

TREE ENCROACHMENT ON
MEADOWS OF THE NORTH RIM OF GRAND CANYON
NATIONAL PARK: LITERATURE REVIEW

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INTRODUCTION

Montane meadow grasslands and subalpine grasslands are natural openings or "parks" located in level basins, in shallow valley bottoms, and sinkholes in high elevations. There are often distinct divisions in these grasslands, a lower wetland portion dominated by sedges and a higher more xeric margin dominated by grasses and showy herbs. The borders of these grasslands are forested often producing an abrupt "edge effect" between the two plant communities.

On the North Rim of Grand Canyon National Park subalpine grasslands and montane meadow grasslands occupy a small percentage of the Park's land area, however, their unique characteristics make them a key vegetation type. For example, meadows are critical habitat for certain wildlife species, and are important for their contribution to the Park's aesthetics, landscape and biological diversity.

Over the past century, many of these montane meadow and subalpine grassland edges have been invaded by small conifers or quaking aspen. This process continues today. It appears that a significant amount of this unique habitat is being lost. Park personnel have observed that "encroachment appears to be occurring on all meadow lands; however, in some areas it seems to be occurring at a faster rate (NPS-RFP 1990)."

There are a variety of factors which may influence the stability (or instability) of the forest-meadow margins such as

soil texture and moisture, snow duration, periodic fire, temperature (especially presence of a cold-air drainage), fossorial animals, and past/present grazing activities.

This literature review is of articles concerned directly with the geomorphology, vegetation, and past management of the subalpine grasslands and montane meadow grasslands of the Kaibab Plateau; of the Southwest; and of similar grassland environments in the western United States.

KAIBAB PLATEAU PARK PHYSIOGRAPHY AND FORMATION

The Kaibab Plateau is the highest plateau in the Grand Canyon complex. It is a broad, asymmetrical arch underlain by the resistant Permian Kaibab and Toroweap limestone formations (Strahler 1944). The altitude of the Plateau ranges from 6,800 to 9,200 feet. On the east side it drops 3,000 feet to House Rock Valley and on the west side the Kaibab Plateau drops several thousand feet down to the Kanab Plateau (Strahler 1944, Merkle 1962).

The highest part of the Kaibab Plateau consists of an elliptical dome with long axis oriented north-south, lying just west of Demotte Park (Strahler 1944). This summit is 9100-9200 feet.

Slightly to the east of this summit and 300-500 feet lower in elevation lie a series of elongate topographic depressions that trend north-south - Demotte Park, Pleasant Valley, Little Pleasant Valley, Little Park, and Round Valley. The largest,

Demotte Park, is about 8 miles long and 1 mile wide. These depressions or parks are anticlinal valleys (valleys which are formed by erosion down through the cap of a dome and along the dome's long axis (Strahler 1944)). The bulk of the limestone erosion to produce the parks was accomplished by surface streams which opened out the anticlinal valleys. Disruption of the surface stream drainage was accomplished through increased limestone solution, and eventually even the remaining surface channels may be abandoned (Strahler 1948).

At one time the parks were thought to follow fault lines. Yet only along the east side of the northern end of Demotte Park and along the east side of Pleasant Valley is there evidence of faults within the parks, and these are small (Strahler 1944, 1948).

The park floors are grassy, and treeless containing occasional outcrops of limestones and numerous solution sinks - sink holes (e.g., Indian and Deer Lakes). Walls of the parks rise abruptly along their east sides and more gradually on the west sides. A number of streams drain the parks through narrow valleys breaking through the eastern walls. These channels to the east are not very important drainages. Most of the precipitation in the parks is carried underground by solution passages in the underlying limestones (Strahler 1948).

CLIMATE OF THE KAIBAB PLATEAU

The general climate of the Kaibab Plateau can be

characterized by cold, wet winters and mild, moist summers. Weather records taken at the Bright Angel Ranger Station, North Rim Park headquarters, at 8,400 feet elevation, show an average January temperature of 21°F and a July average of 62°F, with a maximum of 91°F and a minimum of -25°F (Greening 1941). The average date of the last killing frost in spring is June 14 and of the first in the fall is September 15, giving an average growing season of 93 days. The average annual precipitation of around 27 inches falls in two seasons, the greater amount occurring during winter as snow and in summer as local afternoon showers. Most of the remainder falls from December to March as snow with depths of 4-10 feet frequently recorded (Greening 1941, Merkle 1962, Robbie 1982).

HISTORY OF THE KAIBAB PLATEAU PARKS

The Kaibab Plateau has had an interesting biological history since the white man's settlement in that area. The following account is from Merkle (1962) and has been adapted in part from a more complete history by Rasmussen (1941).

"The first white people, Mormon pioneers, visited the area [Kaibab Plateau] in the 1850's. They found the Indians, Paiutes and Navahoes chiefly, using the Plateau as a hunting ground and, to some extent, as a summer home. The Rocky Mountain mule deer (*Odocoileus hemionus macrotus* Say) was hunted for food and hides; however, the Indians depended more on the smaller animals for food.

Major John W. Powell began the first government exploration of the country north of the Grand Canyon in 1870. The geologist C. E. Dutton explored and described the region in 1880 and 1881. The earliest extensive use of the Kaibab Plateau for livestock was in 1885 and 1886. By 1887, 200,000 sheep, 20,000 cattle, and many horses were using the "unlimited" supply of forage. Presidential proclamation created the Grand Canyon Forest Preserve in 1893 to include the Kaibab Plateau, the Grand Canyon, and the adjoining area on the South Rim. The Grand Canyon National Game Preserve was created north of the Colorado River in 1906. The area south of the River was proclaimed the Grand Canyon National Monument in 1908, and the area north of the River was then called Kaibab National Forest. Grand Canyon National Park was created by an Act of Congress in 1919 to include on the North Rim approximately the southern quarter of the Plateau. The present Grand Canyon National Monument to the west was proclaimed in 1931.

The deer herd achieved national prominence as a result of the ensuing controversy. With the creation of the Game Preserve in 1906 deer hunting was prohibited. There was also a marked decrease in domestic sheep. For several years after 1906 government hunters were employed to kill predatory animals. By 1923, 674 mountain lions (the principal deer predator), 11 timber wolves, 3,000 coyotes, and 120 bobcats had been destroyed. Later the wolves were exterminated and the other predators further reduced. The consequent decrease in competition for forage and

the natural enemies resulted in an increase in the deer population, which was unchecked until 1924 when hunting was again permitted.

An estimated population of 4,000 deer in 1906 had increased to almost 100,000 in 1924, when the range was depleted, and the population started to decrease. Thousands of deer died from causes related to malnutrition and a few thousand were removed by hunting and by trapping. By 1930 the population had decreased to an estimated 20,000 but this number was still excessive for the depleted range, and by 1939 the population as estimated at only 10,000.

In the 1940's the range improved and the deer population increased to an estimated 30,000 in 1955. The range began to show extensive depletion by 1954, with severe browsing on young aspen (*Populus tremuloides*) and Gambel oak (*Quercus gambelii*). Recently the deer harvest has been liberalized and the herd apparently brought under better control."

GENERAL VEGETATION AND SOILS CHARACTERISTICS OF HIGH ELEVATION GRASSLANDS IN THE SOUTHWEST

Parks are natural, treeless openings dominated by graminoids, sedges, and forbs. There are two major types of grassland communities recognized in the high elevations of the Kaibab Plateau and the Southwest, the subalpine grassland and montane meadow grassland (Moir 1967; Lowe and Brown 1973; Turner and Paulsen 1976).

Subalpine grasslands. The subalpine grasslands occupy

valleys, slopes, and ridges on usually flat or undulating terrain adjacent to and within subalpine conifer forests. Size of these grasslands ranges from a small park-like opening within the forest to a thousand acres in the Southwest and on the Kaibab Plateau. These grasslands reach their best development between 2500-3500 m (Brown 1982).

Subalpine grassland soils are variable, and often well drained, and yet appear to be unsuitable for tree growth. Air temperatures are significantly lower and evaporation rates are significantly higher in the grassland than in the adjacent forest, but it is not known whether these microclimate differences are causes or effects. Particularly at the higher elevations short trees often exist at the grassland-forest border, where 2 m. trees at the immediate edge may be the same age as 10 m. tall trees only 5 to 6 m. back in the forest (Brown 1982).

Well drained subalpine grassland sites are dominated by perennial bunchgrasses (*Festuca*, *Stipa*, *Poa*, *Muhlenbergia*, *Agropyron*) and forbs including fleabane (*Erigeron*), mountain dandelions (*Agoseris*, *Taraxacum*), cinquefoil (*Potentilla*), aster (*Aster*), larkspur (*Delphinium*), vetch (*Vicia*), etc. These high elevation "prairies" are replaced in the moister sites by sedges (*Carex*, *Cyperus*) and with more moisture dependent grasses and forbs. There is much intermixing with grasses and forbs of either montane meadow grasslands at slightly lower elevations or alpine tundra at slightly higher elevations (Brown 1982).

More moisture favors the higher subalpine grasslands, which also have lower evapotranspiration rates than montane meadow grasslands. As a result many subalpine grasslands in the Southwest still retain much of their original "wet meadow" characteristics, while many montane meadows are now distinctly drier (Brown 1982).

Montane meadow grasslands. Montane meadow grasslands [or Grassland Association - Mixed Meadow Series; Brown, Lowe, and Pase 1979] are contained largely within the Rocky Mountains, Sierran and Madrean montane conifer forests. These parks are generally restricted to flatlands possessing heavy, poorly drained muck soils. Such soils are unsuitable for tree growth, and the forest edge is frequently abrupt producing a marked "edge effect."

These "flower meadows," dominated by forbs, of lower elevations are distinct from the higher and sometimes adjacent subalpine grasslands (which in the Southwest are usually above 2,600 m. elevation and are commonly dominated by bunchgrasses). Extensions of plains grasslands into the lower ponderosa pine forests (1,800 and 2,500 m.) should also not be confused with montane meadow grasslands (Brown 1982).

Many of the same characteristic meadow species are present in montane habitats in California's Sierras, in the Rocky Mountains and in the Sierra Madres. These include bracken fern (*Pteridium aquilinum*), corn-lily (*Veratrum californicum*), monkey

flower (*Mimulus nasutus*), mountain brome (*Bromus marginatus*), and mountain muhly (*Muhlenbergia montana*). Another common species is iris (*Iris missouriensis*) which may dominate completely in heavily grazed meadows. Other species are regionally restricted for example, pine dropseed (*Blepharoneuron tricholepis*), which occurs only in the Rockies (Brown 1982).

Other characteristic plants in montane meadows include a large number of herbs in the genera *Lupinus*, *Lathyrus*, *Helianthus*, *Aster*, *Penstemon*, *Senecio*, *Solidago*, *Lotus*, *Astragalus*, *Vicia*, *Sphaeralcea*, *Viola*, and others.

Many authors (Mead 1930, Rasmussen 1941, Merkle 1962, Brown, et al. 1979, Robbie 1980, Warren et al. 1982, Brown 1982) recognize distinct divisions of the montane meadow grasslands in the Southwest. The physical factors differentiating these divisions are micro-relief, soil texture, and moisture availability. The low or bottom position of the parks (often saturated soils) contains phreatic plant species, such as sedges, rushes, Bigelow bluegrass (*Poa bigelovia*), iris and alpine timothy (*Phleum alpinum*).

Soils of these meadow bottoms are moderately deep and deep (101 to 152 cm), somewhat poorly drained, and have formed in alluvium from limestone sources (Robbie 1980, Brewer et al 1989). The surface horizon is generally grayish brown or dark grayish brown loam or clay loams. The surface and subsurface horizons (solum) range from 134 to greater than 152 cm. The pH of the solum ranges from 4.8 to 6.2 (very strongly acid to medium acid).

Mottles are present between 60 and 150 cm. indicating poor aeration due to saturated conditions from high water tables (Robbie 1982, Brewer et al. 1989).

