service (1977) Type #20, Douglas-fir; Type #21, ponderosa pine; Type #26, lodgepole pine; Type #25, western larch; and Type #23, subalpine fir/Engelmann spruce. Kuchler (1964) forest types include K-11, ponderosa pine; K-12, Douglas-fir; K-14, grand fir/Douglas-fir; and K-15, Engelmann spruce/subalpine fir. Bailey's (1978) Ecoregions represented in IP include M3111, M3112 and 3120 (bunchgrass/wheatgrass-needlegrass Types), and M2112 (cedar/hemlock/Douglas-fir).

Intermountain province forest habitat type classifications by Pfister *et al.* (1977), Mueggler and Stewart (1980), Cooper *et al.* (1991), Steele and Geier-



Figure 8.--Old-growth *Larix occidentalis* forest, with Douglas-fir and subalpine fir in understory. Note broken-topped snags and mistletoe-infected "witch's-brooms," both of which may serve as *Strix nebulosa* nest sites. Open, wet meadows, filling glaciated depressions occur on nearby sites. Great gray owl sightings have been recorded in this area. Condon District, Flathead National Forest, Montana, within the Intermountain Province. Danny On, October 1965, USDA Forest Service photo.

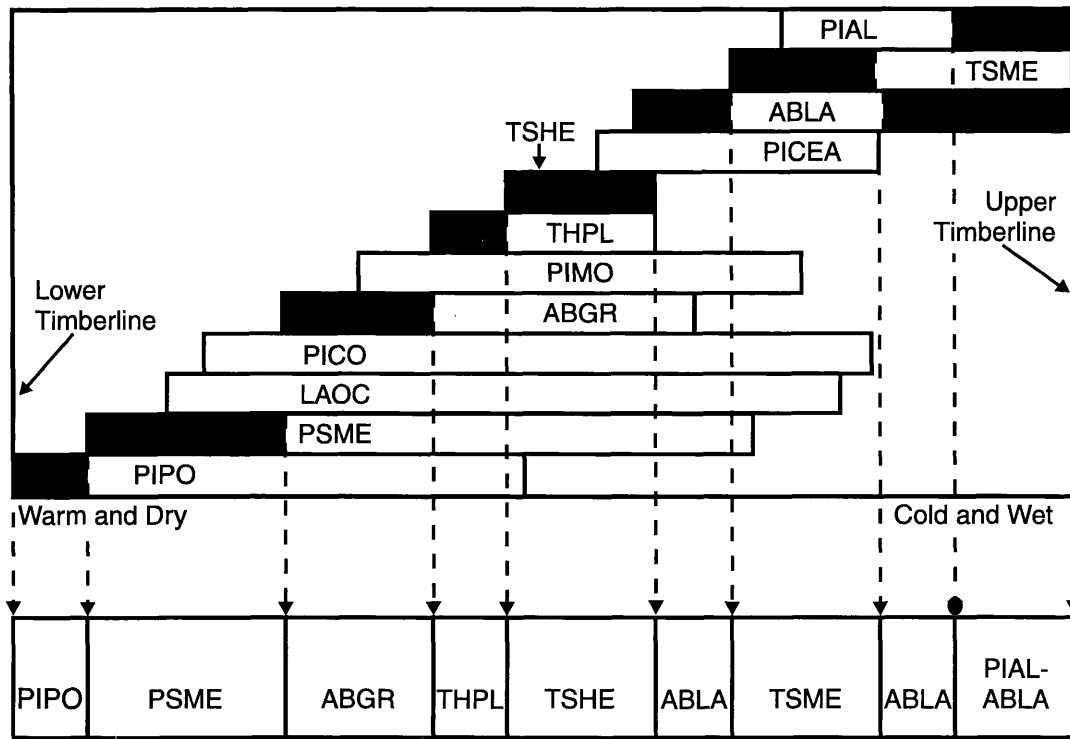


Figure 9.--Schematic distribution of conifers in Montana portion of Rocky Mountains, arranged vertically, showing usual order in which trees are encountered with increasing elevation. Horizontal bars designate upper and lower limits of each tree species compared to climatic gradient. Black areas represent portions of elevational range where each shade-tolerant species exhibits climax characteristics; the climax species are identified on the lower graph. PIPO = ponderosa pine, PSME = Douglas-fir, LAOC = *Larix occidentalis*, PICO = *Pinus contorta*, ABGR = *Abies grandis*, PIMO = *Pinum monticola*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, PICEA = *Picea engelmannii*, ABLA = *Abies lasiocarpa*, TSME = *Tsuga mertensiana*, PIAL = *Pinus albicaulis*. Adapted after Green et al. (1985).

Hayes (1992), provide summarized information on vegetation distribution patterns (zonations). An example is shown in figure 9. Vegetation cover occurring in northeastern Oregon and southeastern Washington are reviewed by Franklin and Dyrness (1973), and Hall (1973, 1980b). Johnson and Clausnitzer (1992) have published a revised classification of the vegetation in the Blue and Ochoco Mountains in Oregon. The role of fire in IP forest types has been addressed in Hall (1980a), Crane and Fischer (1986), Fischer and Bradley (1987), and Walstad *et al.* (1990).

The mountain ranges in IP have well-defined lower and upper timberlines. In pre-settlement times the lower timberline (800-1500 m) was impacted by frequent (10-30 year intervals), low intensity fires ignited by lightning and native Americans (Barrett and Arno 1982, Gruell 1983, 1985a, 1985b, Habeck 1990). Pre-1900 burning perpetuated grasslands and ponderosa pine savannas. This seems true even on mesic-moist sites where Douglas-fir and/or grand fir are the potential climax dominants. After the horse was acquired by American Indians occupying the northern Rockies (1730's), extensive Indian burning for pasture production is likely to have converted mesic montane forests to savanna or grasslands (Habeck 1990). Open park-like stands of old Douglas-fir and ponderosa pine forests were per-

petuated by fires throughout IP montane zones (Habeck 1987).

