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A Gradient Analysis of a Timberline Zone at Logan Pass, Glacier Park, Montana[1]

The ecology of the upper elevational timberlines in the Rocky Mountains has been in vestigated and discussed for many years (Griggs, 1938, 1946; Daubenmire, 195 Habeck and Choate, 1963; Wardle, 1965, 1968; Choate and Habeck, 1967; Arno, 196 and others). A complete understanding of the phytosociological characteristics timberline zones has been hampered by the near absence of quantitative treatments such zones. Lack of agreement among ecologists on a single definition of the ter "timberline" (Habeck and Hartley, 1968) has contributed further to this situation.

In much of the northern Rocky Mountains there exists an upper slope area whe a continuous forest cover composed of erect, well-shaped trees ceases (which may l called the "forest line"), and in this area a variety of vegetational responses can l observed. Often there is a conspicuous stunting or dwarfing of the tree species, a companied by various degrees of discontinuities in the forest canopy. The rapidi of these life-form changes depends greatly upon the steepness of the elevational gradie between 5,000 and 7,000 feet. Examples exist in Glacier Park where the spruce-f (*Picea engelmannii-Abies lasiocarpa*) communities abruptly reach their upper limi at the bases of precipitous slopes; in these instances a krummholz zone is either ve narrow or completely absent. Elsewhere, such as on the upper east-facing slop below Logan Pass (Figure 1), the elevational changes are relatively gentle betwe 5,000-7,000 feet, and as a result a wide krummholz zone dominated by *Abies lasiocar* exists between the forest line and the alpine.

The furthest upward extension of krummholz vegetation coincides with the highe elevation attained by any tree species. This upper limit is referred to as the "tr line." It is common throughout the northern Rocky Mountains for each tree speci to demonstrate different upper elevational limits. Species such as *Pinus albicau* (whitebark pine) and *Larix lyallii* (subalpine larch) are very often stunted, but st erect at elevations where *Abies lasiocarpa* (subalpine fir) exists only as severe dwarfed krummholz mats. Such differential responses complicate the recognition a definition of the timberline zone, but in this study this zone includes the vegetati existing between the forest line and the tree line.

Several features observed within the timberline zone at Logan Pass have attract my attention in recent years. Although cursory examination clearly reveals the li form responses exhibited by subalpine fir, Engelmann spruce and whitebark pine wit

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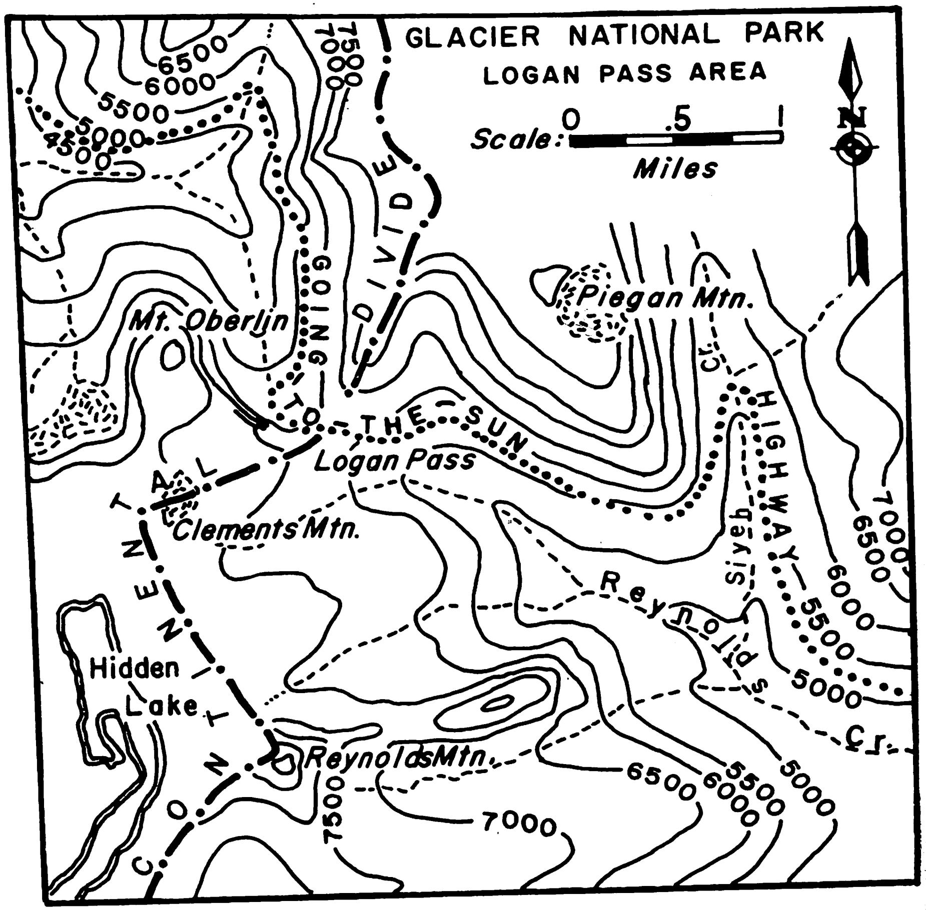