Next, there is an intermediate zone that is grass dominated, finally rising to the higher, well drained, forb-dominated meadow margins. The dominant species occurring in these zones are sheep fescue (*Festuca ovina*), timber oatgrass (*Dathonia intermedia*), tufted hairgrass (*Deschampsia caespitosa*), mountain muhly, Kentucky bluegrass (*Poa pratensis*), June grass (*Koeleria cristata*), needle and thread (*Stipa comata*), and pine dropseed. These plants are commonly found in most meadows of the Kaibab Plateau where soil drainage is not restricted. Aspen and Engelmann spruce normally surround the meadow (Mead 1930a, Rasmussen 1941, Warren, et al. 1982, Brown 1982).

Soils of these well drained areas are moderately deep and deep (101 to 152 cm.), well drained and have formed in residuum and alluvium from limestone sources (Robbie 1980, Brewer et al 1989). Rock outcrops occur within this unit. The surface horizon is pale brown or brown gravelly loam, loam, or clay loam. The solum thickness ranges from 40 to 104 cm. The pH of the solum ranges from 5.4 to 7.0 (Robbie 1982, Brewer et al 1989).

Both the subalpine grasslands and the two distinct communities within the montane meadow grasslands have been and still are subject to grazing because of their abundant herbage. Past and present heavy grazing is not always apparent because of the abundant herbaceous cover and variations in plant composition

between sites. Generally the less palatable forbs, grasses and perennial shrubs tend to increase at the expense of native bunchgrasses (Rasmussen 1941, Merkle 1962).

The stability of the subalpine and meadow ecosystems is not known. Few subalpine grasslands are in a climax condition because of grazing or, less commonly, fire. The stability of the montane meadow grasslands is not known, but is thought to be in a climax condition, except for the meadow-forest edges (Brown 1982).

STUDIES OF THE KAIBAB PLATEAU MONTANE MEADOW GRASSLANDS

The first scientific study and description of the parks on the Kaibab Plateau was a Master's thesis by Mead (1930). Within the Canadian Zone, she compares the meadows and forests and described that:

"The trees are confined to the hills but the tree line does not follow the topography at the base of the hills. In many instances the trees occur on higher ground that stretches out into the meadow, but this is not always the case . . . In a great many cases seedlings of *Picea pungens* occur along the edge of the meadow in the open. This apparently does not signify encroachment since usually no trees of intermediate sizes are found between the seedling and the mature trees. Some that are ten years old are only a foot and a half tall. Natives report that such seedlings have appeared along the edge of the meadow [Robber's Roost

Canyon] for fifty years. Perhaps they germinate in a favorable year, live until conditions are hard, when they are killed off, and the process is repeated. Sometimes, however, they are successful and grow to maturity in the open meadow. In a good many cases it appears that *Populus aurea* [*P. tremuloides*] advances into the meadow making way for *Picea pungens* seedlings. These seedlings are apparently more healthy and in some cases grow to maturity.

Various theories as to the cause of the mountain meadows have been advanced, but no definite conclusions made. Dr. G. A. Pearson [see Pearson 1913 summary in this document] of Southwestern Forest Experiment Station, who has studied the problem for many years in other forests, considers that cold air drainage in the lowlands has considerable detrimental effect on germination and growth of tree seedlings."

To test her hypothesis that microclimate affected the stability of the meadow, Mead conducted a comparative microclimate study. Weather stations were placed in the middle of the meadow, one on the edge of the meadow, and one in the forest (small forest opening). Weekly readings were made of temperature, evaporation, and soil moisture throughout the season. The monthly and seasonal mean showed that in general, the forest had the lowest maximum and the highest minimum temperatures. The meadow had the next highest maximum and the lowest minimum, while the station at the forest edge had a

slightly lower maximum and higher minimum. The average minimum temperature in the meadow was 10.5°F below that in the forest (Mead 1930).

Evaporation data showed a decrease in evaporation from meadow to forest (Mead 1930).

Soil moisture was more uniform in the forest than in the meadow or the meadow edge. The forest soil was not as dry in the dry season nor as wet in the rainy season as that of the meadow. There was also less difference between the moisture content of the subsoil and the surface soil in the forest than in the meadow (Mead 1930). Mead's concluded that microclimate has a significant effect on the stability of these montane meadows, and that the microclimate was more severe in the meadows and not amenable to the growth of tree seedlings.

Mead (1930) also classified the plant communities of the Canadian Zone of the Kaibab Plateau. She grouped the plant communities by communities of the meadow, or communities of the forest. She listed the frequency of plants occurring in quadrants and soil moisture of each community. The meadow communities were grouped as follows: 1) climax meadow type, 2) damp meadow lowlands, 3) north and south face of meadow slope, 4) limestone outcrops, 5) limestone sinkholes, 6) washes, 7) ponds, and 8) springs.

The climax meadow type included the open flat, the hilltop, and the east and west faces of the hill slopes. The soil moisture on the hilltops was more moist than that of the slopes,

and the west facing slopes were drier than the east facing. Soil moisture content of the damp meadow lowlands was about 22% greater than that of the hill slopes. Soil moisture content of the north and south slopes showed that the north facing slopes were 14% damper than the south, and slightly more acid. Washes formed along lines of drainage, and if the slopes are relatively steep then there is considerable erosion.

The plant communities of the forest were grouped as follows (Mead 1930): 1) conifer groves (climax forest type), 2) *Populus aurea* [*P. tremuloides*] groves, 3) canyons.

The dominant tree in the conifer groves plant communities was blue spruce (*Picea pungens*). It grew at the base of the hills and was the common conifer bordering the meadow. Mead considered it a hardy tree and noted that it was the only conifer to encroach upon the meadows. A little higher on the slope and back from the treeline, subalpine fir (*Abies lasiocarpa*), and Englemann's spruce occurred, and still higher Douglas-fir (*Pseudotsuga mucronata* [*P. menziesii*]), ponderosa pine (*Pinus brachyptera* [*P. ponderosa*]), and white fir (*Abies concolor*) are found. On the ridges and hill tops it was common to find pure stands of *Abies concolor*.

Trembling aspen or *Populus aurea* stands were scattered through the forest. Sometimes young aspen was found under mature ponderosa pine and white fir, but it was also found in pure stands, and protecting seedlings of blue spruce.

There was some slope difference in the forest. More aspen,

ponderosa pine, and blue spruce occurred on the south and west facing slopes. On the north facing slopes, white fir and Engelmann spruce were more abundant.

Mead (1930) found no difference in soil moisture content between the north and south facing slopes in the forest as she had found in the meadow.

The canyons studied had fewer plants on the north facing slope, but those plants were more mesophytic (e.g., *Potentilla anserina*, *Linnaea borealis*, *Zygadenus elegans*, *Pyrola* spp.). On the south facing slope and in the bottom of the canyon were plants more typical of the grasslands.

Rasmussen (1941) studied the biotic communities of the Kaibab Plateau from 1928-1930 for his dissertation. Part of his study included the Mountain Grasslands or what he classified as the *Stipa-Carex-Thomomys* Associates, specifically the meadows and parks. Rasmussen stated that:

"There are 10,000 to 15,000 acres (4,000 - 6,000 ha.) of open parks and meadows present on the entire Plateau. These vary greatly in size, but are very similar in their general appearance and features. They are located, as a rule, in fairly level basins and in the bottom of shallow valleys.

Certain localities show an interesting phenomenon is the presence of a near timber-line or Krumholz condition along the meadow border at the foot of a forested slope at an elevation of 9,000 feet (2,740 m.). A factor study in VT

(De Motte) Park, the Plateau's most famous park, showed a marked difference in daily minimum temperatures in adjacent forest and meadow (according to Mead 1930).

Care, however, must be used in not assigning the environment created by the forest as the explanation of its presence. Climatic factors, influenced by air currents and soil differences, may account for the occurrence of these parks and meadows. Explanation of these areas as resulting from forest fires does not seem reasonable on the Kaibab Plateau. There is a usual growth of small conifers along their edges, giving the appearance of invasion of forest species. These trees, however, show by the annual growth rings that they are much older than they appear. Sample blue spruces of less than five feet (1.5 m.) in height present on the edge of the meadow showed as many as thirty annual rings. But in the forest proper, fifteen to twenty feet (4.6 to 6.1 m.) from the edge of the meadow, spruces of six inches (15 cm.) diameter and thirty-five feet (11 m.) height were shown to be the same age.

The explanation of deer presence and variation in numbers in the meadows has been one of the interesting features to observe during this study. From all evidence, it appears that the habit of the deer of visiting the meadows as they now do is a fairly recent change in their activity. The livestock men who have spent years on the Plateau say that deer first began visiting the park [VT or

DeMotte] in large numbers about 1916 and that before that time there was little or no use of the meadow by the deer. T. G. Pearson (1925) reported counting 1,028 deer in VT Park on the evening of August 21, 1924. This was at the time of maximum numbers visiting the meadow. [In 1930 and 1931, the average deer counts were 288 and 188, respectively.] The present poor condition of adjoining summer range and small amount of available food indicated that the deer, by all evidence, were forced into the meadow in order to obtain forage.

The future existence of the herd will depend on a variety of factors affecting biotic balance. Present indications are that the numbers that visit the meadows will continue to decrease with an increase in desirable forage near-by, and that restoration of near natural conditions to the Plateau will limit the number of deer that visit the open parks each evening. This was the situation at the time the area was first set apart as a game preserve. Restoration of the former large show herds would no doubt indicate once again the absence of suitable and sufficient forage in the surrounding forests."

In addition to the observations on the meadow-forest margins, and the deer herds in the parks, Rasmussen (1941) also recognized two definite divisions of the meadows: "One is the low, more mesic portion, where the deer ordinarily concentrate, and where near 90% of the vegetation consists

of netted-veined plants [dicots]. The bulk of this division consists of several species of *Trifolium*, with dandelions, a small fleabane, *Achillea lanulosa*, *Potentilla*, *Ranunculus subsagittatus*, and *R. alismellus*. Species of *Polygonum* occur on newer denuded areas. The grass and grass-like species composing about 10% of the vegetation of this part of the mountain meadows are mainly *Phleum alpinum* and species of *Poa*, *Deschampsia* and *Carex*.

In the higher and more xeric portions of VT park, the grass makes up near 50% of the total ground cover. The grasses consist of species of *Deschampsia* and *Festuca* with *Blepharoneuron tricholepis*, *Stipa comata* and some others. The most conspicuous herb species include species of *Antennaria*, *Eriogonum*, *Potentilla*, *Saxifraga*, a tall *Erigeron*, *Phlox caespitosa*, *Pseudocymopterus montanus*, *Actinea richardsonii*, *Orthocarpus purpureo-albus*, and *O. luteus*.

The favorite food of the deer visiting the meadow is several species of the Mountain clover or *Trifolium* spp. This is preferred to all other meadow species. They eat many other herbs readily, but only a very small amount of grass. The two main areas of clover are in close proximity of the only two springs in the park, one north of the VT hotel and one near Mason Well, four miles (6.4 km.) south of the hotel. In the days of big cattle outfits, VT Park was the summer headquarters, and the area was grazed continually

be horses and subject to overgrazing by herds of cattle that were collected there."

Influential mammals of the meadows, that Rasmussen mentioned in his monograph, included the Mexican badger, Colorado pocket gopher, Rocky Mountain meadow mouse, and the mantled ground squirrel. Of these, the pocket gopher and the ground squirrel were fairly abundant. The pocket gopher preferred areas where the soil was sufficient for burrows and not subject to flooding. It was active year-long. The ground squirrel was especially abundant at the edge of the meadows, enough to influence the plant growth in this ecotone (Rasmussen 1941).

McHenry (1935) published an article on the woodland parks of the North Rim. This article did not contain any quantitative information, yet contained some of McHenry's observations and speculations about the parks. He noted that there were three distinct categories:

"One type of park is represented by such areas as V. T. Park, ... and Little Park. Here we find the broad, flat floor of a shallow valley into which drains the water from the surrounding slopes. Running the length of of such a valley usually is found a series of sink holes, some stopped up and forming small lakes, others still open to the passage of water. The floor of such a valley is composed of a layer of alluvial material resting upon the surface of Kaibab limestone. Thus there is a very shallow water table. With the melting snows this alluvial soil becomes saturated with

drainage water. As the season advances the water from the meadow soil either evaporates or drains off to the sink holes. The ground then reaches an extreme in dryness.