Above the ponderosa pine zone lies the Douglas-fir/grand fir forest zone, extending from 1200-1800 m. Within this zone western larch often prevailed, historically, as a major seral species. This fire-dependent tree often lives 400-500 years, and may achieve diameters of 1.0-1.5 m, and heights over 40 m.

Within the IP subalpine fir dominates the zone between 1800 m and treeline at 2700 m; lodgepole pine extends into this zone and mixes with white-bark pine and Engelmann spruce. Historic wildfires also occurred in this higher forest zone, but intervals between fires were usually more than 100 years, not uncommonly 200-300 years. Some grassland communities dominated by *Agropyron spicatum*, *Festuca scabrella* and *F. idahoensis*, occurred within the IP's montane and subalpine forests. Subalpine meadows dominated by green fescue (*Festuca viridula*) and surrounded by white-bark pine were very common at timberline (2700 m) in northeastern Oregon and west-central Idaho before settlement. Intensive sheep grazing in the early 1900s severely damaged these meadow habitats (Arno and Hammerly 1984); they are now recovering following reduced grazing pressure.

Perhaps the most widespread loss on IP land-

scapes, attributable to logging and post-1900 fire suppression, has been the disappearance of ponderosa pine woodlands in the lower montane zones. As elsewhere in the Northern Rockies, centers of mining activity were the first areas to be heavily logged (Cooper *et al.* 1991). The wood needs for mine timbers, railroad ties, fuel, and building material, as well as clearing for agriculture led to massive forest clearing in IP.

Hutchinson and Winters (1942) compiled a forest resources inventory for northern Idaho that emphasized the heavy removal of western white pine a half century ago. The allowable annual cut of western white pine in 1941 had been established to be 140 million board feet (mm db ft), reflecting a level of white pine harvest that fit a system of sustain-yield forestry. However, they reported that during an earlier four year span (1935-38), western white pine was subjected to an average annual cut of 351 mm db ft! Other conifer species were essentially ignored during this period. This disproportionate cutting of old-growth white pine in northern Idaho strongly impacted this area's forest landscape including the wildlife it supported. The post-World War II building boom accelerated timber harvesting further, especially in the lower and montane zones. On the Clearwater N. F. in Idaho, for example, the annual cut expanded from a high of 18.0 mm bd ft prior to 1946, to 116 mm bd ft by 1959, with similar jumps in other regional forests. Much of this log removal focused on harvesting old growth. See Losensky's (1993) historic forest inventory data, tables 1 and 2).

The belief that the lower montane forests in the Northern Rockies have been changed the most by modern man's influence has also been expressed by scientists contributing to the 1993 Forest Ecosystem Health Assessment Report (Jensen and Bourgeron 1993). Elsewhere, in other IP fire-adapted ecosystems such as in central Idaho and northeastern Oregon, reduced natural fire, increased selective logging of mature late-seral trees, continued livestock grazing, and cyclic drought have collectively disrupted natural forest functions.

Present-day influences have led to epidemic levels of insect infestations (Carlson and McCaughey 1982, McCune 1983) followed by unnatural, high-intensity wildfires degrading overall ecosystem health (Mutch *et al.* 1993). These circumstances have implications to avian habitat management and will require innovative silvicultural strategies to reverse the present trends. Of particular importance is returning a more natural role to fire. In the Blue Mountains, for example, Forest Service resource managers are prescribe burning about 1800-2400 ha per

year, but they realize that 10 times this area requires fire treatment annually to achieve management objectives (Mutch 1992).

Inland Maritime Province

The Inland Maritime Province (IMP) spans northeastern Washington, northern Idaho and northwestern Montana (figure 5). This NRM subregion includes the Selkirk Mountains of northern Idaho, plus adjacent parts of Washington, the northern Bitterroot Range, and Cabinet Mountains, the Whitefish Range, the northern Swan Range and the west slope of the Continental Divide in Glacier National Park. As the province's name implies, IMP is relatively moist. Pacific coastal air masses follow well-defined storm tracks which bring abundant moisture to all elevations. The lowest valleys receive more than 50 cm annually, although some localized rainshadows may record 40 cm or less. Warm, dry weather usually prevails during July and August.

Occurrences of breeding great gray owls are recorded by Bergeron *et al.* (1992) for the Montana portion of IMP. Sighting reports on file at the Forest Service's Northern Region Office place the great gray owl in mature western larch, Douglas-fir and lodgepole pine forest communities within the Swan Valley and the Coram Experimental Forest located on the Flathead N. F. Great gray owl breeding in these localities is only suspected. Large expanses of the Swan Valley consist of a mosaic of old-growth forest, wet marshes and grassy meadows, as well as extensive logged-over units, while the Coram Experimental Forest is contiguous to clear-cut tracts. Great gray owls have also been reported for the Kootenai N.F. (MT), Clearwater N.F. (ID), and Idaho Panhandle N.F. (ID), all of which occur within the maritime climatic province (Idaho Conservation Data Center, Boise, ID). These have included sightings of one adult and one young great gray owl in a riparian western red-cedar forest along the Upper Priest River, Bonner County, ID.

Major Forest Service forest types present in IMP include Type #21, ponderosa pine; Type #22 western white pine; Type #25 western larch; and Type #26, lodgepole pine (1977). Kuchler (1964) potential natural vegetation types include: K-11, ponderosa pine, K-12, Douglas-fir, K-13, cedar-hemlock-pine, K-15, spruce-fir. Within those parts of the IMP supporting western white pine forests, a major biotic influence for the past century has been white pine blister rust (*Cronartium ribicola*). Although western white pine is a fire-dependent seral species, the mortality caused by blister rust no doubt altered natural fire cycles and average fire intensities

throughout IMP's montane zones.

