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FOREST SUCCESSION IN THE GLACIER PARK CEDAR-HEMLOCK FORESTS[1]

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Abstract. A gradient analysis and description was made of forest succession among the *Thuja plicata-Tsuga heterophylla* communities in the vicinity of Lake McDonald in Glacier National Park, Montana. Thirty-three pioneer, seral, and climax communities located on well-drained slopes at elevations between 3,200 and 3,500 ft (1,050–1,150 m) were sampled. Through the calculation of indices of community similarity and dissimilarity, the stands were objectively arranged along a unidimensional gradient. The data summarized along the resulting ordination gradient provide a quantitative description of the basic successional pattern existing among these cedar-hemlock communities. Typically, following burning *Pinus contorta* communities become established, and these in turn are gradually replaced by *Pinus monticola* and *Pseudotsuga menziesii* in various proportions. Climax communities on the upland sites become dominated by *Tsuga heterophylla,* with smaller, but self-reproducing populations of *Thuja plicata* also persisting.

INTRODUCTION

The western redcedar-western hemlock (*Thuja plicata-Tsuga heterophylla*) forests of Glacier National Park in northwestern Montana represent the easternmost development of this forest type in North America. Aller (1960) applied the name "Lake McDonald Forest" collectively to all of the forest communities surrounding Lake McDonald in the western portion of Glacier Park. He described the composition of these communities from a composite of field data collected from a wide elevational transect and from many different seral and climax stands. Actually the forest communities in the vicinity of Lake McDonald demonstrate considerable compositional variability which is related to a long history of fire disturbance. Lumping of stand data from many different successional stages led Aller to conclude that the "Lake McDonald Forest" has a non-homogeneous composition, while his data analysis did not allow him to interpret clearly the successional role of each species.

The general sequence of forest successional stages in the cedar-hemlock zone in the northern Rocky Mountains has been described in the past; however, a quantitative treatment employing gradient-analysis techniques has not been attempted. It was hoped that an application of such methods would clarify the typical patterns of species replacement, as well as the role of each species involved in the successional process in the Lake McDonald area.

The development of the cedar-hemlock communities is best displayed within a narrow elevational zone between 3,200 and 3,500 ft (1,050–1,150 m) on well-drained slopes above the shores of Lake McDonald. Although redcedar and western hemlock occur on the entire perimeter of the lake,

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communities on the east, north, and south sides of the lake are most readily accessible, and these were given particular attention. Both cedar and hemlock occur at elevations between 3,500 and 4,000 ft (1,150–1,315 m), but at these higher elevations one encounters a zone of overlap between cedar-hemlock and spruce-fir (*Picea engelmannii-Abies lasiocarpa*) communities. The transition between these two forest zones on the west slope of the Continental Divide is not narrowly defined; a series of communities within this ecotone received some attention in my investigation, but the principal interest was focused on the communities restricted to the 3,200–3,500-ft zone.

Literature Review

The redcedar-western hemlock forests in Glacier Park and elsewhere in northwestern Montana and northern Idaho represent an eastern extension of this major forest type from Oregon, Washington, and British Columbia. The eastward penetration of Pacific Coast climatic and floristic elements into the northern Rocky Mountains has been frequently described and discussed by others (Kirkwood 1922, 1927, Daubenmire 1943, 1952, Benson 1957, Aller 1960, Habeck 1963, 1967).

Daubenmire (1952) subdivided the *Thuja-Tsuga* zone in northern Idaho into four climax associations, three of which are characterized by the presence of redcedar and/or western hemlock. These include the *Thuja-Tsuga/Pachistima* Association, the *Thuja-Tsuga/Oplopanax* Association, and the *Thuja Pachistima* Association. In each association redcedar and/or western hemlock play roles as major climax species. The fourth climax association is dominated by *Abies grandis*. Other coniferous and broadleaf tree species which function as major or minor seral species in these cedar-hemlock associations include *Larix occidentalis, Pinus contorta, P. monticola, P. ponderosa, Populus tremuloides, P. trichocarpa, Pseudotsuga menziesii, Abies lasiocarpa, Betula papyrifera,* and *Picea engelmannii.* This list includes all of the major tree species occurring in the northern Rocky Mountains and indicates the compositional diversity that is possible in the successional communities in the cedar-hemlock forest zone.