Conditions of extreme wetness and dryness are unfavorable to natural reforestation on the Kaibab Plateau. During the spring and early summer the excessive moisture and cold temperature of the soil make germination of seeds from the surrounding trees unlikely. With the arrival of warm weather the soil becomes as dry as it had been wet, a condition hardly favorable to the germination of these seeds. It is noteworthy that the floral structure of such parks is largely composed of plants best adapted to a very dry environment. Sedges are conspicuously absent in these area except about water holes. There is no evidence that trees ever grew in these open places.

In a few cases limited attempts at natural reforestation may be seen. Here and there a small vanguard of the seedlings of the Engelmann spruce and blue spruce reaches down the slope, encroaching upon the grasslands. These trees are hardly more than eight or ten years old at the most, and probably indicated a recent and very slowly changing condition in that restricted environment. In most cases, however, these parks are bounded very definitely by stands of mature trees with practically no reproduction. It is such parks ...that the visitor today will see bands of deer numbering around a hundred or so. Not many years ago

herds of deer numbering as high as 1,400 were seen in these same parks.

Another category into which the writer would place woodland parks is one which would include definite drainage valleys. On the North Rim of Grand Canyon, drainage takes place from the region of the National Park checking station southward to the Colorado River. This has resulted in the formation of a number of drainage valleys leading into side canyons just below the North Rim. In many of these, intermittent streams resulting from the waters of melting snow and from rains not infrequently assume the proportions of raging torrents. Nor are such drainage basins always confined to restricted areas at the bottoms of narrow valleys. Sometimes they appear as broad areas, as the Coconino Basin, where are found slopes draining from three directions over a rock surface which is sparsely covered by a thin layer of soil. Frequently, also, otherwise narrow valley parks will be broadened in places by alluvial fans at the mouth of tributary draws.

In parks having the type of drainage origin described above, water is usually overly abundant at a time when conditions would otherwise be favorable to germination of seeds from the trees of the forest. Any seedling which might get a slight start is likely to be washed along with the shifting soil. These parks are covered with a characteristic vegetation of grasses and a few semi-arid

flowers. Such vegetation is able to establish itself during the dryer part of the season after the conditions favorable for the development of tree seedlings have passed. In these valley-drainage parks one finds now and then localized areas of sedges. Somehow these have become established during the wet part of the season.

One more category into which we should place woodland parks, includes areas located on south facing slopes in drainage valleys. Examples of such parks are to be seen along the road leading to Point Sublime as it passes through Kanabowits Canyon. Here and there along this delightful woodland road one finds these grasslands reaching up the side of a south-facing slope to the forest above. The north-facing slope opposite will be heavily wooded with a substantial stand of spruce and fir almost to the very bottom of the valley.

In places of the type just described, the natural drainage of the south-facing slope will be greatly aided by the drying effect of the hot, direct rays of the sun and possibly the hot, dry winds from the southwest. Any seed of the trees above which might begin successful germination on such a slope during the moist part of the season would quickly succumb to an advancing drought condition. Occasionally we do find on such slopes a very slow encroachment of the forest from above, as the trees along the forest rim afford a rather meager fringe of protective

shade to a sparse reproduction."

Merkle (1962) gave the fourth published account and conducted a third major study which included the meadows of the Kaibab Plateau and North Rim of the Park. He gave the following description of tree encroachment and vegetation of the meadows:

"The meadows occur in shallow valleys which are surrounded by trees on the upper slopes (elevation about 8,400 to 8,900 ft). The natural maintenance of these meadows provides interesting speculation. No isolated young trees are found out in the meadows, but invasion is suggested by the presence of small trees along the margin. These small trees are 3-6 ft tall; bushy, and at 4 in. above the ground are 0.5-1.7 in. in diameter. At this level there are 25-30 annual rings per inch of diameter. A few feet above, at the edge of the forest, trees of a similar age were 20 to 40 ft tall and 3-6 in. dbh.

Grass and forb cover and competition seem to be minor factors in the exclusion of trees because the area of bare ground in all the meadows is mostly over 50%. Careful search showed that most tree seeds fell within 100 ft of the forest edge. Later observations indicated a very low germination rate and the death of all seedlings by late July. The ungerminated seeds were rotten, and the tree seedlings began dying in late June apparently from scalding near the soil surface. High soil surface temperatures were also fatal to large numbers of grass and forb seedlings that

had developed in the open. Almost all these seedlings were brown by mid-July except those on the gopher mounds, where the rough topography reduced the reflection of the heat from the soil.

High soil moisture until mid-June, following the melting of heavy snow cover, supports the bacteria and fungi responsible for the rotting of tree seeds. Excessive soil moisture probably also causes the slow growth and migration of trees at the edge of the forest and meadows.

One phase of the meadow studies included comparison of the livestock-grazed meadows of the Kaibab National Forest with those ungrazed in the Grand Canyon National Park. These comparisons follow with the descriptions of the meadows in geographic units rather than as vegetation units.

Little Park.—This meadow occurs in a shallow valley just below the highest ridge in the Park and is continuous with V. T. Park and Pleasant Valley meadows to the north in the Forest (8,900 ft elevation). Little Park is grazed and browsed only by deer and small mammals. Mountain muhly and sheep fescue (*Festuca ovina*) occur in the highest frequency but do not dominate the entire meadow. Muhly is dominant on the upper slopes and fescue on the middle ones. In the more moist meadow bottoms *Deschampsia*, *Phleum*, and *Poa pratensis* are the most abundant grasses. *Sitanion*, *Koeleria*, and *Blepharoneuron* are common throughout the two upper zones. Less distinct zonation occurs with the forbs.

Total measured cover on this meadow is 42%. Most is provided by the bunch grasses, mountain muhly, and sheep fescue. Muhly grows in rather large bunches of 8-15 in. diameter at 5 in. above the ground and often forms rings up to several feet in diameter (6 ft was the largest seen). The plants inside the ring are dead and the living plants form the outer circumference of the ring. These rings are larger and more numerous in the Kaibab Forest than in Little Park. All other grass species form smaller clumps or individual stems, except *Poa pratensis*, *Muhlenbergia richardsonis*, and *M. filiformis* which occur in patches of sod. Mutton bluegrass (*Poa fendleriana*) and *Bromus richardsonii* are forest grasses and occurred only in plots near the margin of the woods.

V. T. Park and Pleasant Valley.—These meadows in the Kaibab National Forest are used by cattle, horses, deer, and the small mammals. They are much larger than Little Park, have a more diverse topography and, therefore, more local habitats. This explains the presence of blue grama (*Bouteloua gracilis*) and alpine fescue (*Festuca ovina* var. *brachyphylla*) which occur on steeper slopes and thin soils over rocky outcrops.

The total measured cover in these meadows is 35%. Mountain muhly and sheep fescue provide less cover than in Little Park which allows more space for the spread of other species. As a result several species are more abundant,

including *Blepharoneuron*, *Potentilla hippiana*, *Antennaria rosulata*, *Hymenoxys subintegra*, *Phlox diffusa*, *Erigeron flagellaris*, and others. *Eriogonum bakeri*, *Agrostis idahoensis*, *Stipa comata*, and *Bouteloua gracilis* were not found in Little Park.

Measurements of grasses in these meadows emphasize evident growth differences between the grazed and ungrazed conditions. Heights of leaves and culms were measured at maturity in August. In the grazed meadows individual leaves with intact tips were selected. *Poa pratensis* was not measured in the Forest meadows where it was severely and closely grazed. All foliage was clipped and the only leaves with intact tips were those that had not turned upward. The average height of the bluegrass foliage was 1-1.5 in. as compared to 3-5 in. in the Park. No fruiting culms were seen but they were plentiful in the Park. This species occurs only in a few small patches in the meadow bottoms.

Another difference between the meadows of the National Park and the Kaibab Forest is merely observational and is related to the small mammal population and activity. In the Kaibab Forest the predators are constantly under pressure of control campaigns, including the use of poison to decimate the coyote population. Consequently, the gopher population increases and becomes destructive, so gophers are poisoned and almost eliminated. This also applies to a limited extent to the brown-mantled ground squirrel. The National

Park Service allows these mammals to remain unmolested. However, male coyotes that regularly hunt in the Park are all killed because they are wide-ranging. The Park gophers are not poisoned and carry on their normal activity on the meadow, including burrowing and mounding. As a result, the soil of the Park meadow is spongy and friable. The inside of the rings of mountain muhly are dug up and new plants become established in the gopher mounds. The soil of the Forest is packed solid. The rings of mountain muhly are undisturbed and contain a thick mulch layer which prevents the establishment of new plants. The compactness of the soil may partly explain the shorter stature of the grasses in the Kaibab Forest meadows.

Kaibab Basin.—This meadow, 5 miles west of the North Rim Park Headquarters at an altitude of about 8,400 ft, is in an area in which the Kaibab limestone has an extensive lens of sand, making the permanence of the meadow difficult to explain. No early season observations could be made because of the impassability of the road to the Basin. The total area of this meadow is about 1/2-3/4 sq mile with 56% covered by vegetation *Muhlenbergia*, *Sitanion*, and *Blepharoneuron* are the most abundant grasses. *Koeleria* is common throughout though less abundant. Sheep fescue is a minor species in this meadow and its variety, alpine fescue, was found only in solution depressions of limestone boulders and on the top of one small rocky ridge.

The higher cover values on this meadow is accounted for by the greater abundance and area of *Blepharoneuron*, *Chrysopsis*, *Phlox*, *Achillea*, and *Solidago*. There are several species of forbs [in this park] that are common to the forests of this and lower altitudes.

The isolation of this meadow would make it ideal for animal population and interrelationship studies. Coyotes were seen and heard and small mammals are undisturbed by the activities of man.

Dry Park.—This meadow in the Kaibab National Forest, a few miles north of Kaibab Basin, is relatively small with an area of approximately 40 acres. It is severely overgrazed, since it is the only sizeable meadow in that area of the Forest and the cattle collect there. Observations indicated that it was undersampled. *Muhlenbergia* and *Blepharoneuron* are less abundant than the frequency figures show, and over the whole meadow their importance would be considerably reduced. Sheep fescue was not seen but there were a few scattered specimens of the other meadow grasses.

The forbs appeared to be more accurately represented, as those listed in the higher frequency figures were seemingly as common over the entire meadow. The species list includes all those sampled *Houstonia* was observed only in this area and in some of the small woods openings nearby.

In summary, grasses vary in importance (cover and frequency) under grazed and ungrazed conditions. Grass

cover was reduced under grazing except for *Blepharoneuron*, which is greatly increased, perhaps because it is less palatable to livestock. Many forbs greatly increased in importance in the grazed community. These include *Potentilla hippiana*, *Antennaria rosulata*, *Hymenoxis subintegra*, *Phlox diffusa*, and others. *Eriogonum bakeri* was not found in the National Park meadows. Some forbs were more important in the Park meadows including *Arenaria fendleri*, *Agoseris glauca*, *Erigeron formosissimus*, *Pseudocymopterus montanus*, and others."

STUDIES OF OTHER HIGH ELEVATION GRASSLANDS IN THE SOUTHWEST AND CENTRAL ROCKIES

Pearson (1913) conducted one of the first studies of forest openings or parks in the Southwest. The primary objective of his study was to "determine the influence of the forest cover upon climate locally in the Southwest, in so far as this influence might be of importance in the management of timberlands and the possible afforestation of parks and denuded areas." Although Pearson extrapolated his results to the southwestern ponderosa pine belt, the study was conducted on one park near Flagstaff, AZ, known as Fort Valley. This park is approximately 1.5 miles wide by 2.5 miles long. The average elevation is 7,250 feet. The soils are mainly a gravelly alluvial loam underlain by volcanic cinders. Two-thirds of Fort Valley was under cultivation at the time of the study, and the remainder was covered by a fairly dense growth of a grama grass (*Bouteloua*

oligostachya). A ponderosa pine forest surrounded the meadow and the forest invariably occurred at a slightly higher elevation - in some places the rise was gradual, in other places the rise was 25 to 100 feet.