Reduced summer moisture in IMP sets the stage for wildfire. Historic fires are believed to have perpetuated certain xeric vegetation types in climatically moist parts of IMP. Typically, the forest zones contain combinations of the following dominants, ranked from highest to lowest drought resistance (Minore 1979): ponderosa pine, lodgepole pine, Douglas-fir, Engelmann spruce, grand fir, western larch, subalpine fir, western-red cedar, pacific-yew (*Taxus brevifolia*), western white pine, western hemlock, and mountain hemlock (*Tsuga mertensiana*).

Precipitation increases with elevation, often reaching and exceeding 200 cm annually; a large portion (75-85%) of this annual moisture falls as snow between September and March. Spruce-fir forests are developed on the higher IMP mountain slopes, while white-bark pine is locally abundant on warm aspects that experience some mid-summer moisture shortages. Although mountain hemlock joins subalpine fir, forming closed-canopy forests on the Montana-Idaho state line, this hemlock is very intolerant of summer drought and heat as well as severe continental winters (Habeck 1987). Upper timberline develops at 2000-2300 m and features krummholtz subalpine fir, white-bark pine, and partly wind-shaped alpine larch (*Larix lyallii*). White-bark pine, a five-needled pine like western white pine and limber pine, has shown significant recent reductions in its abundance throughout NRM due to white pine blister rust epidemics of mountain pine beetle (*Dendroctonus ponderosae*) (Arno and Hoff 1989, Hoff 1992, Keane and Arno 1993).

Fires occur at much lower frequencies (100-200 yr intervals) in this moist geographic subregion. When fires do occur, however, they are often high-intensity, stand replacing fires. The high intensity is due to greater organic fuel accumulations. When the right combination of midsummer weather occurs (lightning, low humidity, wind, dry ground fuels, etc), IMP forests experience wildfires capable of removing all aboveground plant cover (Habeck and Mutch 1973). Western larch, lodgepole pine and/or western white pine are important post-fire seral species which form dense, even-aged pioneer stands. Examples of short-interval "double" or "triple" burns have historically occurred in parts of IMP, and forest recovery may be retarded for many decades.

The deep snow accumulations in IMP mountains cause frequent snow avalanches. Tons of flowing snow and fierce winds smash and mangle the vegetation in the snow track. Snow slide chutes often support vegetation dominated by such woody dicots as mountain alder (*Alnus sinuata*), service-berry

(*Amelanchier alnifolia*), mountain maple (*Acer glabrum*), black cottonwood (*Populus trichocarpa*) and quaking aspen.

Historical Changes in Rocky Mountain Vegetation

Over the past century, the Northern Rocky Mountain forest cover that has served as forest owl habitat has undergone significant change in structure and composition. Popular news media have reported on the diminishing conifer timber volume available for harvest throughout the Rocky Mountains, focusing especially on the current scarcity of old-growth forests, lost after a century of logging.

The descriptions and discussions of each Rocky Mountain phytogeographic province included brief assessment of the ecological roles of climate, fire, logging, and grazing in terms of their impact on early-day and present-day cover. A review of pertinent forest ecology literature for western North America clearly identifies several anthropogenic influences as critical in altering forest and grassland landscape patterns. Native American burning significantly supplemented natural lightning ignitions in establishing fire regimes that altered forest cover types over much of the northern Rockies. Throughout much of the NRM, the lodgepole pine cover type was perpetuated by pre-1900 fires. Lodgepole pine communities occupy a wide range of elevations, and in association with clearcuts or mountain meadows, are often identified as important great gray owl habitat throughout the Rockies. Historic, high-intensity, stand-replacing fires in many cases created even-aged stands but also generated landscapes that prominently displayed a heterogeneous mosaic of lodgepole pine communities of multiple ages (Clements 1910, Lotan *et al.* 1985).

In some parts of its Rocky Mountain range, lodgepole pine appears to function as a climax species, forming communities with several age classes. In the GYA (parts of Idaho, Wyoming, and Montana), fire-free intervals in some lodgepole pine stands historically spanned several centuries (Romme 1980, 1982). Further north, in western Montana and the Glacier Park Ecosystem, lodgepole pine forests were originally subject to stand-replacing fires at intervals of 50-100 years. Brown (1975) provided a graphic interpretation (figure 10) of the complexity of interactions between lodgepole pine community dynamics and fire cycles. In close physical association with many lodgepole pine-dominated stands were groves of fire-dependent quaking aspen that form distinct communities.

Ponderosa pine, a widely distributed forest species in the Northern Rockies, occupies warm, dry lower timberline forest zones that in pre-settlement times frequently burned. These fires perpetuated ponderosa pine savanna/grassland communities with old-growth forest structure. When observed by Leiberg (1899), portions of western Montana mountain ranges displayed a fire-generated ponderosa pine-dominated zone extending from valley bottom to the spruce-fir zone spanning the entire Douglas-fir zone. Such observations suggest that frequent fires maintained potential mesic Douglas-fir types as pine savanna and bunchgrass communities (Habeck 1990). In the more moist mountains of northern Idaho, northeastern Oregon and northwestern Montana, western larch and western white pine serve as major post-fire seral dominants. Western larch and western white pine are relatively long-lived with fire intervals of a century or longer. These two species formed expansive old-growth forests that became the targets of early logging activity (Hutchinson and Winters 1942).