Much of the variation in forest composition in the forest zones of western Montana is clearly the result of disturbance by fire, though species and community distributional patterns are also conspicuously influenced by physiographic factors. Fire in the northern Rocky Mountains has been the subject of numerous published reports dating back to the early 1900's (Whitford 1905, Kirkwood 1922, Gisborne 1928, Larsen 1929, Marshall 1928, Hubermann 1935, and many others). These earlier investigations provided a general understanding of the probable successional stages within the various forest zones of this region.

Within the cedar-hemlock zone in northern Idaho and western Montana, pioneer forests established following fire usually will be dominated by *Pinus contorta* and/or *Larix occidentalis.* These communities, in turn, will often be replaced by *Pinus monticola* and/or *Pseudotsuga menziesii.* Finally the climax dominants, *Thuja plicata* and/or *Tsuga heterophylla,* in various proportions, will tend to replace all of the pioneer and seral species (Habeck 1963). Such a successional sequence is greatly complicated by the potential occurrence of many major and minor seral species on a given site at a given time. The seral species display wide variation in their longevities too; relatively short-lived species such as *Pinus contorta, Populus tremuloides,* and *P. trichocarpa* make only brief appearances in forest recovery, whereas others such as *Larix occidentalis* and *Pinus monticola* are very long lived and often persist in the climax communities.

In a subsequent treatment of the vegetation of northern Idaho, Daubenmire (1966) indicated that climax communities codominated by both *Thuja plicata* and *Tsuga heterophylla* are not likely to develop, since a given homogeneous habitat will favor the ultimate dominance of one of these species or the other, but not both. Daubenmire (1966, Fig. 2) portrays redcedar as a species occurring at somewhat lower elevations and in slightly more xeric habitats than western hemlock. Redcedar is described as capable of producing and maintaining self-reproducing populations only in habitats or areas outside the ecological range of hemlock. In consequence, whenever the two species do exist together, it can be expected that the hemlock will display competitive superiority over redcedar. These conclusions are in contrast to those presented earlier by the writer (Habeck 1963) for cedar-hemlock communities in Glacier Park, wherein the climax communities composed of varying proportions of both species are described. Moisture and drainage features have considerable influence on the specific composition of the climax communities in the Lake McDonald region, with hemlock dominating redcedar on well-drained slopes, redcedar dominating the wet ravines or poorly drained depressions, and both species present and regenerating themselves on sites with intermediate moisture conditions.

Description of the Study Area

The western portion of Glacier Park is characterized by a cool, moist climate. Total precipitation, which varies between 25 and 30 inches annually, is generally distributed evenly over the year. Winter temperatures average about 21°F; July temperatures average 65°F. These climatic conditions are responsible for the existence and persistence of redcedar, western hemlock, and other Pacific Coast species in Glacier Park.

The slopes surrounding Lake McDonald support Brown Podzolic soils generally as described by Nimlos (1963). These soils have developed over limestones, shales, and sandstones belonging to the Belt Series. Typically an A_{00} layer of 1–3 inches overlies a well-developed B_{ir} layer which varies between 8 and 20 inches in thickness. Leached A_2 layers are occasionally encountered, but such layers when present are not often more than 1 inch deep.

The forests surrounding Lake McDonald (elevation 3,144 ft), regardless of their age and composition, all reveal evidence of fire disturbance. The most recently burned (1928) areas near Lake McDonald contain abundant charred cedar and hemlock remains; older communities exhibit numerous dead snags and windfalls, most of which are *Larix occidentalis*. The study area has been protected from cutting since the park was established in 1910.