The meteorological observations were taken from six weather stations which extended from the forest on the west side of the park, across the park, into the forest on the east side. Daily readings of temperature, precipitation, relative humidity, and wind movement were kept for about four years. Soil temperature and evaporation readings were made during the growing season.

The results of his study are as follows:

"Summary of Results of Meteorological Study. The records show that the mean annual temperature in the forest is 2.7°F higher than in the park. The most important difference, however, is in the extreme temperatures. The maximum averages 0.9°F lower, and the minimum 6.4°F higher in the forest than in the park. The mean daily range is 7.3°F smaller in the forest.

The evidence at hand supports the opinion that the above relation is due to the influence of the forest canopy. The influence upon minimum temperatures, which is by far the greatest and most important, appears to be exercised partly by the action of the tree crowns in checking the loss of heat by radiation, but mainly by the deflection of cold air currents from surrounding mountains and high mesas. A final and absolute determination of the extent to which the

presence of trees is responsible for the amelioration of temperature conditions in the forest, and the determination of the manner in which its influence is exerted demands further investigation.

The temperature of the soil in the forest during the summer, when shaded by trees, is about 5°F lower at a depth of 2 feet than at the same depth in the park.

The available data on atmospheric humidity show no definite relations between forest and park, excepting that the relative humidity appears to be slightly higher in the forest during the summer time and slightly higher in the park during the winter time.

The only appreciable effect of the forest upon precipitation is in its influence upon the distribution and disposal of snow and rain. Considerable amounts of snow and rain are collected by the tree crowns. Probably the greater portion of this blows or drips off, but an appreciable amount is lost by evaporation. The snow falls more evenly and accumulates to a slightly greater depth in the park than in the forest in the winter time, but it remains on the ground from two to three weeks later in the forest. A greater proportion of the snow waters is absorbed by the soil in the forest than in the park.

The average wind movement is only 51 per cent as great in the forest as in the park.

The evaporation from a free water surface is only 70

per cent as great in the forest as in the park.

The influence of the forest upon all factors studied, with the exception of relative humidity for which our data are inadequate, is similar to that shown by European observations. In the European forests, as in those covered by this study, the extremes of temperature are modified; but in European forests the maxima are lowered more than the minima are raised, with the result that the mean temperature is lower in the forest than in the open, while in our forests the maxima are lowered less than the minima are raised, with the result that the mean temperature is higher in the forest than in the open. The influence of the forest in decreasing evaporation is 30 per cent greater in Europe than is shown in this study.

Forestation of Parks. As regards parks, this study indicates that climatic conditions on such areas are decidedly unfavorable to the establishment of forest growth; that the invasion of such areas by forest trees can as a rule not be expected, and that if their afforestation is ever accomplished it must be by artificial means.

It is believed that atmospheric conditions in the Fort Valley Park are fairly representative of other parks in the region. With respect to wind and consequent evaporation there can be no great difference. In larger parks these factors will be higher and in smaller parks lower than at Fort Valley. They will also vary with the location in the

park, the lowest wind and evaporation being found along the south and west borders, since the prevailing winds are from the southwest. We might expect a great variation with respect to minimum temperature, but since nearly all parks are so situated as to receive cold-air drainage from the surrounding country, very low minimum temperatures resulting from this cause as well as from radiation may be looked for. On prairies, which are on the same level as the surrounding timbered country and are thus exempt from cold-air drainage, the only reduction of minima would be that due to radiation, and here we may expect to find about the same temperature conditions as on a cut-over area namely, a slight increase of the maxima and a reduction of the minima by 2°F or 3°F as compared with the forest.

The action of drought, through excessive evaporation from the soil and from the plant itself, and of low temperature in the form of unseasonable frosts, is very destructive to young seedlings before they have developed deep-root systems and woody stems. Annual observations on marked plots on the Coconino and Apache¹ National Forests show that even under the partial protection afforded on cut-over lands over 95 per cent of the seedlings die during the first year. The loss among seedlings which might spring up in a park under full exposure to the wind and frosts can only be conjectured.

¹Forest Service Bulletin 125, pp. 23-28.

A practical demonstration of the protective influence of the forest upon the action of wind and evaporation is afforded by a planting experiment in the spring of 1909. Fifty 2-year-old western yellow-pine transplants were planted on April 22 under similar conditions as on the forest-park margin, where wind and evaporation are practically the same as in the park, and some were planted in the forest. Western yellow pine at this age is not very susceptible to frost, and therefore the losses are attributable to other causes. On May 21 only 11 percent of the plants on the forest's edge were alive, while of those transplants in the forest, 90 per cent were alive. Soil samples taken on May 21, however, showed a moisture content of 17 percent within the forest, and 17.5 per cent at the forest-park margin, in the zone occupied by the roots, which were about 8 inches long. The moisture content is abundant for pine seedlings on both soils under reasonably favorable atmospheric conditions. No evaporation records are available for this period, but the wind movement at the edge of the forest was almost twice as great as in the forest. The conclusion is therefore that the plants in the edge of the forest, with an abundant water supply at their roots, dried up simply because the water loss from the foliage exceeded the amount supplied by the roots. In the forest, on account of a lower rate of evaporation from the foliage, a safe balance between the supply and expenditure of water

was maintained.

As a result of the above experience, planting in parks was almost despaired of, but another attempt was made in 1912 with excellent results. This success is attributed entirely to the use of a superior grade of plants. It has been demonstrated that western yellow-pine can be planted successfully in parks if good stock is used; but we have no assurance that plantations will grow to maturity. It is possible that the absence of natural forests in parks may be explained by the presence of adverse atmospheric conditions which make it impossible for seedlings to survive the first year; but it is probably that there are also other factors, such as unfavorable soil conditions. The bulk of our park areas in the yellow-pine type will eventually be given over to agriculture; but such portions as are too rocky for farming should be forested if possible."

Reynolds (1966) compared cattle, elk, and deer use in created openings (logged areas) and natural openings in spruce-fir forests of the Kaibab Plateau and the White Mountains of east-central Arizona. He found that:

"1. Cattle, elk, and deer use natural grassland openings in spruce-fir forests of Arizona differently, as measured by accumulated dropping groups. 2. Cattle make greater relative use of grassland openings than adjacent forest, elk make about equal use of the two situations, while deer use adjacent forests more than openings. 3. For

deer and elk, use of openings relative to adjacent forest is about the same for openings created by clearcutting as for natural grassland openings. Cattle do not use created openings relative to adjacent forest as intensively as natural openings. Possibly the sparsity of perennial grass and the presence of logging debris discourage more intensive use of created openings by cattle. 4. Deer and elk use is higher close to the border, on both forest and opening sides, than in areas more remote from borders. Cattle use increases from borders into openings, and decreases at greater distances from borders into the forest. 5. Openings smaller than 20 acres receive heaviest use by deer and elk. Circular openings larger than 20 acres are little used except around perimeters. Cattle preference for openings did not vary with size of opening. [Reynolds concluded by stating that] maintenance of natural openings and creation of small opening by cutting should improve deer and elk habitat."

Patton and Judd (1970) studied the role of wet meadows as wildlife habitat in the Southwest. They examined two meadow areas in the Apache National Forest. They noted that:

"wet meadows in the Southwest are slowly changing to drier sites. Dry conditions are more favorable for trees, and the meadows are gradually shifting to a forest type. [Their study determined that] three sites (meadow, transition, and dry forest) influence herbage production and plant

composition. Average per acre production for a 3-year period was 2,690 lb., 1,330 lb., and 170 lb. in the meadow, transition, and dry forest sites, respectively for the two areas studied. Deer and elk spent more time in the adjacent forest edge than in the meadow, but time spent in the meadow may be more important for quantity and quality of forage."

Turner and Paulsen (1976), in "Management of Mountain Grasslands in the Central Rockies: The Status of Our Knowledge, summarizes the results of several studies:

"Mountain grasslands of the central Rockies are closely associated with the subalpine forests in Wyoming, Colorado, New Mexico, and Arizona. The forest types commonly occur at elevations between 8,000 and 11,500 feet, or between the upper limits of the ponderosa pine forests and timberline. Within the timber stands, mountain grasslands are interspersed as parklike openings that vary in size from a few to several thousand acres. The grasslands may be found on gentle to steep slopes, wide valleys, and broad, rounded ridges. Commonly their distribution and major physical characteristics are described on the basis of the more extensive forest types.

Mountain grassland vegetation is a continuum expressing many interacting factors of the local environment. Most grasslands support, or are capable of supporting, numerous kinds of perennial grasses and forbs. Annual plants seldom are abundant except on recently disturbed or severely

overgrazed areas.

Two major but intergrading plant communities comprise the bulk of the mountain grassland type. Most extensive is the mountain bunchgrass community characterized by Thurber fescue (*Festuca thurberi*), where that plant has not been eliminated by grazing. The range of Thurber fescue extends from southern Wyoming southward through Colorado into northern New Mexico. The Wyoming bunchgrass community occurs mainly in Wyoming, but fingers southward in northern Colorado. It is typified by Idaho fescue (*Festuca idahoensis*), which is commonly associated with bluebunch wheatgrass and sagebrush (mainly big sagebrush) at lower elevations and on the drier sites (Williams 1963).

Other grasslands are found in the high-elevation broad valley floors between major mountain ranges in central and southern Colorado. Species are often an admixture of elements from lower ranges with those of the higher and somewhat more mesophytic dry mountain meadows (Costello 1944).

On more moist sites, wet meadow communities occur throughout the major plant communities. Sedges dominate these areas, but tufted hairgrass, Kentucky bluegrass, and alpine timothy are frequently abundant together with a number of moisture-loving forbs.

Vegetation varies greatly. Conspicuous and distinct differences between plant communities frequently accompany

marked changes in soil texture or exposure. Differences are less conspicuous with gradual changes in elevation or other features of the environment.

Mountain grasslands occupy sites where soils tend to be finer textured, deeper, and less well drained than on adjacent forested areas. Tree growth apparently is precluded from grassland areas because of competition from herbaceous plants, low temperatures, soil heaving, poor drainage, or other limiting factors. Where grasslands intermingle with timbered areas on hillsides, differences in site characteristics are usually less pronounced and trees are more likely to invade.

Under pristine conditions, Thurber fescue or Idaho fescue evidently comprised much of the vegetation, lending a grassland aspect to many high mountain parks. Forbs doubtless were locally abundant and conspicuous on recently disturbed sites. Within the subalpine zone, forbs tend to be more prominent at higher elevations and shrubs at lower elevations. A grassy understory commonly is overtopped by big sagebrush on relatively dry sites and by silver sagebrush on more mesic sites at upper elevations. Gambel oak and associated shrubs frequently comprise part of the plant cover on grasslands near the lower limit of the subalpine zone in Colorado.

Plant development varies from year to year as well as with the microclimate of local sites. At high elevations,

growth begins later but stages of development tend to be shorter than at low elevations; plants thus complete their life cycle in a relative short period (Costello and Price 1939, Pond and Smith 1971). Temperature and moisture during the growing season, of course, influence the rate of development.

Range readiness also varies considerably, since development of the forage crop to a stage suitable for grazing depends on when the snow disappears and ensuing temperatures (Costello and Price 1939). According to guidelines of the USDA Forest Service (1962), most ranges are ready for grazing between mid-june and mid-July. However, when the snowpack is usually deep and slow in melting, the grazing period may begin even later.

Herbage production on mountain grasslands occasionally exceeds 3,000 pounds per acre; however, yields of 1,000 to 2,000 pounds are much more common (Turner and Dortignac 1954, Hurd 1961). Above-average yields are produced on deep, fertile soils at intermediate elevations during years of favorable growing conditions. Highly productive sites may support a relatively dense cover of bunchgrasses, although some produce large yields of tall forbs. A variable mixture of grass and forb herbage is characteristic of mountain grasslands. Browse (mainly sagebrush or rabbitbrush) may be locally abundant.