Beginning in the late 1800s, logging removed large expanses of the most accessible montane-zone timber throughout the area designated as the Northern Rockies. The demand for railroad ties, mine timbers, home construction, fuel, and

other uses associated with frontier development during the 1870-1900 period, led to the extensive removal of timber cover and disruption to the original landscape mosaic. Mineral prospecting in western Montana and northern Idaho sometimes involved wholesale burning of the forest simply to expose bedrock. Clearing lands by logging and burning was also done by pioneer farmers, ranchers, and other homesteaders. Sheep and cattle grazing enterprises started by using natural mountain grasslands and alpine meadows; such grazing soon expanded into logged and burned timberlands throughout the middle and northern NRM. Logged and heavily grazed lands were invaded by exotic plants (Losensky 1987, Tyser and Key 1988, Rice *et al.* 1992). The exotic plant species further altered the structures and compositions of native grasslands, meadows, range lands, and even clearcut forest habitats, all of which, in their original condition supported rodent populations used by forest owls.

An analysis of USDA Forest Service timber inventory data dating back to the 1930s (Losensky 1993) provides an opportunity to make a tentative comparison of early-day vegetation cover values with similar modern data compiled from LANDSAT photo interpretations (NDVI map = Normalized Difference Vegetation Index map; Hann *et al.* 1993).

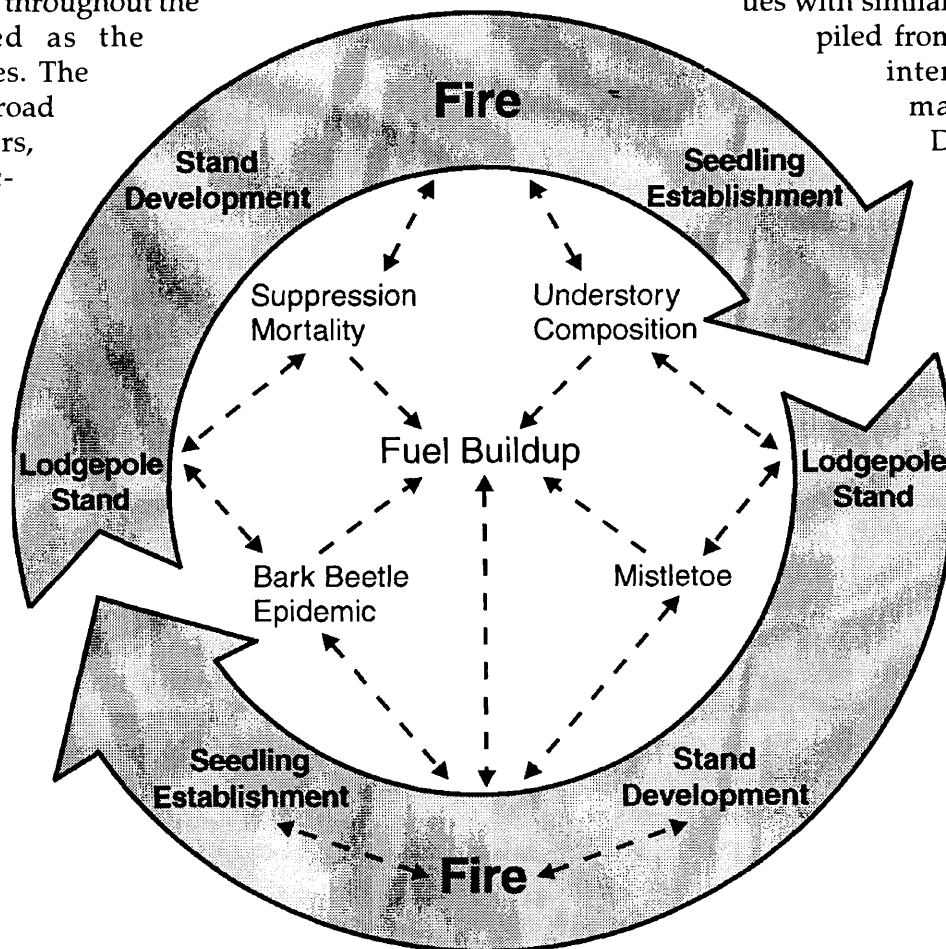


Figure 10.--Typical *Pinus contorta* fire cycle showing interactions between fire and various biotic influences in the northern Rocky Mountains. After Brown (1975).

This comparison allows a coarse scale assessment of historical changes over a 72.5 million ha portion of the Rocky Mountains (USDA Forest Service, Northern Region National Forests and contiguous lands of all ownerships). Table 3 demonstrates that some forest types have been greatly reduced in acreage over the past six decades, though some have increased. This tabulation, however, does not reveal the fact that many of the earlier acres supported old growth. Ponderosa pine savanna, western white pine, and grasslands have been reduced significantly throughout the northern Rocky Mountain region, while sagebrush and agricultural cropland cover types have expanded. Furthermore, alterations in native vegetation and natural ecosystem processes (fire and succession) in the Rocky Mountains have contributed to insect, fungi and disease impacts on the ecosystems of this region (Monnig and Byler 1992, Mutch *et al.* 1993).

OREGON CASCADES AND CALIFORNIA SIERRA NEVADA MOUNTAINS

Introduction

Range maps published by Johnsgard (1988) and Forsman and Bull (1989) describe the great gray owl's range as including the Cascades in Washington and Oregon, southward into the Sierra Nevada Mountains of central California. Specific studies by Goggans and Platt (1992) place breeding populations of *Strix nebulosa* in the central-western Oregon Cascades (Willamette National Forest). Similar studies in the south-central Cascade Range owl studies have been reported by Forsman and Bryan (1984), Bryan and Wise (1985), Bryan and Forsman (1987), and Wise and Lightly (1988), all of which have been centered east of Crater Lake National Park. The volcanic Cascade Range in southern Oregon becomes interrupted by the Klamath River Valley near the Oregon-California border. North of this gap in the Cascades, the mountains are covered with dense montane and subalpine forests adapted to moist conditions (Arno and Hammerly 1984). Southward from the Klamath River, the Cascades display more open-canopied montane forests, adapted to a drier climate. Within northern and northeastern California, the Cascades merge into the granitic Sierra Nevada Range. Our understanding of great gray owls in central California's mixed conifer forests is mostly the result of studies conducted by Winter (1986). He discovered that great gray owl concentrations were greatest in the Yosemite Ecosystem, which includes Yosemite National Park plus the adjoining

Stanislaus, Inyo, and Sierra National Forests.