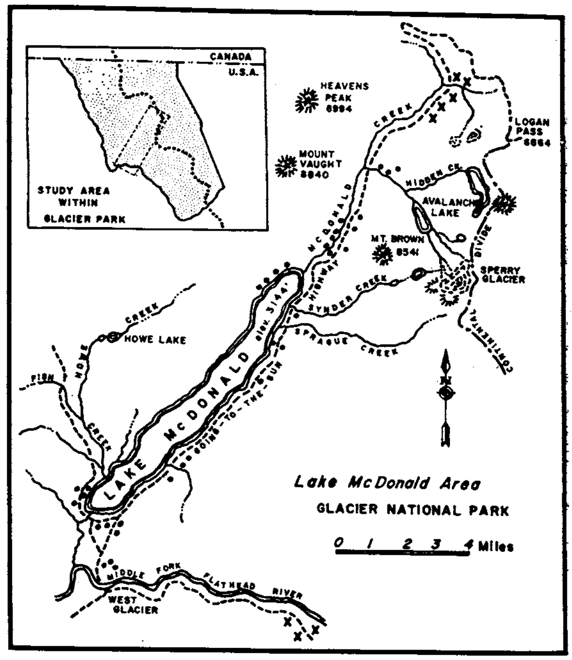

Fig. 1. Detailed map of the Lake McDonald area in Glacier National Park in northwestern Montana. Darkened circles indicate the locations of the study areas. Crosses indicate the locations of sampled stands in the ecotone between the cedar-hemlock and spruce-fir zones.

Methods

Thirty-three forest stands on well-drained, upland sites were studied in detail during the summers of 1962 and 1963 (Fig. 1). Ten ecotonal stands above 3,500 ft (1,150 m) were also included in the field investigations. Eight of these transitional stands were located in the Lake McDonald area (Fig. 1); the remaining two were located near Essex, Montana, on the park's southern boundary.

Stands were selected at random during the summer of 1962; any community which appeared homogeneous in composition was accepted. A chi-square test applied later on the sample data indicated that all but one stand was homogeneous at the 5% level of significance. In 1963, after examination of the 1962 data, additional stands were selected subjectively to include communities which differed significantly in composition from those sampled earlier.

The trees and tree saplings in each stand were sampled by the quarter method (Cottam and Curtis 1956). Twenty points were used in each stand sample. Trees were defined as individuals over 4 inches dbh, which when mature can ordinarily be expected to occur in the main canopy of the community. This criterion excluded western yew (*Taxus brevifolia*) and mountain maple (*Acer glabrum*) which on occasion achieve tree size. Tree saplings were designated as individuals between 1 and 4 inches dbh. Tree seedlings (less than 1 inch dbh) were sampled, along with other vascular understory species, in meter-square quadrats established at each of the 20 sampling points. The nomenclature used in this paper follows Davis (1952).

Relative density, relative frequency, and relative dominance were calculated for each tree species in each stand. These three values were summed to arrive at a single importance value for each species. Similarly, relative frequency and relative density were determined for saplings in each stand; these two values were summed to arrive at a sapling importance value. Absolute densities for trees and saplings were calculated; dominance per acre was also determined for each stand. The quadrat data were used to calculate frequency percentages for tree seedlings and other understory species.

A simple linear ordination of the 33 communities was constructed using the basic approach described by Bray and Curtis (1957). A multidimensional ordination was also made of these communities, but the basic features of forest succession (compositional change with time) were suitably described by a unidimensional gradient. Since the sampled communities were confined to a narrow elevational range and to well-drained slopes in the vicinity of Lake McDonald, there appeared no need for additional ordination axes.

