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PLANT SUCCESSION ON TALUS SLOPES IN NORTHERN IDAHO AS INFLUENCED BY SLOPE EXPOSURE[1]

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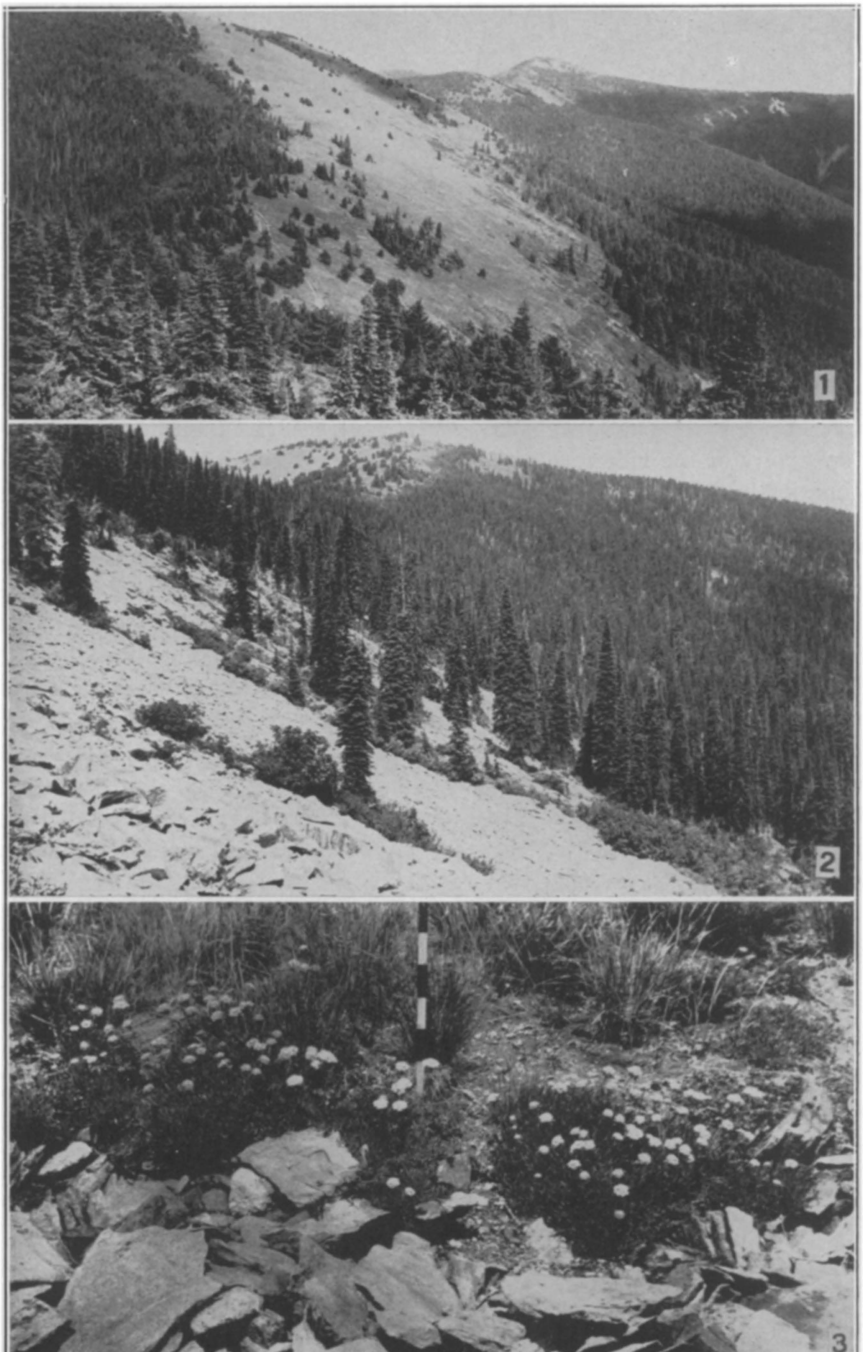
One of the most conspicuous features of the forested regions of northern Idaho is the small treeless areas which occupy portions of the southerly exposures of especially prominent peaks and ridges. These areas, sometimes referred to as parks or balds, begin at the summits of the prominences and extend down over the south-facing slopes sometimes as much as approximately 200 m. Each park is essentially an island of prairie-like vegetation surrounded by belts of shrubs and scattered trees, and then by dense forest. Few if any of the mountains of northern Idaho are high enough to have a climatically determined upper timberline, so these parks are not to be confused with alpine vegetation.