All along the crest of the northern and southern Cascades, numerous volcanic peaks and cones rise above the forested mountain slopes. Timberlines and alpine habitats are present at the highest elevations along the crest (3700-4200 m). The north Cascades exhibit a distinct maritime climate with precipitation reaching or exceeding 250 cm annually. Southward the maritime influence diminishes with dry summers (July-August) common in the southern Cascade Range, although winter snow depths are still considerable (13 meters on some mountain peaks). Throughout the Cascade and Sierra Nevada mountain range systems, the eastern slopes lie within a conspicuous rain shadow zone. Thus, while the west slopes display dense stands of Douglas-fir and western hemlock supported by the constant supply of moisture, the dry, warm, sunny east slopes support savanna communities dominated by ponderosa pine.

Subalpine fir, according to Arno and Hammerly (1984), becomes less common at timberline in the southern Cascades, and very scarce in northern California. Perhaps it is less capable of withstanding the dry summer conditions prevailing in the Sierra Nevada. In southern Oregon pacific silver fir (*Abies amabilis*) is replaced by California red fir (*Abies magnifica*). In California red fir may reach upper timberline but is less common than mountain hemlock or white-bark pine at the highest elevations. Dry summers and soils derived from volcanic rocks (including pumice) in the southern Cascades create circumstances where moist mountain meadows become less common. The dry soils with reduced fertility support only sparse vegetation in pumice flats ecosystems (Franklin and Dryness 1973, Arno and Hammerly 1984, Volland 1985).

Fire has been a major influence throughout Pacific Northwest (PNW) forests, shaping the landscape's vegetative cover for thousands of years (Agee 1990, Walstad *et al.* 1990). Modern fire suppression has reduced the acreage burned by free-ranging wildfires, which has changed in the forest mosaic, creating more uniform landscapes and higher fuel loadings all across the Cascade Mountains. The ponderosa pine forests in the Cascades historically experienced frequent, low-intensity fires that formed a mosaic of different-aged patches. Fire exclusion has led to major disruptions in ponderosa pine communities, creating stagnated, two-story stands with ladder fuels that threaten the surviving, remnant old-growth pines (Agee 1990).

The Sierra Nevada is a fault-block granitic mountain range that extends over 600 km north-to-south

from the Oregon Cascades. The Sierra Nevada crest (over 3050 m) is off-centered to the east, with the west slope a gradual incline (Arno and Hammerly 1984, Barbour 1988). The west slope receives ample, dependable moisture from the Pacific, except during the dry summer months. Yosemite National Park's montane forest zone receives 100-125 cm annual precipitation. Timberline and alpine zones receive even more, mostly as snowfall. Great gray owl habitat in the Sierra Nevada consists of mixed-conifer forests found between 1200 and 2450 m (Verner 1980, Winter 1982, 1986). Meadows and forests with abundant large snags appear to be important.

The forest vegetation known to be associated with the great gray owl in Oregon's Cascade Range and California's Cascade/Sierra-Nevada Mountains will be discussed below. The conservation assessment prepared for the California spotted owl (Verner *et al.* 1992) includes detailed reviews of the history of California's central Sierra-Nevada mixed-conifer forest types, and should be consulted.

Central-Western And Southcentral Oregon Cascades

Central-Western Cascade Range

The central-western Cascade Range, which includes the Willamette National Forest east of Eugene, Oregon, occupies the central portion of the Western Cascade physiographic province as described by Franklin and Dryness (1973) occupying the montane forest zone between the Willamette Valley and the High Cascades. It is in this geographic area that Goggans and Platt (1992) made their breeding-season observations of great gray owls. Also, it coincides with the mountain landscape (vicinity of the H.J. Andrews Experimental Forest) where Morrison and Swanson (1990) provided a detailed analysis of fire history and vegetation patterns. The lower west slopes (300-1050 m) fall within Kuchler's (1964) potential vegetation Type K-2, western red-cedar/western hemlock/Douglas-fir, while the mid-to upper west slopes (1050-1550 m), are included in Type K-3 where Pacific silver fir-Douglas-fir prevail. Kuchler's Type K-4, subalpine fir-mountain hemlock occupies the Cascade Crest.

Within Type K-2 ("western hemlock zone"), the principal seral species is Douglas-fir, with western white pine, incense-cedar (*Libocedrus decurrens*) and sugar pine (*Pinus lambertiana*) present as occasional seral species (Franklin and Dryness 1973, Morrison and Swanson 1990). Western red-cedar, a tolerant climax species, codominates with western hemlock. Western red-cedar may initially appear with Dou-

glas-fir immediately after fire disturbance or invade gradually over a century following a burn. In Type K-3 ("Pacific silver fir zone"), Pacific silver fir is the climax dominant, with western hemlock and western red-cedar joining as minor climax associates. After logging or fire disturbance in the silver fir zone, Douglas-fir and/or noble fir (*Abies procera*) are the most common seral species. Western white pine is a minor seral species within this higher west slope forest zone.