Herbage production and composition vary considerably

from year to year. During an 11-year period in which production on moderately grazed pastures in western Colorado averaged 1,456 pounds per acre, yields ranged from 23 percent above to 27 percent to the total herbage. Although such variability is readily apparent, the underlying causes are obscure.

Pocket gophers and other small animals also influence floristic composition and the microenvironment. On Grand Mesa in western Colorado, available herbage was reduced by 20 percent or more where gophers numbered 25 to 30 per acre (Turner 1969). They may substantially reduce ground cover and may be the primary cause for the exposure of bare soil (Ellison 1946, Turner and others 1973). Gopher effects on infiltration, runoff, soil erosion, and moisture content of the soil vary with local conditions. On many areas their burrowing activity has resulted in mixing of soil horizons, and much vegetation has been covered by the soil they excavated (Ward and Keith 1962). Other studies of mountain grassland and aspen communities, however, have indicated gophers performed a useful function through cultivating and aerating the soil without reducing total herbage production (Ellison and Aldous 1952).

Often, however, responses caused by rodent activities cannot readily be distinguished from effects of livestock grazing and weather. Influences of fire, soil erosion, phytotoxins (allelochemicals), and soil nutrients also

complicate understanding of the composition and succession of mountain grassland vegetation (Ellison 1949, Miller 1963, Wright 1971).

On Colorado ranges that are grazed too heavily by cattle, Thurber fescue commonly is replaced by Idaho fescue and associated bunchgrasses on relatively coarse-textured soils, and by Kentucky bluegrass on fine-textured or compacted soils. Western wheatgrass and mulesear sometimes occur on fine-textured soils along with or instead of Kentucky bluegrass (Turner and Dortignac 1954). Moir (1967) reported similar findings for Kentucky bluegrass on fine-textured soils in southern New Mexico."

Dye and Moir (1977) studied the spruce-fir forest at its southern distribution near Sierra Blanca Peak in southern New Mexico. As part of this study the authors also examined the relationship of the spruce-fir forest to adjoining *Festuca thurberi* communities. Langenheim (1962) observed that fires within the spruce-fir forest at Crested Butte, Colorado, could initiate a Thurber fescue stage of succession. Dye and Moir (1977) felt in their study that:

"There is little evidence, however, that such Thurber fescue communities at Sierra Blanca (Moir, 1967) would develop into spruce-fir forests. Herb- and shrub-dominated states of forest development typically show a wealth of forest species, most of which are entirely absent from *Festuca thurberi* meadows. Although mollic soils of the

spruce-fir forest are morphologically similar to those of the grass-dominated openings (Moir, 1967), the mull humus in the two communities could be contributed by different plant species and does not necessarily reflect a history of similar vegetation. The rarity or absence of many fescue meadow species in the shrub thickets also suggests that the former is not a fire precursor to the *Ribes* stage of forest development. Our observations indicate that *Ribes montigenum* and *R. wolfii* (neither of which occurs in fescue meadows) are dominants of the earliest stage of fire-induced forest clearings at most sites within the spruce-fir habitat. Stahelin (1943) reported that forest regeneration after fire was most rapid on cover types dominated by forest understory species such as *Vaccinium*. He observed that grass-dominated communities of subalpine regions of the central Rocky Mountains exhibited very slow rates of coniferous invasion. In New Mexico the fescue communities also seem to be unfavorable environments for forest advance under present climates. Hypsithermal stress may not only have contributed toward near extinction of forest species, as discussed earlier, but also may have served to initiate the grass-dominated meadows. Subalpine grass-dominated communities seem inimical to tree invasion even at sharp ecotones (Franklin et al. 1971). Therefore the cooler, wetter period of the 1960-1969 decade (Namias, 1970) did not cause tree establishment in *Festuca thurberi* communities.

In the single fescue meadow where young fir and spruce trees are apparent (Moir, 1967), tree invasion is confined to the immediate proximity of old nurse trees. A possible explanation for this unusual instance of forest advance is that isolated old trees within this particular fescue meadow served as bedding areas for livestock. An old sheep camp existed nearby, and animals may have initiated succession by manuring, soil compaction, grazing or other reasons (F. E. McDermaid, pers. comm., 1967).

At upper elevations along the main ridge between Sierra Blanca Peak and Lookout Mountain young trees have become established in *Festuca thurberi*, *F. ovina* and alpine communities. Accelerated erosion caused by recent ski developments here may have caused at least some of this tree establishment as soils became shallower and more skeletal (Ellison, 1954). Very recent climatic changes may also be partly responsible, especially for invasion into lithosolic alpine communities. Our present evidence suggests that spruce-fir forests are generally static with respect to herb-dominated fescue communities at lower elevations and dynamic at upper elevations."

Butler (1986) wrote the following about conifer invasion of subalpine meadows in central Lemhi Mountains, Idaho:

"In the mountains of the western United States, subalpine forest environments are difficult sites for tree establishment (Agee and Smith 1984). When trees do become

established in locations such as above present treeline or in subalpine meadows, the establishment is often attributed to some form of climate change which has made conditions more amenable for tree survival (Franklin et al. 1971), Schimpf et al. 1980, Kearney 1982, Ostler et al. 1982, Winter 1984). Other factors, particularly land-use practices, must also be examined as possible causative factors in successful tree establishment at formerly inhospitable sites (Dunwiddie 1977, Vale 1981b).

A recent study from the Lemhi Mountains of east-central Idaho revealed a major historic treeline advance, initiated in the 1920's (Winter 1984). This advance was correlated with a broad climatic warming and drying that occurred across western North America during the same period, and which has also been identified by examination of the ages of invasive trees in subalpine meadows (e.g., Franklin et al. 1971, Nisle 1981, Agee and Smith 1984). Other studies in western mountain meadows have also identified successful tree establishment in the same period, but did not directly attribute these tree invasions to climate change (Koterba and Habeck 1971, Vale 1981a).

The present study was concerned with 1) identifying the period(s) of successful tree invasion into mountain meadows in the central Lemhi Mountains of Idaho, 2) comparing the period(s) of meadow invasion to the period of treeline advance in the same range, identified by Winter (1984), and

3) attempting to identify causal factors which allowed the meadow invasions to occur.

Vegetation surrounding the meadows is largely mature Douglas-fir forest. Vegetation in the meadows is primarily sheep fescue (*Festuca ovina*) or Idaho fescue (*F. idahoensis*), with very little bluebunch wheatgrass (*Agropyron spicatum*). Bluegrass (*Poa secunda*) is a secondary species (U.S. Forest Service 1964). Sagebrush (*Artemisia* spp.) is found in all three meadows. Various members of the aster family (Compositae) are found in all three meadows.

Periods of invasion vary among the three meadows studied, suggesting that 1) no one causal agent is responsible for invasion, or 2) the same causal agent operated at different times in each meadow. Suggestions as to the causal agents in each meadow are outlined below.

In Deer Creek Meadow (DCM), initial invasion correlates temporally with the dry period of 1920-1940, and with the period of introduction of grazing. Other studies in the region have shown that warmer and drier conditions during these decades produced longer snow-free periods in subalpine meadows, drying the meadow soils and therefore allowing tree invasion (Franklin et al. 1971, and Agee and Smith 1984, in the Pacific Northwest; Ostler et al. 1982, in the Uinta Mountains of Utah; and Schimpf et al. 1980, in the northern Wasatch Mountains of Utah). This same period also saw an

upper treeline advance at least partially attributable to milder climatic conditions (Winter 1984), so it is reasonable to assign climate as one of the most likely causal agents for the onset of the tree invasion.

Cessation of grazing has been cited as conducive to tree invasion in some studies (Vale 1981a, 1981b), whereas other work suggests that moderate levels of grazing result in abundant tree invasion, by reducing competition with meadow vegetation (Dunwiddie 1977). The introduction of grazing around 1920, at an initially moderate level, probably assisted the establishment of seedlings in DCM. As grazing pressures increased, however, seedling establishment declined except during the immediate post-fire period. Although reduced grazing was recommended in 1950 and imposed in 1951, DCM continues to experience severe grazing disturbance in most summers. This grazing probably precludes continuing invasion of the meadow, in that seedlings are trampled and destroyed before they can become well established and sufficiently large to survive. Cessation of grazing would probably result in a renewed initiation of seedling invasion.

The two periods of pronounced invasion in Harry's Meadow (HM), 1905-1919 and 1925-1945, are probably climate related, with a possible grazing influence in the second period. The first period correlates with the termination of cold, late Neoglacial climatic conditions in the Lemhi

Mountains (Knoll 1977, Butler 1983). Snow retention into the summer season was therefore reduced, allowing for the initiation of meadow invasion. The second peak of invasion probably represents a continuation of the invasion process, favored by the drought conditions prevalent in that time period. The onset of grazing in the 1920's may have contributed further to the second phase of invasion.

The period of initial invasion in HM coincides with the cessation of limber pine establishment in all three meadows, suggesting climate change as the primary invasion instigator. Post-1905 trees in the meadows represent species such as Douglas-fir and lodgepole pine, species which are more tolerant of warmer and drier conditions. The limber pine is a tree frequently found near upper treeline (Winter 1984), and is associated with cold climatic conditions. Given the change from late Neoglacial to post-Neoglacial conditions about 1905 in the Lemhis, it is not surprising that limber pine was no longer able to successfully invade and compete in the warmer and increasingly drier meadow environments.

Meadow invasion has essentially ceased in HM, with no tree present (except for the few unsampled seedlings) younger than forty years in age. Reasons for this are unclear, in that no grazing has been observed in this meadow in five summer field seasons, nor is the soil of the meadow churned and disrupted as in the heavily-grazed DCM. Fire

has not been a factor, nor has human disruption,...No evidence of cutting or stump removal of small trees is present. The total absence of grazing (associated with an absence of seedlings) may lend support to the theory that moderate (but not heavy) grazing levels assist in tree establishment.

Invasion of First Meadow (FM) predates the invasion in HM by approximately ten years. In the absence of grazing or fire corroboration, climate remains the most likely causal agent for invasion. FM is more exposed and sunny than HM, and 50m lower in elevation. These factors may have allowed warming and drying, and subsequent meadow invasion, to begin sooner in FM than in HM.

Once begun, the invasion in FM has remained steady, except for a surge in the 1940-1944 pentad. Although no fire scars were located on trees in FM, the presence of modern charcoal suggests that this surge could be a result of post-fire succession. The large number of invasive lodgepole pine also suggests fire succession. Invasion since the 1940-1944 peak has continued.

Previous studies of invasion of trees into subalpine meadows have cited several possible causal agents. In this study, the influences of these same causal agents have interacted in a complex fashion. Some periods of invasion onset or cessation are attributable to climate changes, whereas others are related to changing grazing pressures

interacting with climate change. Each meadow examined had its own history, depending on which potential causal agents had interacted in that meadow."

Aldon and Barstad (1987) studied several montane grasslands in the Escudilla Mountain Natural Area in the Apache-Sitgreaves National Forest near Alpine, Arizona. Some of the results that they found are as follows:

"Three undisturbed montane grassland meadows were studied during the summers of 1984 and 1985. Toolbox Draw, Bead Springs, and Middle Meadow were monitored using community structure analysis to measure each plant community's composition and diversity, as well as cover, density, and frequency of individual plant species.

Toolbox Draw was dominated by Arizona fescue (*Festuca arizonica*), a sedge (*Carex oreocharis*), sheep fescue (*Festuca ovina*) and mountain muhly (*Muhlenbergia montana*). Bead Springs was strongly dominated by Thurber fescue (*Festuca thurberi*), the only known location of this grass in Arizona, Arizona fescue, sheep fescue, and tufted hairgrass (*Deschampsia caespitosa*). Middle Meadow was dominated by a forb (*Geum triflorum*), Arizona fescue, and mutton bluegrass (*Poa fendleriana*). This fescue species, which occurred in both Bead Springs and Middle Meadow, is robust and may be an ecotype different from the Arizona fescue found in Toolbox Draw, which is the typical species common in the Southwest.