Figure 1.

in the limits of the timberline zone, the distributional features displayed by other associated species, the shrubs and herbaceous plants, were at first not easily understood or interpreted. Within the timberline zone at Logan Pass, mixtures of floristic elements from lower spruce-fir forests and higher alpine communities have been observed. Such mixtures may not seem unusual since the timberline zone is basically a vegetational ecotone between forest and alpine. But an accumulation of observations suggests that the timberline in the vicinity of Logan Pass currently exists in an unstable condition. What appears to be taking place is an upward advancement of the timberline. The occurrence of krummholz island communities on some portions of Logan Pass (6,660 feet) seems to be the result of a relatively recent invasion during the past 100 years.

The exact cause of this zonal instability can only be surmised at this time. Field studies support the hypothesis that an earlier forest/krummholz vegetation did exist on portions of Logan Pass that are presently alpine meadows. Fire, in combination with severe snowslides, very likely destroyed this forest cover, but little evidence re-

mains today. Some charcoal has been found in soils at elevations above 6,000 fe Charred stumps and logs, however, have not been seen on these upper slopes; su surface evidence of past fires may have been eroded by snowslides, by soil movemer or by snowmelt waters.

Following the destruction of the former forest/krummholz cover, alpine pla moved downward into the denuded areas, and what is seen today is a stage of for recovery or reinvasion. The rate of upward timberline movement is indeed very slo due, in part, to the harsh climatic conditions at these elevations, and to the setba caused by snowslides. On gentler slopes directly on Logan Pass, krummholz islan are expanding rapidly around their perimeters as a result of vigorous vegetative rep duction by *Abies lasiocarpa.*

Within this setting of timberline instability, an investigation of community co position and species distribution was undertaken in the Logan Pass area. Field pha of this study were conducted during the summers of 1962, 1964 and 1965, with ad tional visits to Logan Pass each summer since 1966.

Field Methods and Data Analysis

Fourteen communities located at various elevations between 5,700 and 7,200 feet w selected for detailed analysis. All of these occur on the east-facing slope of the Co tinental Divide, or directly on Logan Pass (Figure 1). Specific stand locations, ho ever, also include some south and west exposures. Stands at elevations below 6,0 feet occur primarily on the slopes above Siyeh Creek, in the vicinity of where Going-to-the-Sun Highway intersects this creek. Stands at higher elevations were lected from many available between this highway and the slopes below the peak o Piegan Mountain.

Twelve of the 14 stands classed as either forest or krummholz are dominated *Abies lasiocarpa.* A total of 20 points were sampled by the quarter method (Cott and Curtis, 1956) in each of these stands. Trees with diameters of two inches more at ground level were regarded as tree-sized individuals; those smaller than t inches were tabulated as tree saplings. This arrangement was thought necessary si few trees exceeded eight inches in diameter anywhere along this timberline gradie The majority were between two and five inches. Vascular understory plants w sampled with meter square quadrats established at each of 20 points in each stand.

Data collected for each tree species in each stand were summarized in the fo of importance values by combining relative frequency, density and dominance val (Curtis and Cottam, 1962). Total densities of trees and saplings were determir for each stand, as were quadrat frequency values for each understory species. Nom clature used in this analysis follows Davis (1952) and Moss (1959).

Although an arrangement of the fourteen communities based entirely on ea stand's elevational position may have provided a satisfactory ordination useful gradient analysis of the data, it was decided to employ the techniques described Bray and Curtis (1957) for objectively ordering communities. Through the calcu tion of coefficients of community similarity, based on comparisons of stand compo tions, the 14 communities were linearly arranged along a compositional gradient (Ta 1).