Forest cover in the west-central Cascade Range is essentially continuous with occasional interruptions by talus slides, rock outcrops, snow avalanche tracks, some dry and wet meadows, and bogs. Actually, according to Goggans and Platt (1992), few natural openings existed previous to modern logging. Morrison and Swanson (1990) determined that their study areas experienced natural fire intervals from 95 years (lower elevations) to 149 years (cooler, moist sites); the latter sites generally experienced stand-replacing burns, the former sites, fires of lower severity. Between 1800 and 1900 fires created a complex mosaic of stands or forest patches, mostly less than 10 ha in size. Fire suppression has operated effectively since 1900.

Great gray owl roosting and nesting habitat in the west-central Cascades features remnant old-growth Douglas-fir. Owl nests were reported by Goggans and Platt (1992) in broken topped, dead Douglas-fir trees, 90-128 cm dbh, all on west-facing slopes. Natural meadow communities are uncommon in the owl sighting areas. Logging activity, however, had occurred within 200 m of all nests. These investigators believe that timber harvesting created "temporary meadows" with hunting perches (tree stumps and snags) suitable for the great gray owls (Miller 1991).

Southcentral Cascade Range

The southcentral Cascade Range (figure 11) falls primarily within Franklin and Dryness's (1973) Basin and Range physiographic province. The area is characterized by fault-block mountains enclosing basins with internal drainage. Bryan and Forsman (1987), reporting on the biogeography and ecology of great gray owls in this segment of the Oregon Cascades, specifically identified Deschutes, Klamath, Lake, and Jackson Counties as the localities of greatest great gray owl abundance.

Much of the forested portion of the eastern flanks of the Cascade Range in Washington and Oregon, including the south-central Cascades, falls within Kuchler's (1964) Type K-10, Ponderosa Shrub Forest (ponderosa pine, *Ceanothus velutinus*, *Cercocarpus ledifolius*, *Purshia tridentata*, *Agropyron spicatum* and

Festuca idahoensis). This same forested region is classified as the ponderosa pine zone by Franklin and Dryness (1973), and in Oregon the pumice plateau area occupies elevations between 1450 to 2000 m. At its upper limits the ponderosa pine zone grades into forests dominated by Douglas-fir, grand fir, or *Abies concolor*. At its lower limits the pine zone abuts *Artemisia tridentata* steppe or western juniper (*Juniperus occidentalis*).

Franklin and Dryness's (1973) literature review of the ponderosa pine zone in Oregon emphasizes the major role that historic fires played in shaping the vegetation mosaic in south-central Oregon. They report on fire history studies, such as those made by Weaver (1943), that indicate fire occurrences at 8-20 yr intervals in the ponderosa pine zone. Frequent fires maintained ponderosa pine dominance even on mesic habitats where the potential climax species, such as Douglas-fir, would attain dominance without frequent fire treatments. Fire exclusion over the past half century has allowed the development of dense, stagnated ponderosa pine stands, or invasion of shade tolerant climax species. Fire suppression combined with heavy livestock grazing has altered understory vegetation, too. Heavy grazing often favors increased shrub cover and reduced grass cover (Franklin and Dryness 1973). Logging in the ponderosa pine forests has accelerated the conversion to shade-tolerant species such as Douglas-fir and grand fir.

The forest types primarily used by great gray owls in south central Oregon are dominated by mixtures of mature and/or old-growth lodgepole pine and ponderosa pine forest (Bryan and Forsman 1987), especially stands adjacent to wet meadows. Quaking aspen is associated with lodgepole pine on mesic-moist sites in their owl study areas.

California Sierra Nevada Range

The southern Oregon Cascades merge physically and phytogeographically with the Sierra Nevada Range in California. A pronounced moisture-temperature gradient means the cool, moist environments of western Washington and northwestern Oregon give way southward to warmer, drier climates. Southern Oregon displays an increase in the number of California-centered floristic elements, such as sugar pine, incense cedar and tanoak (*Lithocarpus densiflorus*). These elements, along with others typical of the mixed conifer and mixed sclerophyll forests, are parts of the transition to typical northern California vegetation types (Franklin and Dryness 1973).

Arno and Hammerly (1984), include the mountain-

OREGON CASCADE AND CALIFORNIA SIERRA NEVADA

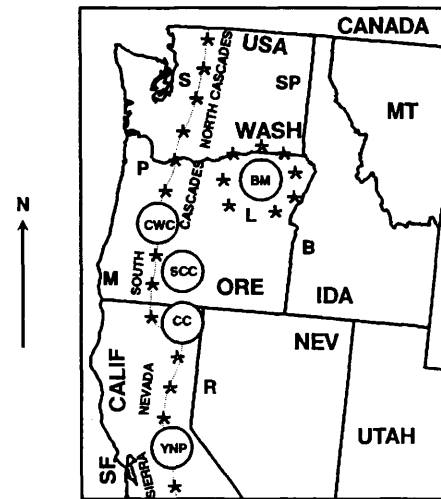


Figure 11.--Cascade and Sierra Nevada mountain ranges and general localities where great gray owl studies have been reported. BM = Blue Mountains, CWC = Central Western Cascades, SCC = South-Central Cascades, CC = California Cascades, and YNP = Yosemite National Park. Other geographic points: B = Boise, ID; SP = Spokane, WA; S = Seattle, WA; P = Portland, OR; L = La Grande, OR; M = Metford, OR; R = Reno, NV; SF = San Francisco, CA.

ous northeastern portions of California, southward to Lassen Peak (the region north of the Feather River), within their "Southern Cascade Range" designation. The similarities are so great between northeastern California's forest vegetation (Klamath N. F.) and that which occurs in Oregon's south-central Cascades that Miller (1991) undertook a detailed habitat analysis to assess the great gray owl's status in the northern California extension of the Cascade Range but he found no owls occupying his California study site.