Since the 900 acres of the proposed Escudilla Research

Natural Area have been unused or only lightly and infrequently used by cattle and have not been greatly affected by other land use, they are ideal as study sites. These montane grasslands, while not strictly pristine, may be excellent indicators of conditions before various human uses of the land forced species to change."

STUDIES OF HIGH ELEVATION GRASSLANDS IN THE PACIFIC NORTHWEST AND THE SIERRAS NEVADA MOUNTAINS

Franklin et al. (1971) discussed invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Their study areas included Paradise Valley at 1600-1800m on the south slope of Mount Rainier; Mount Rainier National Park and the Goat Rocks Wilderness southeast of the park; Mount Hood and Mount Jefferson in Oregon, and in the Mount Baker and Harts Pass areas in the North Cascades. Closed forest, older tree groups in meadows, meadows, and all invading trees were examined and the following contains some of their observations and results:

"Shifting boundaries between subalpine meadows² and adjacent forests in mountain areas have important implications in land management. The meadows are often prime recreational attractions or are prized as sources of

²Our terminology is based upon recommendations by D. Love (1970). In particular, usage of the term "subalpine" refers to that belt between upper altitudinal tree line and the lower closed-canopy, more or less continuous coniferous forest. The term "subalpine meadow" refers to herb- or shrub-dominated communities in the forest-tundra ecotone where trees do not, at present, dominate.

game or livestock forage, so that shifts toward forest dominance merit considerable attention.

Recent invasion of subalpine meadows has been widely reported in mountainous areas of the Pacific Coast of North America from British Columbia to the Sierra Nevada, although the tree species involved and probable causes vary. In 1966, we surveyed and dated meadow invasion by trees at Mount Rainier National Park, Washington, with the support and encouragement of the National Park Service.

Several significant features of meadow invasion are revealed in this study. First, the invasion occurred during a restricted time span earlier in this century and has essentially ceased for about the last 20 years. Second, it was a massive invasion unrelated to the gradual expansion of forest onto meadow areas normally expected. Finally, it has occurred in many subalpine areas along the coast of the northwestern United States and adjacent British Columbia. Before considering possible causes for the invasion, we will briefly discuss each of these features.

The widespread and massive nature of subalpine meadow invasion is confirmed by both our reconnaissance data and published accounts. Brink (1959) reported extensive invasion of heather communities by *Abies lasiocarpa* and *Tsuga mertensiana* in coastal British Columbia. Douglas (1970) found it to be widespread in heather communities in the northern Cascades of Washington. Fonda and Bliss (1969)

and Kuramoto (1968) encountered the phenomenon in the Olympic Mountains, with *Abies lasiocarpa* the major invader in drier northeastern areas and *Tsuga mertensiana* more common on western slopes. Van Vechten (1960) and Swedberg (1961) reported invasion of subalpine meadows by *Tsuga mertensiana* in two portions of the Oregon Cascade Range.

Our data clearly show that establishment of invading seedlings and saplings was essentially limited to a 20- to 30-year period in the first half of this century. Establishment reached a peak in the late 1920's and early 1930's and seedlings younger than 25 years in age are rarely seen. These ages correlate well with those reported by other investigators. For example, Brink's (1959) trees were mostly 20 to 40 years old, indicating a similar chronology. The only significant exceptions are the data reported by Fonda and Bliss (1969) who found age groups of 8 to 15, 20 to 25, and 35 to 45 years in their invading trees. The 8 to 15 group and 1- and 2-year old seedlings which they report are found only rarely in our study areas.

In the Mount Rainier area, invasion of meadow areas by tree groups has been typified as a gradual process (Franklin and Mitchell 1967). Development of tree groups would begin with the establishment of one or two seedlings of a pioneering species. Around these tree foci, additional trees would be established from seed or by layering as the first specimens ameliorate the meadow microenvironment,

particularly by accelerating snowmelt and extending the growing season. In this way, tree groups or copses, would gradually extend over meadow areas by expanding their margins. In his studies in the subalpine region of the northern Rocky Mountains, Patten (1963) suggested that seeds of Engelmann spruce falling in the open at the forest margin, where spring temperatures are higher than within the forest, would have enhanced germination stimulus and thus caused forest advance into meadows.

Possible Causes for Meadow Invasion. The gradual successional encroachment of forest on meadow is often encountered in subalpine areas, but massive changes of the type reported here are not expected. Several possible causes have been suggested, including fire control programs, grazing, modifying effects of adjacent forest, and climatic changes.

Fire is often considered an important factor in creating and maintaining meadow areas. For example, Kuramoto (1968) felt that fire was the major factor responsible for subalpine meadows in the Olympic Mountains. The microclimate of the fire-created opening would determine whether or how fast trees would reinvade. At Paradise Valley there are large open areas in the lower part of the subalpine zone which were created during the last century by extensive fires (Haines, 1962). However, these are, in general, easily identified as potentially forested sites by

old logs and snags, presence of several herbs and shrubs typical of forested sites (e.g., *Vaccinium membranaceum* Dougl.), and an abundance of charcoal. Tree regeneration on these fire-created openings is generally dense and vigorous and exhibits a full range of age classes down to 1- or 2-year-old seedlings, all of which indicates a strong and continuing successional pressure toward forest.

We conclude that fire has had little to do with the creation and maintenance of the subalpine meadows considered in our study. There is little or no evidence that the meadow sites studied have been forested in postglacial time--neither charcoal nor rotten wood is common in soils except near older tree groups and forest. Consequently, fire control programs instituted in this century could have little to do with the tree invasion reported here.

Excessive grazing of meadow areas often encourages tree invasion by reducing herbaceous competition. Many of the meadow areas examined have no grazing history, however, except for an occasional native herbivore. The only case observed where grazing was felt to have had a significant effect was in the Goat Rocks Wilderness. There, extensive tracts of what were probably *Festuca viridula*-*Lupinus latifolius* meadows were heavily grazed by domestic livestock earlier in this century. Tree invasion is quite common on these degraded meadow types in contrast to the nearly pristine *Festuca*-*Lupinus* communities examined in Mount

Rainier National Park, where cattle grazing permits were issued for only three summers during and after World War I (McIntyre, 1952).

Conditions on the study area at Paradise Valley suggest that the modifying influence of adjacent forest or tree groups was of little importance in aiding seedling establishment. Invading clumps of seedlings and saplings are not closely associated with older trees. This situation generally agrees with that described by Fonda and Bliss (1969), who found greatest densities of invading trees to be within 5 to 8 m of the center of treeless areas. Perhaps if the meadows we studied had had larger segments free of older trees, we would have observed an edge effect, which could reflect both increased seed supply and more favorable microenvironments.

The simultaneous, temporary occurrence of conditions favorable for conifer invasion over such a widespread area strongly suggests a climatic flux favorable for conifer seedling establishment. Snowpack, through its influence on length of growing season, is known to be one of the most important factors in determining the position of forest-meadow ecotones in subalpine zones. A climatic flux which reduced duration of snow cover (i.e., increased the length of the growing season) would favor conifer invasion (Brink, 1959). Fire control programs and livestock grazing could have made only localized contributions to the phenomenon.

Meadow invasion would require at least one other major element in addition to one or several favorable growing seasons—an adequate supply of tree seed. Good seed crops are not produced annually, but generally at 3- to 6-year intervals in the case of *Abies lasiocarpa* (Franklin, 1968). Consequently, we would expect significant tree establishment only in years when a good seed crop (produced the previous summer) coincided with a favorable growing season. With adjustments for probable underestimation of ring counts, some peak years of establishment are strongly suggested — 1928, 1933, and 1937. If we go back in 3- or 6-year increments from the bumper *Abies lasiocarpa* seed crop experienced in 1968 (data on file, Forestry Sciences Laboratory, Corvallis, Oregon), we can hypothesize abundant seed production in 1932. This seed would germinate in the spring of 1933. The growing season that year began late (snow-free about July 15), but the snow-free period was one of the longest on record, and the snow-free season in 1934 began exceptionally early. There could, therefore, have been a combination of factors favorable for conifer establishment at that time. The snow-free seasons in 1928 and 1937 were similarly longer than average. These interpretations and extrapolations of climatic seed production, and seedling age data are less than definitive but are interesting nevertheless.

Relation to Community Type. The greater abundance of

invading conifers in *Phyllodoce* and *Potentilla* communities but greater growth of established trees on *Valeriana* and *Festuca* types may have considerable ecological significance and is worthy of further detailed study. Kuramoto (1968) noted a similar pattern in the Olympic Mountains. Both the *Valeriana* and *Festuca* communities typically have a dense, herbaceous cover 0.5 m or more in height and are on sites with somewhat warmer and longer snow-free seasons. The minimal amounts of tree invasion in these communities suggest that one important factor limiting conifer establishment may be herbaceous competition. Under these conditions, increased tree invasion in response to a longer, snow-free season should be minimal, as seems to be the case. Once competition is overcome and trees are established, however, seedling growth rates would logically be superior on these somewhat warmer habitats and better drained soils.

Management Implications. Conifer seedlings have invaded large portions of subalpine meadows in the Pacific Northwest, including many sites where the meadows are key recreational attractions. Except in the case of overgrazed meadow areas, this appears to be an entirely natural phenomenon. Although the invasion was essentially completed two decades ago, trees are only now reaching sufficient size to be conspicuous and to significantly alter meadow composition and scenic vistas.

The land managers responsible for these landscapes must

decide whether they will remove invading seedlings from all or a portion of the affected area or will allow developments to proceed unhindered. If control of tree encroachment is deemed desirable, removal of seedlings and saplings by cutting should be very effective. Successional pressures are not great, and reinvasion will not occur until favorable environmental conditions again exist for establishment of conifer seedlings. Even if reinvasion were to take place again the next year, which seems most unlikely, it would be 20 to 30 years before trees were again sufficiently large to constitute a threat to meadow communities.

If tree removal is not carried out, some subalpine meadow area will undoubtedly be lost to forest. This is not necessarily serious, however, as the higher subalpine meadows and some of the most luxuriant types (e.g., *Valeriana*) are least affected."

Ratliff (1985) reported on the status of knowledge on the meadows in the Sierra Nevada of California:

"Meadows in the Sierra Nevada of California are wetlands or semiwetlands supporting a cover of emergent hydrophytes and mesophytes and dry herbland of the subalpine and alpine zones (Ratliff 1982). They may be classified in a number of ways, including by wetness, range type, altitude, physiography, vegetation, and sites. A single classification is usually applied to an entire meadow, with little if any recognition given to different sites. Wet,

moist, or dry meadows can be further classified, however, by range type, which indicates the vegetation type and dominant species (Forest Service 1969).

Meadows of Gaylor Lake Basin in Yosemite National Park were classed as wet, moist, and dry (Klikoff 1965). The wet type is the shorthair (*Calamagrostis breweri*) type of Sumner (1941), and the dry type corresponds to the short-hair sedge (*Carex exserta*) type described by Bennett (1965).

Similarly, in Yosemite Valley, meadow sites were classified in relation to a drainage gradient (Heady and Zinke 1978). Sedges (*Carex* species) decreased in percentage of species composition from depression bottoms to sites excessively drained. Grasses generally increased in the composition, becoming more prevalent than sedges on the better drained sites.

Kings Canyon National Park meadows have been classified into wet, woodland, and shorthair types (Sumner 1941). The wet meadow type consists of sphagnum, coarse-leaved sedge, fine-leaved sedge, and grass subtypes, and division of the woodland meadows into broad-leaved and coniferous subtypes was suggested (Bennett 1965).

Meadows have been classed as montane (midaltitudinal) and subalpine and alpine (high altitudinal) (Sharsmith 1959). Three classes - level meadows, hanging meadows, and stringer meadows - have been used along Rock Creek in Sequoia National Park (Harkin and Schultz 1967).

A physiographic classification with two classes in the top category was proposed (Benedict 1981). The classes were meadows with vegetated margins (type 1) and meadows with sandy margins (type 2). A lower level category contained topographic classes (basin, slope, and stream), and within these were classes of a geological category. The classification, like most others, dealt with meadows as the individual units to be classified.