On an east-west ridge in Bonner County, Idaho, approximately midway between Priest and Pend Oreille lakes, the writers were attracted by a series of open talus areas on the north slope where the climax vegetation is forest, and to one which is located on exactly the opposite slope in a park (fig. 1). These talus areas seemed to offer an exceptionally good opportunity to compare the effects of conditions associated with slope exposure upon the course of vegetational development on bare areas otherwise identical. Talus slopes are abundant in the northern Rocky Mountains, but observations were confined to the opposite sides of this single ridge in order to eliminate variations in macroclimate between bare areas. The two rock slides studied are exactly opposite, about 300 meters down the slope on either side of the crest of the ridge.

The talus on both exposures consists of blocks of metamorphosed granite which for the most part vary between one-quarter of a meter and one meter

[1] The writers are indebted to the Northern Rocky Mountain Forest and Range Experiment Station for the use of laboratory and other facilities of the Priest River Experimental Forest which were of material assistance in making this study.

FIG. 1. General view looking east along Looking Glass Ridge. The rock slides studied are in the distance just below the highest knob on the horizon but not visible in this photograph. Just within the forest toward the top left corner of the picture is an area where the topography favors such a heavy accumulation of snow that the trees are extremely dwarfed and misshapen. FIG. 2. General view of fir forest on the north side of Looking Glass Ridge. Note upper edge of park on opposite (south-facing) slope in distance. Elongate strips of vegetation on talus in foreground consist chiefly of *Menziesia ferruginea* and *Abies lasiocarpa*. FIG. 3. Edge of talus on south-facing slope showing mats of *Eriogonum subalpinum* invading the rock mass and preparing the way for grasses. The stake is marked off in decimeters.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in diameter. Among these angular boulders there is practically no finer detritus to serve as soil material. This lack of soil and the instability of the surface layers of rocks are the two major factors which have long retarded the colonization of these areas by plants.

SUCCESSION ON THE NORTH SLOPE

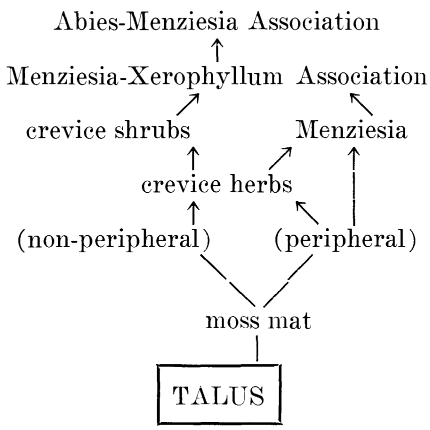
Succession is initiated on the north slope by mosses which become established in the niches formed by the accidental arrangement of boulders. Around the periphery of the open expanse of talus, where nearby trees can exert a sheltering influence, the mosses are very aggressive in that they seem not to demand a better substratum than is provided by the bare rock surface, and the colonies soon spread so as to completely cover the walls of the niches. Toward the central part of the open talus area mosses seem more dependent upon a previous accumulation of weathered rock fragments or bits of litter blown from the forest, and the colonies do not spread so vigorously as near the edge of the forest. The advent of vascular plants, and therefore the continuation of the sere, seems in every case to be dependent upon these moss colonies which provide lodging for the disseminules and hold sufficient moisture to supply the seedlings until their roots have extended down through the cool moist cavities among the talus blocks to the more permanent moisture supplies which lie below.

The pioneer vascular plants which enter upon the mosses likewise reflect a slight differentiation between the central and peripheral portions of the talus habitat. Usually herbs such as *Cheilanthes gracillima* D. C. Eaton, *Cryptogramma acrostichoides* R. Br., *Aquilegia flavescens* S. Wats., *Angelica sp.*, *Penstemon fruticosus* (Pursh) Greene, and *Arnica sp.* follow the mosses, but in peripheral regions the shrub *Menziesia ferruginea* Smith may enter the sere at this point. Over most of the talus a wider variety of shrubs including *Ribes viscosissimum* Pursh, *R. lacustre* (Pers.) Poir., *Sorbus occidentalis* (S. Wats.) Greene, *Sambucus melanocarpa* A. Gray, *Rubus,* and *Amelanchier* follows the establishment of the herbs. Thus far there is hardly enough interrelationship between the individuals representing a given stage in succession to refer to each stage as an association. However, the next clearly marked stage of development is a closed association dominated by *Menziesia ferruginea* Sm. and *Xerophyllum tenax* (Pursh) Nutt. The slight difference in successional trend between peripheral and central parts of the talus slope practically disappears with the development of the *Menziesia-Xerophyllum* thicket.