TABLE 1. Summary of data from a series of timberline communities at Logan Pass, Glacier National Park, Montana. Importance values and densities (number/acre) are provided for tree species; quadrat frequency data are given for the most common vascular understory species. x = indicates presence only.

	Timberline Communities													
	12	13	14	1	10	2	4	9	11	3	5	8	6	7
Elevation	5800	5900	5950	5700	5700	6200	6500	6650	6800	6650	6900	6750	6950	7200
Importance Values														
Abies lasiocarpa	239	223	264	281	244	284	289	290	278	288	300	300	0	0
Picea engelmannii	49	59	36	0	41	0	0	0	0	5	0	0	0	0
Pseudotsuga menziesii	12	18	0	0	7	0	0	0	0	0	0	0	0	0
Pinus albicaulis	0	0	0	19	8	16	11	10	22	7	x	x	0	0
Tree Densities	155	191	154	541	211	279	418	1290	1875	376	275	329	0	0
Sapling Densities	94	188	229	148	172	152	111	165	230	40	37	60	0	0
Quadrat Frequency														
Actaea arguta	70	60	55	0	0	0	0	0	0	0	0	0	0	0
Tiarella unifoliata	25	25	25	0	0	0	0	0	0	0	0	0	0	0
Alnus sinuata	10	20	10	0	0	0	0	0	0	0	0	0	0	0
Menziesia ferruginea	100	100	95	15	0	0	0	0	0	0	0	0	0	0
Sambucus melanocarpa	35	40	20	x	0	x	0	0	0	0	0	0	0	0
Rubus parviflorus	65	x	55	65	0	60	0	0	0	0	0	0	0	0
Heracleum lanatum	30	50	45	30	45	5	0	0	0	x	x	x	0	0
Ribes lacustre	35	25	25	35	45	5	0	30	5	x	x	x	0	0
Vaccinium membranaceum	55	45	40	0	0	5	45	0	0	10	x	25	0	0
Thalictrum occidentale	25	10	20	100	100	70	65	80	75	20	55	30	0	0
Galium triflorum	5	20	15	0	10	5	0	0	50	0	0	0	0	0
Polystichum lonchitis	25	50	40	10	0	5	0	x	5	0	0	0	0	0
Lonicera involucrata	15	25	20	0	0	0	0	10	0	x	0	0	0	0
Senecio triangularis	5	5	10	45	100	15	0	35	45	15	0	x	0	0
Smilacina stellata	0	55	0	35	0	5	0	0	0	0	0	0	0	0
Achillea millefolium	0	15	5	0	25	0	x	10	5	0	0	10	0	0
Epilobium angustifolium	0	10	10	90	55	100	x	0	0	0	5	0	0	0
Veratrum viride	0	0	0	25	0	x	5	10	0	10	20	20	0	0
Xerophyllum tenax	0	0	0	x	50	95	100	5	5	15	95	15	0	0
Erigeron peregrinus	0	0	x	0	0	35	0	0	0	5	0	55	60	90
Valeriana sitchensis	0	0	0	25	20	15	10	10	5	85	55	80	0	40
Hypericum formosum	0	0	0	0	0	x	x	0	0	0	0	25	50	45
Potentilla diversifolia	0	0	0	0	0	x	0	0	0	0	0	50	100	65
Erythronium grandiflorum	0	0	0	0	0	0	5	0	0	100	45	75	0	0
Veronica alpina	0	0	0	0	0	0	x	0	0	0	0	65	0	20
Gentiana calycosa	0	0	0	0	0	0	x	0	0	40	x	35	55	20
Sibbaldia procumbens	0	0	0	0	0	0	x	0	0	10	0	20	80	65
Luzula wahlenbergia	0	0	0	0	0	0	0	0	0	100	25	70	0	0
Pedicularis contorta	0	0	0	0	0	0	0	0	0	0	0	35	0	0
Kalmia polifolia	0	0	0	0	0	0	0	0	0	0	0	0	90	0
Anemone parviflorus	0	0	0	0	0	0	0	0	0	0	0	0	40	5
Senecio subnudus	0	0	0	0	0	0	0	0	0	0	0	0	35	35
Castilleja rhexifolia	0	0	0	0	0	0	0	0	0	0	0	0	15	25
Carex tolmiei	0	0	0	0	0	0	0	0	0	0	0	0	5	35
Arnica diversifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	35
Luzula glabrata	0	0	0	0	0	0	0	0	0	0	0	0	0	45
Arenaria capillaris	0	0	0	0	0	0	0	0	0	0	0	0	0	80

Results and Discussion

A gradient from low to high elevations is closely approximated in the ordination developed (Table 1). Since some variation does exist in site exposures among these communities, a perfect correlation between elevation and stand composition is unlikely to be attained. Past disturbance in each community is also variable and not necessarily related to elevation.