At the Blodgett Forest Research Station in California, rush (*Juncus*), forb, and dry grass meadow vegetation classes were identified (Kosco 1980). A fourth class contained rushes, sedges, grasses, and forbs in about equal proportions.

Sites within meadows are considered individual units (Ratliff 1979, 1982). Fourteen meadow site classes are described on the basis of current vegetation. The classes are viewed as approximations to series within meadow subformations (Hall 1979).

In developing the classification scheme provided in his technical report, Ratliff drew from the authors cited, classifications of meadows from other areas, and his own experience. The scheme follows the basic concepts of Hall (1979). The basic units of classification are meadow sites. Ratliff defined a meadow site as an area of meadow with a homogeneous species composition and a general species composition different from that of adjacent areas (Ratliff 1979). Major

categories of the system are subformations, series, and associations. Although the classification is still largely heuristic, Ratliff believed it serves as a vehicle for communication between land managers and researchers.

Ratliff (1985) in this report discussed four management problems that plague a meadow manager: animal activities (specifically livestock grazing and human use), lodgepole pine invasion, fire, and gully erosion. The following discussion from Ratliff concentrates on the meadow invasion and fire:

"Invasion of Meadows. Sierra lodgepole pine is listed as *Pinus contorta* var. *murrayana* (Krugman and Jenkinson 1974). It is also considered a separate species (Munz and Keck 1959). Common names for the species are Sierra lodgepole pine, lodgepole pine, and tamarack pine (Little 1979). Other varieties of lodgepole pine—*P. contorta* var. *contorta* and *P. contorta* var. *latifolia*—are in close kinship with Sierra lodgepole pine; available information on them should be considered. For convenience, this report uses *lodgepole* or *lodgepole pine* to refer to all varieties.

Lodgepole pine's remarkable physiological adaptability and its occurrence around and in mountain meadows make it a focus of concern to land managers. It has invaded many meadow sites. The trees reduce the area of open meadow, alter light and moisture available for herbaceous plants, and produce undesirable changes in species composition and productivity.

Invasion of meadow sites by lodgepole pine has been documented primarily by observations spanning many years. A sharp transition from open meadow to large, older trees gives the impression of a stable relationship between forest and meadow. A transition from open meadow to scattered small trees to larger trees to large mature trees suggests instability and change.

The best quantified data on invasion are provided by Vankat (1970). He determined ages of trees in and around meadows and dated the invasion by lodgepole pine as 1900 to 1905. Lodgepole pine reproduction was scarce between 1865 and 1900—the period of heavy grazing by sheep.

The following hypotheses related to invasion of meadows by lodgepole pine have been proposed (Leonard and others 1969):

The establishment of lodgepole pine seedlings is inhibited or prevented at the germination stage by sod, dense meadow vegetation or dense organic surface material, and by saturated soil. Seedlings are inhibited from rooting by saturated soil and are highly susceptible to trampling on grazing sites free of exposed rocks. Growth and development beyond the vulnerable seedling stage are further inhibited by constantly saturated soil, and by trampling and browsing.

A lodgepole pine that has developed beyond the

seedling stage on a meadow site can be expected to follow a normal course of development and to grow relatively rapidly even in seasonally saturated soil, or constantly wet but well aerated soil. The development of a stagnant, constantly saturated root environment is one exceptional circumstance that can lead to the decline and death of a sapling or mature tree over a period of several years.

Assuming that these hypotheses are true, in order to stop or reverse the invasion process, we need to understand the requirements of lodgepole pine for seed germination and seedling establishment. And we need to understand how management can modify the meadow environment to prevent occurrence of those requirements.

Growth and establishment. Lodgepole pine can become established, grow well, and reproduce in soil environments that apparently are unfavorable to other conifers. It also grows under conditions in which the other conifers grow, including near tree-line environments. Although not always the dominant tree species, lodgepole pine probably grows in most montane and subalpine meadow edges of the Sierra Nevada.

Sierra lodgepole pine grows in an elevational range of about 5,000 to about 11,000 ft (1,525 to 3,353 m), the trees grow from 50 to 130 ft (15 to 40 m) tall. They produce pollen in May and June (Krugman and Jenkinson 1974), and

cones ripen and disperse seed in September and October. Sierra lodgepole pine does not have serotinous cones; rather, the cones open soon after maturity and do not persist long on the trees. Seed production can start at 4 to 8 years of age, and normally a large seed crop is produced each year. The average number of cleaned seeds is 117,000 per lb (257,938/kg). About 200 lb (91 kg) of cones are required to obtain a pound of seed. Stratification of fresh seed is not needed to induce germination; however, for stored seed, stratification at 33° to 41° F (0.6° to 5° C) in a moist medium is recommended. Germinative capacity averages about 75 percent. A 70 percent germination of lodgepole pine seed collected at Rock Creek in Sequoia National Park was reported (Harkin and Schultz 1967).

Lodgepole pine regenerates best on mineral soil or disturbed duff free of competing vegetation and in full sunlight (Tackle 1961). The seed of lodgepole pine requires a small amount of light for germination, but the seedlings require considerable light to ensure satisfactory reproduction (Mason 1915). The best seedbed is a mineral soil with plenty of heat and available moisture; layers of needles or undecomposed humus may dry out before roots can reach the mineral soil. In Oregon, seedbeds of mineral soil supported about twice the number of seedlings as undisturbed litter (Trappe 1959). In summary, lodgepole pine needs a mineral seedbed in well-lit warm, moist environments.

One study reported on effects of low temperatures and compared lodgepole and ponderosa pine seedlings (Cochran and Berntsen 1973). Thirty-six-day-old seedlings suffered greater mortality from night temperatures of 18° F (-7.8° C) than did 22-day-old seedlings. Younger seedlings of lodgepole pine can therefore stand lower night temperatures in spring than older seedlings. If a period of warm temperatures (just above freezing) is followed by temperatures of 20° F (-6.7° C) or less, mortality is reduced. Also, seedlings grown until fall under natural photoperiods can withstand minimum night temperatures of 15° F (-9.4° C), showing that shortening photoperiods are conducive to hardiness. It appears that only extremely cold night temperatures in spring could prevent lodgepole pine establishment in meadows. Such temperatures may occur in some meadows because of cold air drainage.

If other conditions are suitable, abundant germination of lodgepole pine seed may be expected in meadows soon after soil warms in spring. A study of the effects of temperature on germination of lodgepole pine seeds found that the optimum temperature was about 70° F (21.1° C) (Bates 1930). Temperatures above 82° F (27.8° C) or below 60° F (15.6° C) reduced germination. Fluctuating temperatures with the daily mean at 65° to 70° F (18.3° to 21.1° C) gave the best rates of germination. The response to fluctuating temperatures was considered to be linked with the species'

habit of reproducing in exposed areas with great daily extremes in temperatures. The maximum and minimum temperatures of 48° and 38° F (8.9° and 3.3° C) at one centimeter from the south side of rocks (Leonard and others 1968) approximate the fluctuation stated earlier.

At 50 percent full light intensity, lodgepole pine seed germination was 22 percent (Boerker 1916). At 16 percent of full light intensity, germination was 7.5 percent; at 2 percent of full light, 3.5 percent. These data indicate lodgepole pine's need for light.

Moisture Effects—Physiological responses of lodgepole pine to soil moisture were studied along Rock Creek in Sequoia National Park (Leonard and others 1968, 1969). Pressure chamber readings on cut branches were taken as measures of physiological response. A branch (with its cut end protruding through a stopper) was sealed in a pressure chamber. The chamber was gradually pressurized with dry nitrogen gas; the pressure was recorded when water became visible at the cut surface.

Except on a porous moraine (dry site) in 1968, lodgepole pines under all site and seasonal conditions registered pressures almost entirely below 200 pounds per square inch (psi) (14 kg/cm²). Diurnal pressures in September, however, peaked at about 225 psi (16 kg/cm²). Pressures on the dry site approached 250 psi (18 kg/cm²) toward the end of summer. A pressure of 200 psi (14 kg/cm²)

represents a level of stress of significance for lodgepole pine. That pressure was exceeded only under circumstances of depleted soil moisture, excessively high evaporative stress, fungal infection of the needles, or an obviously poor crown condition.

Midwinter pressure readings showed that soil moisture was readily available. Except for a few surface centimeters, the soil was not frozen. Water and nutrients are therefore available for metabolic processes of lodgepole pine even in the dead of winter. Water movement in the trees is normal, at least when leaf tissue is not frozen.

Lodgepole pine is tolerant of soil saturation, thus able to survive and grow in meadows. No differences in physiological response were found among trees along a gradient from saturated meadow soils to porous moraine soils. Soil saturation did not appear detrimental to lodgepole pine. Deliberately flooded trees had low pressures and high rates of transpiration, indicating efficient water absorption by the flooded roots.

Continuous saturation lasting for several years could nevertheless contribute to tree mortality. Mortality of lodgepole pine in some normally saturated situations was observed. Long-term saturation of the trees may result in preferential attack by fungal infections of the needles. Characteristic fungal reproductive structures in needle specimens indicated that damage was caused by *Hypodermella*

montana. Crowns of weakened trees were sparser than uninfected trees and showed some yellowing. Severely affected branchlets had shed all but the current crop of needles and their terminal buds were often dry and brown. Although such fungal infections may not kill the trees, they can weaken them. These trees may then become susceptible to secondary attack by bark beetles. Evidence of bark beetle attack was observed in dead trees.

Disturbance by Livestock and Rodents—Grazing

disturbance by livestock is the usual reason given for the invasion of meadows by lodgepole pine. Grazing—especially sheep grazing—and its influences on the vegetation and soil modified the meadow environment creating a suitable niche for lodgepole pine (Vankat 1970), and Ratliff believes that statement to be true. However, Ratliff also believe the proposition must be accepted that meadow invasion by lodgepole pine can be autogenic—the result of plant succession—and not always the result of allogenic effects.

On biologically and geologically stable meadows, the opportunities for invasion by lodgepole pine are few (Benedict 1981, 1982). Instability can result both from natural causes and from human activities.

If geologic or climatic change can induce instability in a meadow system by permitting lodgepole pine invasion, geologic or climatic change can induce instability in a forest system by permitting meadow invasion. That such

events occur in the Sierra Nevada has been well demonstrated (Wood 1975). Over geologic time, meadows have developed, disappeared, and redeveloped at the same geographical locations.

From studies of stand age structure of trees contiguous with meadows, it has been hypothesized that sheep grazing and fires set by shearherders to facilitate the movement of their flocks prevented regeneration of lodgepole pine, hereby stopping the process of invasion (Vankat 1970). This situation was photographed at Jackass Meadow on what is now the Minarets Ranger District of the Sierra National Forest (Sudworth 1900). The picture shows a fence line situation. The caption states that within the fenced area lodgepole pine reproduction was abundant, but outside, where sheep graze regeneration in the Rock Creek area of Sequoia National Park (Sudworth 1900).

Certainly, we can associate overgrazing with soil disturbance and loss of vegetative cover. Sheep grazing during one 9-year period (1864-1873) was blamed for creating "a gray sea of rolling granite ridges, darkened at intervals by forest, but no longer velveted with meadows and upland grasses" on the Kern Plateau (King 1902, p. 351). Sheep, through trampling and grazing, can destroy fragile sods and effectively denude some meadows.

Although it prevented or checked the invasion of meadows by lodgepole pine, heavy grazing may have provided

bare mineral soil and reduced mulch and competition, thereby predisposing meadows to invasion. We know that large areas of meadow were invaded by lodgepole pine soon after 1900, and that this invasion coincides with the end of heavy concentrations of sheep. We can therefore hypothesize that human activities, within historic times, have both impeded and encouraged lodgepole pine invasion.

Probably, lodgepole pine invasion of meadows is most strongly related to sheep grazing; however, cattle can cause severe disturbance to meadows. That continued invasion by lodgepole pine into meadows can be ascribed to forces set in motion during the time of sheep grazing is difficult to determine. We know that the current invasion has been occurring on ungrazed meadows and on meadows grazed continually since about 1900.