Coefficient of community values were calculated using 78 quantitative characteristics from each stand. These included importance values for trees and saplings in each stand as well as the quadrat frequency values for a majority of the common understory species. In constructing the primary axis of the ordination, the reference stands of greatest dissimilarity were a young *Pinus contorta* community that had developed after a 1928 fire and an old-aged *Tsuga heterophylla* community. Based on similarity and dissimilarity values the remaining 31 stands were arranged between these two end communities. The resulting ordinational gradient was partitioned into six equal segments, and stand averages for various community features were determined.

Results and Discussion

The compositional changes which portray the general sequence of species replacement during secondary forest succession in the Lake McDonald area are summarized in Table 1. In this table

Table 1. Average importance values for each tree species within the six successional gradient segments

Species	Gradient segments					
	I	II	III	IV	V	VI
Pinus contorta	241.4	76.4	2.2	3.4	0	0
Populus tremuloides	2.2	0	0	0	0	0
P. trichocarpa	3.6	0	0	0	0	0
Abies lasiocarpa	3.0	8.8	1.4	0	0	0
Picea engelmannii	6.8	14.0	3.2	12.8	3.4	0
Pseudotsuga menziesii	16.0	25.4	9.4	8.6	11.4	3.2
Betula papyrifera	0	6.8	5.6	6.2	4.6	1.0
Pinus monticola	1.2	14.4	18.6	21.2	22.4	6.0
Larix occidentalis	25.8	75.2	109.0	46.2	42.2	29.8
Abies grandis	0	0	0	0	1.4	0.8
Thuja plicata	0	70.0	103.4	111.8	61.0	45.6
Tsuga heterophylla	0	9.0	47.2	89.8	153.6	213.6

the average importance values for each tree species in each of the six ordination segments are given. The communities composing segment I of this gradient average less than 50 years of age; other gradient segments are of continuously greater age, with the stands composing segment VI averaging about 400 years old. The data provide firm support to earlier qualitative descriptions of secondary succession in the cedar-hemlock zone elsewhere in the northern Rocky Mountains. However, the compositional changes between pioneer and climax stages of succession are very gradual and distinct stages can only be arbitrarily delineated.

The averaging of values from several communities within each of six gradient segments conceals the fact that some compositional variability does exist among the stands representing pioneer, seral, or climax stages of succession. The variation, however, is not great and does not negate the attempt to provide a simple, linear ordering that reflects forest community changes over a long period of time. Daubenmire (1952) discusses this specific aspect of succession in the cedar-hemlock associations in northern Idaho. His remarks indicate that a predictable sequence of species in the cedar-hemlock forests is not possible due to the numerous biotic and chance factors that operate on the species and habitat following one or more fires. Daubenmire also suggests that any physiologic differences among seral species are apparently too slight to be of much importance in producing an invasional sequence among the seral species. To the contrary, the data presented here for the cedar-hemlock communities in Glacier Park provide a definite invasional sequence.

Following fire *Pinus contorta* generates a single population on sites surrounding Lake McDonald, but displays an inability to perpetuate itself in the absence of fire. *Pinus contorta* is short lived, and importance values for this species are reduced markedly in the intermediate and later stages of succession. *Larix occidentalis* is a close associate of *Pinus contorta* in the pioneer communities. Following single burns *Larix* exists only as a minor component in the lodgepole pine-dominated communities, but its proportions are greatly increased on sites that experience repeat burns during the early stages of succession. The large number of older *Larix* individuals in present-day stands representing later stages of forest development probably indicate that in former times multiple burns were common in the Lake McDonald area.