The California Sierra Nevada (figure 11) forest vegetation is treated (literature review) in detail by Arno and Hammerly (1984), and Barbour (1988). Within the USDA Forest Service's California spotted owl conservation assessment (Verner *et al.* 1992), McKelvey and Johnson (1992) and Weatherspoon *et al.* (1992) discussed forest vegetation and fire ecology of the central Sierra Nevada. Their reports cover the historical impacts of early logging and pre-settlement fire regimes.

Barbour (1988) provided a gradient analysis diagram (figure 12, redrawn from Vankat, 1982) of Sierra Nevada vegetation types. This ordination encompasses the central Sierra Nevada forest vegetation types used by great gray owls and was studied in detail by Winter (1982, 1986). The major forest types, as classified in the 1977 USDA Forest Service treatment include Type #21, Ponderosa Pine; Type #23, Fir-Spruce; and Type #26, Lodgepole Pine. All

of the Sierra Nevada, under consideration here, falls within Bailey's (1978) Ecoregion M2610, "Sierran Forest Province."

The forests of the Sierra Nevada between 600 and 2000 m mostly fall within Kuchler's (1964) Type K-5, "Mixed Conifer Forest," in which white fir (*Abies concolor*), incense cedar, ponderosa pine and Douglas-fir codominate. On a revised Kuchler map of California's natural vegetation, dated 1977, this same category is designated as Type K-15, "Sierra Montane Forest," positioned above Type K-7, "Sierra Yellow Pine Forest" which features ponderosa pine. Present, at higher elevations (1800-2750 m), is Kuchler (1964) Type K-7, "Red Fir Forest," featuring California red fir as a primary dominant, with white fir, lodgepole pine, Jeffrey pine (*Pinus jeffreyi*), and western white pine as common associates. On Kuchler's 1977 revised vegetation map, this latter zone is redefined and described as K-17, "Upper Montane-Subalpine Forest."

Winter (1986) identified the Sierra Nevada elevational range occupied by breeding great gray owl populations to be between 1219 and 2438 m. Foraging sightings were nearly always in or near montane meadows, and nests in the tops of broken-off large snags. Winter (1986) estimated that old-growth red fir/mixed conifer forests in the central Sierra Nevada national forests and national parks have been reduced from nearly 2,000,000 ha down to about 400,000 ha, an 80% reduction; he also suggested that earlier logging on national forests led to significant reduction in large-diameter snags available as owl nest sites.

Within the central Sierra Nevada mixed conifer forest type, Barbour (1988) identifies ponderosa pine as "the thread that holds the type together," although on drier and colder sites, Jeffrey pine may replace ponderosa pine. Prior to modern fire suppression, the pine-dominated mixed conifer forests had an open, park-like appearance with groups of large-diameter, taller pines alternating with openings, with few trees of intermediate height present. Overstory and understory structure in the mid-montane mixed conifer forests changed during the past century in response to fire suppression.

Prior to 1875, fires occurred in the Sierra Nevada mixed conifer zone at intervals of about 8 years on pine-dominated sites and about 16-year intervals on the more mesic fir-dominated sites (Barbour 1988). Most early-day fires, of Indian or lightning origin, were low-intensity ground fires and of limited areal extent. Frequent fire created conditions for successful conifer seedling establishment. The periodic burning routinely thinned out conifer reproduction,

maintaining the open-canopied park-like conditions. After 1900, when fire suppression became successful, the original, open pine-dominated forests experienced invasions by white fir. The forests now have higher amounts of dead and living fuels, which enhance the potential for crown fires in the Sierra Nevada mixed conifer communities (Weatherspoon *et al.* 1992). Opportunities for ponderosa pine establishment have also been reduced considerably.

The California red fir forests type, occupying the upper montane zone of the Sierra Nevada, often features lodgepole pine as a common associate; lodgepole pine also extends upward into the subalpine forest zone. Barbour (1988) describes the presence and dominance of red fir on mesic habitats where lodgepole pine is only a minor component. Where lodgepole pine is prevalent, it forms stands that are moderately dense, with 55-80% cover. Barbour (1988) states that lodgepole pine in the Sierra Nevada does not form a fire-type as it does in the Rocky Mountains.

Both red fir and lodgepole pine form old-growth stands; but the fir achieves ages over 300 years and diameters over 100 cm dbh, while lodgepole lives less than 300 years and measures under 70 cm dbh. Studies of lodgepole pine in California have shown

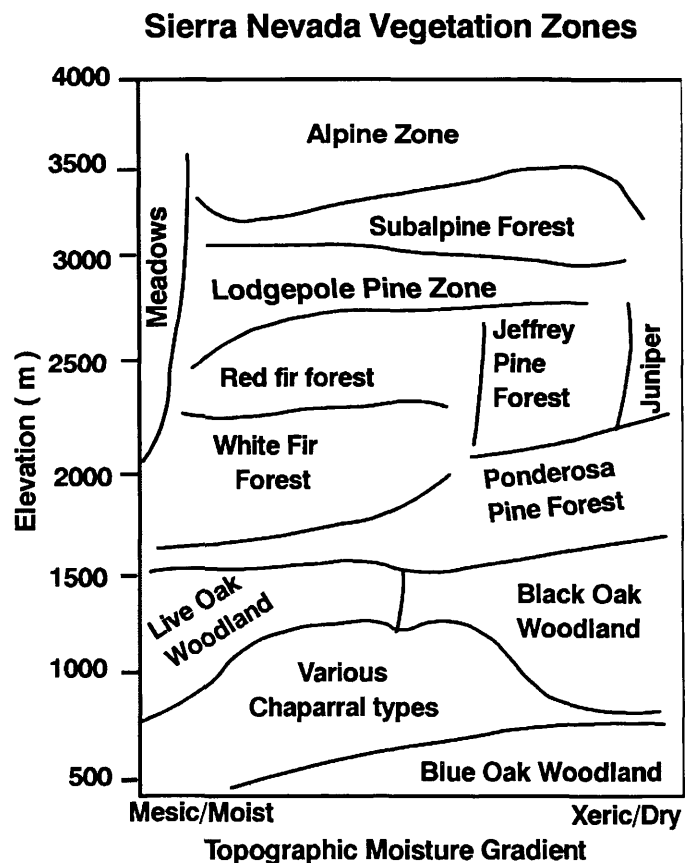


Figure 12.--Ordination diagram representing general arrangement of major vegetation zones along elevation and topographic-moisture gradients in the Sierra Nevada Range, California. After Barbour (1988) and Vankat (1982).