The climax dominant, *Abies lasiocarpa* (Hook.) Nutt., germinates in the shelter of the *Menziesia-Xerophyllum* association, and the final adjustments leading toward stability come about as the trees increase in size and abundance so that a closed forest is formed. *Menziesia* and *Xerophyllum,* which are the dominants of the preclimax association, persist as the most important plants in the dense undergrowth of the forest. Stability is finally attained by the replacement of relic herbs and shrubs of the open talus by minor constituents of the climax forest.

In general, the initiation of succession upon this north slope is nearly independent of talus activity, but the continuance of succession at a given point of origin depends upon comparative stability which may be provided by either topographic or substratal features. Rolling fragments tend to converge into valley-like depressions down which boulders roll frequently, leaving alternating strips of relatively stable material. Also, less extensive but more permanently stabilized areas may be provided in the lee of exceptionally large boulders which are too deeply imbedded in the detritus to be affected by surface movement. Small rocks are diverted to each side of these larger boulders leaving quiescent areas on the slope immediately below. The island-like thickets which develop at such places always expand most rapidly in a direction at right angles to the contour lines, down the strips of quiescent material which alternate with paths along which the movement of boulders is active. The forest stage makes its first appearance as a narrow strip extending down the axis of these elongate islands of shrubby vegetation (fig. 2).

The sere on the north slope, as described above, may be expressed in a simplified diagram which shows the chief stages as follows:



SUCCESSION ON THE SOUTH SLOPE

The surface of the talus area on the south side of the ridge is not so steep as that on the north slope, so that instability is here not so important a factor in retarding plant invasion. However, the lack of a substratum with adequate water-holding powers appears to be so much more important on this slope that despite the greater stability of the surface, plant invasion of the talus here is at least as slow as on the north slope.

Moss patches, which on the north slope fostered the development of islands of vegetation at scattered loci over the talus surface, are almost entirely lacking on the dry south slope and invasion is accomplished by the marginal encroachment of vascular plants unpreceded by cryptogams. The crustose lichens, which are fairly abundant on the rocks here, seem to be wholly inconsequential in the establishment of higher vegetation.

Eriogonum subalpinum Greene is the most characteristic species leading the mass encroachment of vegetation onto the loose rocks (fig. 3). The dense mat of low stems and leaves produced by this plant is admirably suited for the accumulation of litter and wind-borne mineral fragments. The fringe of *Eriogonum* about the open talus is thin and frequently discontinuous, and in places dead, wind-eroded *Eriogonum* mats demonstrate that plant succession on this slope is vulnerable to reverses during seasons of exceptional drought.

Immediately behind the *Eriogonum* fringe occur the species which compose the prairie-like climax. As stated previously, the permanent plant cover on the most exposed portions of the park is a grassland, while on less exposed situations occur individual trees or small groves of *Pinus albicaulis* Engelm., *Pseudotsuga taxifolia* (Poir.) Brit., and occasionally *Abies lasiocarpa* (fig. 1). There is no evidence whatever that the trees can increase to replace these grasslands under the existing climatic conditions. Among the most conspicuous vascular plants of the grasslands are: *Festuca idahoensis* Elmer, *Agropyron spicatum* (Pursh) Scribn. & Smith,[2] *Xerophyllum tenax* (Pursh) Nutt., *Carex geyeri* Boott., *Arenaria formosa* Fischer, *Lupinus sp., Achillea lanulosa* Nutt., *Aster stenomeres* Gray., *Senecio integerrimus* Nutt., *Hieracium albertinum* Farr. The relatively simple succession on the south slope may be diagrammed as follows:

Forest Association
↑
(less exposed sites)
↑
Festuca–Agropyron Association
↑
Eriogonum
|
TALUS

ENVIRONMENTAL DIFFERENCES ON THE TWO SLOPES

In spite of the short distance separating the two talus areas described above, there is an extremely sharp difference in the seres and the climaxes

[2] In this particular park most plants are of the awnless form, although a few individuals possess short awns.

in which they culminate. Even the floras are almost wholly distinct—the only species in common is *Xerophyllum tenax*. These facts must be interpreted as indicating the existence of some factor or factor-complex which produces a net environmental difference proportionally as great as the vegetational difference.