The interaction of *Thuja plicata* and *Tsuga heterophylla* on upland sites involves an early domination by redcedar (segments III to V) which is maintained well beyond the intermediate stages of succession, but which is finally reversed in the subclimax and climax stages. The earlier appearance of redcedar is indicated in the reproduction data also (Table 2). Although the appearance of western hemlock reproduction is only slightly delayed over that of redcedar, the difference in time is sufficient to allow redcedar to establish an overstory which brings about a marked reduction in light reaching the forest floor. Although the hemlock is highly shade tolerant, its reproduction is apparently retarded due to the

TABLE 2. Average importance value for each tree sapling species, and average quadrat frequency for *Thuja* and *Tsuga* seedlings, in six successional gradient segments

Species	I	II	III	IV	V	VI
	Gradient segments					
Pinus contorta	69.3	2.5	0	0	0	0
Populus tremuloides	4.2	0	0	0	0	0
P. trichocarpa	2.9	0	0	0	0	0
Abies lasiocarpa	5.1	13.3	11.8	3.1	4.4	0
Picea engelmannii	51.1	44.0	11.4	2.3	0	0
Pseudotsuga menziesii	10.4	14.5	2.7	0	0	0
Betula papyrifera	3.2	2.4	1.4	0	0	0
Pinus monticola	11.9	4.7	21.9	0.7	3.0	0
Larix occidentalis	40.5	9.6	0	0	0	0
Abies grandis	0	0	0	0	2.0	3.2
Thuja plicata	0.7	72.3	62.1	97.5	84.4	31.5
Tsuga heterophylla	0	36.7	88.7	96.4	105.4	163.3
Average quadrat frequency						
Thuja seedlings	3.0	13.0	28.0	34.0	22.0	2.0
Tsuga seedlings	0	19.0	36.0	43.0	34.0	17.0

light reduction and perhaps to the scarcity of rotting logs and stumps that provide ideal seed beds for hemlock seedlings.

Redcedar reproduction shows a general decline on upland sites during later stages of succession. Observations indicate that seedlings and saplings of this species generally originate from seed in the young, open, pioneer communities that allow considerable light penetration to the forest floor. Communities with closed canopies do not favor sexual reproduction of redcedar. On poorly drained habitats, however, redcedar is generally successful in reproducing itself via branch layering. The frequent absence of adequate moisture in the upper soil layers on well-drained slopes is responsible for redcedar's reduced ability to shift from sexual to vegetative reproduction on these upland sites. The rate of redcedar reproduction is not reduced to zero, however, and some reproduction can nearly always be found in even the oldest hemlock-dominated communities in the Lake McDonald area.

The data from the upland slopes support the view that western redcedar is either a major seral species or a minor climax species in Glacier Park. In either case, western hemlock appears to have the potential of achieving dominance over redcedar on the upland slope habitats. The ability of redcedar to regenerate itself even to a small degree in the face of intense competition from western hemlock does not conform to conclusions drawn by Daubenmire (1966) that *Tsuga heterophylla* will completely replace redcedar when both are competing on the same habitat. Daubenmire's interpretation of the sociologic roles of redcedar and western hemlock in northern Idaho are predicated on ideas associated with habitat homogeneity. Homogeneity has been a fundamentally important concept in vegetational analysis for many years; however, its definition and measurement have been the object of recent discussions among ecologists (Daubenmire 1966, Cottam and McIntosh 1966, Daubenmire 1968). A habitat with perfectly uniform features may well be capable of supporting only a single climax tree species as Daubenmire has indicated; such habitats, however, are rarely encountered in nature on any sizeable scale. This is certainly apparent in mountainous terrain, at least where such habitats may not occupy more than a few square meters. In traveling even a short distance one notes gradual changes in elevation and/or slope exposure, and such habitat changes are accompanied by community compositional changes. Daubenmire (1968, p. 26) has clearly indicated that the most significant aspects of community homogeniety, from his point of view, involve those habitat features that are relatively permanent to the site, such as parent material, microclimate, or drainage. Of lesser importance are homogeneity features related to spatial distribution of species occurring on the habitat; these distribution patterns may be constantly changing and subject to numerous chance factors.