Grazing may indirectly cause invasion by lodgepole pine by affecting gopher activity and populations of some seed-eating rodents. Overgrazing often aggravates the normal effects of gophers. And overgrazing may expose other rodents to greater predation, thereby reducing the amount of lodgepole pine seed consumed and improving chances for seedling establishment.

Although he did not fully evaluate the effects of pocket gophers, Buchanan (1972) suggests that they may play a role in lodgepole pine invasion. Surface soil deposits may benefit survival of lodgepole pine seedlings. These

deposits provide the mineral seedbeds apparently required. Gopher mounds are slightly raised, not as deeply shaded by herbaceous vegetation as the undisturbed soil surface, and are relatively free of competing vegetation. Pocket gopher mounds covered about 5 percent of the meadow and 4 percent of the meadow-forest ecotone, providing a sizable area of suitable seedbed (Buchanan 1972). Where livestock no longer graze—as well as where they do—gopher activities may contribute to meadow invasion by lodgepole pine.

Snow Depth—In the Sierra Nevada, most lodgepole pine seedlings become established in years of low snowpacks (Wood 1975). Length of the snow-free period may be the most critical variable in tree invasion of subalpine meadows (Franklin and others 1971). Tree invasion is related to periods of below-normal snowpacks and earlier snowmelt or to a long snow-free period after melt. A good seed crop followed by an early melt of snow can be expected to result in significant tree establishment. Where snow is deep, conifers do not usually reproduce (Billings and Bliss 1959). In the "ribbon forests" of the Rocky Mountains, tree seedlings were protected by snowpacks on their windward side (Billings and Bliss 1969). Deep snowpacks resulted from the ribbon of trees immediately to windward. Adjacent to and in the lee of that ribbon, snowpacks were generally too deep and melted too late to permit tree establishment.

From these reports, we may expect that deep, long-

lasting snowpacks tend to inhibit lodgepole pine invasion of meadows. But studies have not proven this to be fact.

A weather modification that increases snowpack could enhance conditions for lodgepole invasion (Buchanan 1972). Lodgepole pine seedlings, 2-0 stock, were planted in meadows, forests, and forest-meadow ecotones of the Bridger Range, Montana. Survival of the seedlings was lowest in the meadows and increased with increasing snow depth up to 7.9 ft (240 cm). Naturally occurring lodgepole, 1.7 to 6.7 ft (0.5 to 2 m) tall, increased in frequency with increasing snow depth ($r = 0.7$). Frequency of small seedlings was significantly correlated ($r = 0.36$) with snow depth on the meadows. Survival of planted lodgepole pine and presumably natural reproduction was explained by the relationship of snow and availability of late-season moisture. From this, we may expect the greatest invasion activity at the forest-meadow ecotones where snow accumulates to depths of not over 8 ft (244 cm) and melt is slow.

It seems reasonable that periods of low snowpack and early melt may be necessary for seedling establishment. Once established, the young trees are protected from cold temperatures, wind, physiological drought, and browsing by a deep, long-lasting blanket of snow. If the snowpack is deep enough and lasts long enough, survival of invading lodgepole pines should be reduced.

In the Sierra Nevada, lodgepole pine is frequently cut,

piled, and burned to enlarge or reclaim a meadow. Although cut for lumber, it is not usually considered prime timber for manufacture. It is cut commercially for fence posts and firewood. Size and orientation of the openings from harvest or other removal of lodgepole pine influence snowpack depth and melt. General references on forest-opening effects on snow accumulation and melt are available (Anderson 1956, 1967, Berndt 1965, Gary 1980, Niederhof and Dunford 1942).

The largest snowpacks are observed on southern edges of openings shaded by trees, a few meters immediately to the lee of bordering trees, or where opening width is about equal to the height of the trees around it. Snowpacks on large forest openings disappear before the pack in long, narrow openings with an east-west orientation. Because of reduced radiation the pack melts more slowly in openings with a north aspect and on well-shaded openings. Northern edges of openings usually accumulate less snow because of direct solar radiation and back radiation from trees. Where meadow reclamation is an objective, lodgepole pine harvest should be planned to take full advantage of these relationships.

Soil Conditions—The nature of the soil may influence whether lodgepole pine is able to invade a meadow. Lodgepole pine grows in shallow depressions (Howell 1931). There, clay pans form resulting in a perched water table. Lodgepole has been observed growing on two general soil

types--well and excessively well-drained, moderately coarse to coarse-textured soils, and poorly and very poorly drained, organic soils (Stephens 1966). Medium to moderately fine textured soils and moderately well drained, but moderately coarse to coarse textured soils lacked lodgepole pine. Lodgepole pine is considered a pioneer species on droughty, low fertility soils and on wet, organic soils (Stephens 1966). It is also considered a pioneer on bars of cobbles, rocks, and sand along the Kern River (Hubbard and others 1966).

A relationship of seedling, sapling, and larger trees with rocks in meadows has been observed (Leonard and others 1968). Higher maximum soil temperatures immediately adjacent to rocks and absorption of energy by the rocks could provide a more favorable environment for lodgepole pine than meadows away from rocks. Other microenvironmental conditions near rocks that may favor lodgepole establishment include exposed mineral soil, better soil texture, better aeration and drainage, and early snowmelt.

Soil moisture near rocks was 143.3 percent. But 4 ft (1.2 m) away from rocks, soil moisture was 351.3 percent. Soil particles 2 mm or less averaged 83.5 percent of the bulk sample near rocks and 96.3 percent of the bulk sample four feet (1.2 m) away from rocks (Giffen and others 1970). Moisture content is not independent of the percentage of fine soil particles.

Lodgepole pine roots have an affinity for rocks (Preston 1942). Roots tend to group adjacent to a large rock and some roots may penetrate the rocks. This affinity may be a nutrient response in an otherwise rather sterile soil.

In Ratliff's studies of mountain meadows, he observed an apparent affinity of lodgepole pine for rocks in some, but not all, meadows. Where the soils are mainly of organic origin, rocks may provide a better habitat. On mineral soils, texture and drainage may be the controlling characteristics.

Fire - Fire as a part of the natural environment of many vegetation types in California has been receiving greater recognition during the last several years (Botti and Nichols 1980, Gordon 1967). Evidence strongly suggests that fire plays a significant role in the evolution and maintenance of meadows of the Sierra Nevada (Sharsmith 1959). Fire has been thought to influence the forest-meadow boundary (DeBenedetti and Parsons 1979, 1984; Parsons 1981).

Fire has a role in meadow evolution and maintenance in other mountain regions as well. In the Cascades of Washington and Oregon charcoal and rotting wood are uncommon in meadow soils and fire is not an important variable (Franklin and others 1971). In the Olympic Mountains of Washington, however, fire is a major variable in meadow creation and maintenance (Kuramoto and Bliss 1970). Between

1870 and 1880 fire destroyed much of the subalpine forest around James Peak, Colorado, permitting downward extension of alpine vegetation (Cox 1933). Destruction of ribbon forest by fire could result in new snowdrift patterns and replacement of forest by alpine or subalpine meadows in the Rocky Mountains (Billings 1969). And old records show fire is a natural ecosystem component of "Crex Meadows" in northwestern Wisconsin (Vogl 1964).

Meadows are not likely to burn when the herbage is grazed or in years of normal precipitation. Meadows may burn when herbage is tall and dry and during droughts. A fire crossing a meadow having high soil moisture usually consumes only current growth and some mulch. With very dry conditions, fire may damage the meadow considerably (DeBenedetti and Parsons 1979, Parsons 1981). To understand how fires affect meadows, we need to know how fire frequency and fire incidence relates to meadows and their watershed.

Fire frequency is the time between fires at particular points; fire incidence is the time between fires within a particular area (Kilgore and Taylor 1979). The larger the area considered, the greater the fire incidence. A higher fire incidence may be expected on its surrounding watershed than on a particular meadow. And, with their normally drier fuels, points in forests may be expected to burn more frequently than points in adjacent meadows. Fires in their watersheds are therefore apt to influence meadow ecology more often than fires directly on meadows. Increased water

flows and sedimentation are likely the most significant effects of fires in the watershed. Fires that directly burn meadows will, of course, have greater and immediate effects on meadow ecology.

Fire History - Fire frequency in portions of Kings Canyon National Park and Sequoia National Forest was 8 to 18 years between 1478 and 1875 (Kilgore and Taylor 1979). Fire incidence in the watershed areas was 1.7 years during that period.

Fuel conditions at higher elevations are lighter and fire crowning is currently not as serious a problem as at lower elevations (Kilgore 1971). Fire scars at the higher elevations were less frequent than at the lower elevations (Kilgore and Taylor 1979). Above about 7500 ft (2286m), any role played by fire in meadow development diminished in importance (Sharsmith 1959). Lower elevation meadows are likely more often affected by forest fires than are higher elevation meadows.

Major fires (or at least fires of more than a few acres) may be required to produce geologic effects on meadows. Evidence of fire is frequently found in profiles of meadow soils. Five layers of charcoal were deposited in one meadow (Wood 1975). The deposits were all less than 1200 years old. These layers support that idea that major fires in the watersheds normally occur at intervals of 250 to 300 years.

Because of its relatively thin bark, lodgepole pine is more susceptible to fire damage than other pines (Mason 1915). Fire is most destructible to dense young stands. Although many mature lodgepole pines were killed, burning appeared to provide conditions favorable to lodgepole pine seedling establishment.

Fire Management - Not enough is known about fires in meadows to prescribe their use as a management tool. We have much to learn about the use of fire in the meadow environment, and it must be used with proper safeguards. A few observations are available, however.

A light fire across a meadow appears to affect vegetative composition only slightly. But changes in herbaceous vegetation that would result after a hot fire in a meadow appear undesirable. Because of this, any prescription for the use of fire must consider the soil moisture condition.

It appears possible to use fire to manipulate succession on the edges of meadows. Succession to forest was set back at Cabin Meadow on the Sierra National Forest (pers. com. Ronald Bertram, Wildlife Biologist, Fresno, CA 1982). Tree invasion at Ellis Meadow in Kings Canyon National Park had been slowed by fire and no trees were established in burned areas through 1981 (DeBenedetti and Parsons 1979, 1984; Parsons 1981). Trees growing in hummocks in the meadow, however, survived the fire. Light

fires may kill some seedlings. Fires hot enough to kill trees established in the meadow proper will likely do great damage to the meadow itself. Under conditions suitable for a hot fire, restriction of the fire to the target area may be almost impossible."

CONCLUSIONS

The studies referenced above have cited possible causal agents for tree invasion into high elevation grasslands. The causal agents include climate, cold air drainage, soil texture and moisture, grazing, fire, snow duration, and gophers.

The authors that studied the forest-meadow edges of the large parks on the Kaibab Plateau cite soil texture and cold air drainage as the major factors that maintain these montane meadow grasslands (Mead 1930, Rasmussen 1944, Merkle 1962). These authors do not believe that fire played a major role in maintenance of the North Rim meadows, which agrees with the conclusions of other studies conducted in similar montane meadow grasslands in the Southwest (Pearson 1913, Dye and Moir 1977, and others). However, fire did play a major role in the subalpine grasslands, and these grasslands are often adjacent to the meadows on the Kaibab Plateau (Brown 1982). In addition, it is reasonable to assume that fire, grazing, snow duration and fossorial animals may play a strong role in the stability of the forest-meadow border.

This study, "Tree encroachment on meadows of the North Rim

of Grand Canyon National Park,* will be concerned with:

1. identification of the present forest-meadow border,
2. identification of the forest-meadow border prior to European settlement in the area (i.e., 1880),
3. determination of the rate of change of the meadow edge under certain environmental conditions over the past 100 years,
4. determination of the period(s) of successful tree invasion,
5. determination of the species and ages of the invasive trees, and finally,
6. attempt to identify the causal factor(s) which allowed tree invasion to occur. The causal agent(s) may be interacting and may vary for each meadow examined.

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