Frequently the obvious difference in water balance associated with north and south slopes has been attributed to insolation which causes higher transpiration, evaporation, and temperature on the south slope, with the result that both the soil and air are drier there. To determine the extent to which this explanation might be applicable to the ridge studied, comparative measurements of evaporation stress were made. Stations were established in open talus areas on both slopes, as well as in the climax forest on the north slope and the climax grassland on the south slope. The data obtained (table 1)

TABLE 1. *Mean daily water-loss in milliliters from standardized spherical atmometers operated during a 4-week period: June 29–July 27, 1941.*

Location of instruments	North slope	South slope
Open talus		
Large area	41.0	....
Small area	29.8	40.5
Climax vegetation	11.2	36.1

show that (a) the evaporation rate is consistently lower in the climax communities than on the primary bare areas, (b) the severity of this factor decreases less as a result of succession on the south than on the north slope, and (c) the evaporation rate alone is not a critical factor governing plant succession here, for the evaporation rate on large talus areas on the north slope may be greater than the rate on a small area on the south slope. The type of vegetational development is correlated with direction of exposure rather than with the size of the talus area; the successional pattern is essentially identical on large and small talus areas on either slope, regardless of differences in evaporation stress.

Other environmental measurements directly applicable to the present problem have been made on both north and south slopes near the west end of the ridge by Hayes.[3] He maintained stations in open situations on both slopes during the summer months for a period of three years. His data show that although summer precipitation and mean daily relative humidity (at 4.5 feet above the ground) are approximately equal on both slopes, wind velocity on the south slope averages 1.1 m.p.h. greater than on the north, and the 3-year average of median maximum duff surface temperatures was 148° F. on the south slope in contrast to 111° on the north slope.

[3] **Hayes, G. C.** 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. U.S.D.A. Circ. 591: 1–39.

The possible importance of lethal soil surface temperatures in the present problem can be discounted at once, because species characteristic of the north slope cannot grow even in the shade cast by the dense tall grasses which cover the south exposure.

Although measurements of wind and of duff moisture both indicate a less favorable water balance on the south exposure, even their cumulative influence is not commensurate with the great difference in vegetation on the two slopes. Clearly none of the atmospheric conditions measured by Hayes or by the writers differs sufficiently in midsummer to account for the vast difference in xerism which is indicated by the vegetation itself.

Two aspects of winter climate seem to deserve consideration with regard to this problem of environmental differentiation. There is abundant evidence in the Rockies that at upper timberline strong winter winds may evaporate more water from trees than can be absorbed from the cold soil so that winter killing results. This form of injury invariably results in strikingly asymmetrical trees, and since the pines and Douglas firs around the open grassland on Looking Glass Ridge are neither uniformly nor strongly asymmetrical, the writers do not believe that winter winds are sufficiently strong to account for the differences in water balance on the two slopes.

Another phenomenon associated with winter is the difference in amount of snow accumulation on the north and south slopes. A very high percentage of the snow which falls on the south slope is transferred to the north slope by wind action, even though the wind is not strong enough to distort the trees. So deep is the accumulation of snow just to the lee of the crest of Looking Glass Ridge that in places the trees exhibit an extreme degree of dwarfing and distortion (fig. 1). The lower surface temperatures on the north slope, combined with the greater accumulation of snow, enable the snow cover to linger here until very late in the spring, and as a result the season of active plant growth does not begin on the north slope until long after a comparable stage is attained on the south slope. In consequence, the critical dry season on the south slope is lengthened by a period of time equal to this difference in the initiation of vegetative activity on the two exposures. In the opinion of the writers such a difference in the length of the season of cumulative drought, during which plants are active yet must rely almost entirely upon soil moisture accumulated during the winter, constitutes the only influence sufficiently great to be commensurate with the pronounced differences in vegetation on the two slopes.

SUMMARY

Plant succession is described on talus slopes on the north and south faces of an east-west ridge in northern Idaho. Although the two areas studied are located very close to each other and at approximately the same elevation,

the environments differ so greatly that the processes of vegetational invasion, the seral communities involved, and the climax communities attained on each are strikingly different. The relative dryness so evident on the south slope is attributed primarily to the fact that the scanty snow accumulation operating together with high surface temperatures greatly advances the inception of the growing season here, and as a result the season when temperature is favorable for growth is so long that soil moisture reserves are exhausted before the summer is over.