The importance values for *Abies lasiocarpa, Picea engelmannii, Pinus albicaulis,* and *Pseudotsuga menziesii* reveal definite types of patterning along this ordinational gradient. Subalpine fir dominates all communities with a forest or krummholz cover, with the other three species serving as minor associates. The interactions between *Abies lasiocarpa* and *Picea engelmannii* appear to be very similar to those observed and described for these two species elsewhere in Glacier Park and in other portions of the spruce-fir zone in northwestern Montana (Habeck, 1967, 1968). At elevations between 4,500 and 5,500 feet, *Picea engelmannii* often attains dominance over *Abies lasiocarpa* on habitats that have been burned, but the capability of spruce to reproduce itself is reduced once subalpine fir becomes reestablished. As a consequence the ecologic role of Engelmann spruce is frequently that of a minor climax species. Above 6,000 feet in the Logan Pass area, *Picea engelmannii* is nearly absent. This reduced abundance of spruce near timberline is in sharp contrast to the behavior of Engelmann spruce in Colorado (Wardle, 1965, 1968) where it often dominates in timberline communities.

Pinus albicaulis attains its highest importance values at elevations above 6,000 feet, but as can be noted in Table 1 this pine does not become more than a minor community associate of subalpine fir. These data, however, do not reveal the true importance of the relationship existing between these two conifer species. Extensive observations in the Logan Pass area, supported by observations published by Brink (1959), Franklin (1966), and Franklin and Mitchell (1967) for timberline forests elsewhere in the Pacific Northwest, clearly point to the fact that *Abies lasiocarpa* establishment in upper timberline areas is often dependent upon the presence of *Pinus albicaulis.* Commonly, the first trees initially to invade the Logan Pass alpine meadows are whitebark pine. As isolated individuals or as small clumps of several trees, this pine appears to serve as a nucleus around which *Abies lasiocarpa* seedlings become established. Old-aged, open-grown whitebark pine trees can often be observed within the central portions of the krummholz islands on Logan Pass. The established subalpine fir expands rapidly via vegetative reproduction, and nearby krummholz islands may fuse together, forming larger stands.

This interesting and important relationship between whitebark pine and subalpine fir, however, appears to be nearing a stage of complete disruption because of heavy infections of whitepine blister rust (*Cronartium ribicola*) on the *Pinus albicaulis* in the Logan Pass area. Complete mortality of whitebark pine can be forecasted for this area, and its loss would no doubt slow the rate of krummholz reinvasion on the wind-swept alpine meadows.

Density values for trees and saplings (Table 1) are rather wide ranging, and do not appear directly related to elevation. Communities located below 6,000 feet have generally lower tree densities than those above this elevation. Trees in stands No. 12, 13 and 14 are larger in size, averaging seven inches in diameter, and show very little stunting. Their canopies are well developed, but generally do not overlap. With increasing elevation, the densities increase, but the trees become dwarfed and disfigured, and snowpack and spring snowslides cause large gaps in the stand canopies. The communities appear as a collection of tree-thickets, with treeless areas separating them. Some krummholz communities, however, do remain intact, with high tree densities and nearly continuous canopies. Stands 9 and 11 are of this type. The ecological importance of tree and sapling densities and the continuity of canopy covers is related to the distribution of understory species within this timberline zone.

Quadrat frequency data for the common understory species appear to relate well to the compositional changes described for the trees. Collectively the distributional patterns of these understory species form a vegetational continuum lacking abrupt discontinuities. Although the inclusion of a greater number of stands in this analysis would probably have provided additional detail and refinement to this vegetational gradient, it does appear that the major compositional changes within this timberline zone are illustrated very well in Table 1.