it to be bimodal in its site distribution pattern, capable of occupying both arid, wind-swept, shallow soils and successfully invading wet meadow edge and lake shore sites in cold-air drainages (Barbour 1988). On such wet sites lodgepole pine and red fir may also be co-associates, with quaking aspen and black cottonwood also present. Barbour (1988) cites studies by Vankat and Major (1978) suggesting that lodgepole pine invasion of wet meadows may be related to fire cycles. Other biologists have implicated episodic insect infections in lodgepole pine population dynamics in the upper montane Sierra Nevada zone.

The forest dynamics, involving several pairs of tree species, within the ecotone between the mid-montane and the upper montane is discussed by Barbour (1988). Basically, white fir gives way to California red fir, ponderosa pine to Jeffrey pine, and sugar pine to western white pine. Mixed through these conifer forest types may be quaking aspen stands, occupying an elevational range between 1500 and 3000 m. According to Winter (1986) mesic-moist meadows are well represented in the Sierra Nevada below 1200 m elevation, but he found no evidence that such sites were used for breeding by great gray owls. He suggested that summer heat at lower elevations might be stressful to great gray owls, which evolved in boreal holarctic climates.

Historical Changes in Cascade and Sierra Nevada Vegetation

As with Rocky Mountain vegetation, the lower and upper forest zones in the Cascade Range and Sierra Nevada have experienced a century of major disturbance by elements of western civilization. Mining, logging, grazing, and altered fire regimes have all combined to change vegetation patterns in the lower and upper montane zones where great gray owls historically occurred (Forsman and Bull 1989, Verner *et al.* 1992, Winter 1986). Systematic field investigations in the Oregon and California mountains were initiated before 1900. The U.S. Geologic Survey (USGS) prepared reports on the condition of natural resources within federally established forest reserves, areas which later became the national forest system. McKelvey and Johnson (1992) have summarized USGS data on pre-1900 tree species distributions, timber volumes, and logging intensities in what now constitutes Yosemite National Park and adjacent national forests.

McKelvey and Johnson (1992) cite circa 1900 data compiled by USGS's forest examiners George Sudworth (1900) and John Leiberg (1902), wherein

the claim is made that about 0.6 million ha had been logged in the northern Sierra Nevada between 1850 and early 1900s, leaving about 0.9 million hectares uncut at the beginning of this century. The timber volume removed per stand, however, was highly variable, ranging from an estimated 5% to 99% but averaging about 50% for all areas examined by the early USGS field observers. Log transport limitations, namely horse-drawn wagons, prevented clearcutting in many instances and necessitated "light high grading" of old-growth ponderosa pine and sugar pine. Thus, some Sierra Nevada old growth survived by simply being out of easy reach. Wherever railroad transportation was available, logging was more intense. The volume of timber removed from Sierra Nevada national forests rose steadily between 1900 and 1960, then declined somewhat and leveled-off until the 1980's when it rapidly declined. Rates of timber harvest rose again during the early 1990s (McKelvey and Johnson 1992).

McKelvey and Johnson (1992) concluded that the Sierra Nevada Range currently supports very little pristine forest cover. They state that logging, grazing and altered fire regimes have converted the pre-1900 forest system dominated by large, old, widely spaced trees, and with high structural heterogeneity, into a system characterized by densely stocked, even-aged stands in which most of the largest trees are in the 80-100 yr class. The modern Sierra Nevada forest appears, to these two investigators, unstable, to be highly susceptible to drought-induced mortality and threatened by insect infestations. In their current condition, many Sierra Nevada forests display very high fire potential, a subject which is thoroughly discussed by Weatherspoon *et al.* (1992).

Summary: Relationships Between Forest Dynamics and Management of Great Gray Owls

In summarizing what we know about the character of forest and meadow types used by the great gray owl in western U.S., a two-part theme repeats itself: great gray owls use old-growth forests near openings. The old-growth forests provide large-diameter (over 50 cm dbh) trees or snags having abandoned raptor nests, and the openings provide huntable populations of rodents. During the past century, human activities, including widespread harvesting of mature and old-growth forests, have reduced the abundance of potential nest trees. Furthermore, the altering of natural (pre-settlement) fire regimes have disrupted the generation and maintenance of a distinctive fire mosaic covering the west-

ern North American landscape.

Timber harvesting, whether clearcuts or even selective removal of large-diameter trees, has reduced nesting opportunities for all forest raptors, including great gray owls. Studies show that logging can and does generate "temporary meadows" capable of supporting rodent populations used by breeding great gray owls. But unlike naturally occurring mountain meadows, forest clearings created by logging undergo rapid forest re-establishment; successional development makes the usefulness of such openings short-lived. Some montane grasslands have experienced gradual conifer invasions, attributable to reduced fire occurrence and fostered by shifting climatic cycles. This means shrinking great gray owl foraging habitat throughout western North America. Sustaining populations of great gray owls is possible, but only as a product of innovative ecosystem forest management.

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