A gradual shift takes place from understory species that characterize the groundlayers of spruce-fir communities occurring below 6,000 feet, through a series of species found in both forest and alpine habitats occurring in the krummholz communities, and finally terminating with a group of plants typically restricted to alpine communities above timberline. Several species located at opposite ends of this gradient exhibit narrowly restricted distributions, occurring in only one or several of the communities. In contrast, this list of understory species includes nearly a dozen that occur in seven or more of the 14 stands, encompassing a wide elevational range. Each species demonstrates an individual response along this ordinational gradient, when both abundance and stand occurrence are considered. Some species reach either their upper or lower elevational limits rather abruptly, such as *Actaea arguta, Tiarella unifoliata, Alnus sinuata, Arenaria capillaris* and *Luzula glabrata.* A majority of the species, however, commonly display gradual increments or reductions in values as their upper or lower elevational limits are encountered.

Stands 6 and 7 occur at the highest elevations included in this study. These alpine communities lacking tree species are in close proximity to several developing krummholz islands. Many of the species occurring in these two alpine stands are not present in any other stands (Table 1). Certain alpine meadow species that attain their highest frequency values within stands 6 and 7 also occur within many of the krummholz communities at lower elevations. Some of these include *Hypericum formosum, Veronica alpina, Erigeron peregrinus* and *Sibbaldia procumbens.* If it may be assumed that stands 6 and 7 represent the type of alpine meadow communities being invaded by *Abies lasiocarpa* and *Pinus albicaulis,* it is then possible to designate certain differential responses exhibited by the alpine flora following tree invasion. Since many alpine species require full sunlight for their development, the reduction in light reaching the groundlayer when a tree canopy begins to develop leads to a direct loss of the most shade intolerant members of the alpine communities. Such losses are evident in the understories of stands 9 and 11 where canopy covers are heavy and very little light penetrates to the understory. Certain alpine species persist in krummholz communities with open canopies (stands 3, 5, and 8, for example).

Although observations on the upper, east-facing slopes of the Continental Divide in the vicinity of Logan Pass, strongly suggest that a forest/krummholz cover is gradually encroaching upward into the alpine meadow communities, the compositional gradient presented in Table 1 should not be accepted in its entirety as a "successional blueprint" of this upward invasion. It does seem true that certain alpine plants do extend themselves to lower elevations on sites that are disturbed, and do not become heavily shaded, and some or all of these will eventually retreat upward as forest or krummholz cover is gradually reestablished.

In a similar way, shrubs and herbaceous species characteristic of the lower spruce-fir communities retreat downward or advance upward in response to the loss or re-establishment of forest cover in this timberline zone. These vegetative oscillations should be viewed as dynamic phenomena superimposed upon a natural elevational/environmental gradient. This physiographic gradient is important in itself in bringing about pronounced life-form modifications among the woody species; physiography in the Logan Pass area imposes upper and lower limits of occurrence on herbaceous species even in the absence of disturbance.

The severe winds, deep snowpacks, snowlides, and low temperatures characteristic of Logan Pass would certainly inhibit the development of spruce-fir communities of the type occurring at elevations below 6,000 feet. Nevertheless, there is no reason to doubt that a continuous forest cover, dominated by *Abies lasiocarpa,* could develop throughout the 5,500 to 7,000 foot zone in the absence of fire disturbance. Such an unbroken forest cover would still exhibit the gradual stunting associated with increasing elevations, and would also illustrate a gradual compositional shift among the associated understory species.

The ultimate height of timberline advancement in the Logan Pass area can only be speculated upon at this time. With many of the krummholz islands near 7,000 feet showing evidence of rapid expansion around their perimeters, environmental factors at Logan Pass seem to be well within the range for tree development. Expansion above 7,000 is likely to be hindered by the very steep slopes above Logan Pass, with small clumps of trees becoming established only on favorable microsites above this elevation. Much of the alpine vegetation on Logan Pass is below 7,000 feet, so krummholz vegetation should eventually invade many of the alpine communities.

Studies of timberline advancement in British Columbia by Brink (1959) and in the Cascade Mountains by Franklin and Mitchell (1967) have resulted in descriptions of krummholz establishment similar to that presented in this investigation. These workers, however, have given greater importance to the influences of climatic change in bringing about vegetational changes in the upper timberlines in these other Pacific Northwestern areas. Amelioration of climates in the northern Rocky Mountains has also been described, and timberline advancement in Glacier Park may also be related to a general moderation in climates above 6,000 feet. Still, evidence of past fire in the vicinity of Logan Pass and the rapid rate of krummholz island expansion after initial establishment within alpine communities give strong support to the hypothesis that a form of secondary forest succession is currently taking place.

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