In the Lake McDonald area it may be that redcedar is reproducing itself within *Tsuga heterophylla*-dominated communities on atypical microhabitats. Depressions created by windfalls do provide suitably moist microhabitats for successful branch-layering by redcedar. Such depressions are likely to always exist and perfectly uniform habitats will never be realized. As Goodall (1965) has pointed out, habitats may often consist of a mosaic of microhabitats, with species giving individual response to the resulting patternization within a particular site. Vegetative redcedar reproduction seems to respond somewhat independently of western hemlock in the Lake McDonald communities; the heavy shade cast by a hemlock overstory precludes the establishment of sexual redcedar reproduction, while the critical factor in vegetative reproduction of cedar is not shading, but the occurrence of adequate soil moisture.

Species that can be designated as major seral species in the Lake McDonald region include *Picea engelmannii, Pseudotsuga menziesii,* and *Pinus monticola* in addition to *Larix occidentalis* mentioned earlier. Each of these species achieves its highest importance values in one or another of the intermediate gradient segments. *Picea engelmannii* is a common understory component in the lodgepole pine-dominated stands. However, the occurrence of spruce saplings is sharply reduced in communities that have developed a dense canopy. *Pseudotsuga menziesii* generates sapling populations in the pioneer stands only, but this species is relatively long lived and its occurrence continues well into the late stages of forest succession. *Pinus monticola* reproduction invades at both early and intermediate stages of succession. Western white pine is also long lived, and individuals approaching 30 inches dbh are not infrequent in the Lake McDonald area. Glacier Park closely coincides with the eastern range limits of *Pinus monticola* in western North America, and seldom does this species display the population densities or growth rates in western Montana that it demonstrates in northern Idaho and southeastern British Columbia.

The remaining species in the successional series are either minor seral or minor climax species. These include *Populus tremuloides, P. trichocarpa, Abies lasiocarpa, Betula papyrifera,* and *Abies grandis.* The first two were encountered in a few lodgepole pine stands located on a glacial moraine which forms the southern shore of Lake McDonald; these species are not common elsewhere in the study area. *Abies lasiocarpa* is an infrequent member of the communities composing the cedar-hemlock zone in Glacier Park. Subalpine fir makes its appearance generally in the early pioneer stages of succession, and even though it can withstand severe suppression it does not reproduce well in communities dominated by redcedar and western hemlock. This inability is markedly reduced, of course, at higher elevations.

Betula papyrifera occurs in all of the gradient segments although it never achieves more than minor importance. Scattered clumps of this species that have developed entirely from vegetative sprouting are common, and this reproductive habit probably accounts for its presence and maintenance in some of the older-aged cedar-hemlock communities.

The least common tree species in the immediate Lake McDonald area is grand fir (*Abies grandis*). It occurs jointly with both redcedar and western hemlock in a few isolated stands on the northwest shore of the lake. As the tree-reproduction data in Table 2 indicate, *Abies grandis* is capable of maintaining small populations in competition with *Thuja* and *Tsuga,* but the restricted distribution of grand fir in the study area somewhat reduces the significance of these data. Daubenmire's interpretation of the sociologic role of grand fir (1966, Fig. 2) in northern Idaho includes the view that *Abies grandis* functions only as a seral species when in competition with *Thuja plicata* and *Tsuga heterophylla.* My data seem to support the view that grand fir may function instead as a minor climax species.

Aller's (1960) data indicated a much greater abundance of *Abies grandis* in the Lake McDonald area than is revealed in my study of these forest communities. The absence of data in Aller's study for *Abies lasiocarpa* in the 3,200- to 3,500-ft (1,050–1,150 m) zone suggests that these two fir species were incorrectly identified in his study.

Several community characteristics are closely correlated with the successional ordination (Table 3). Average total tree and sapling densities follow similar patterns with exceptionally high densities in the pioneer stages and very low densities in

TABLE 3. A summary of community characteristics, expressed as averaged values for stands within each of the gradient segments

Community characteristic	Gradient segments					
	I	II	III	IV	V	VI
Average tree density (number per acre)	568	370	304	275	254	182
Average sapling density (number per acre)	430	391	289	188	184	120
Average stand dominance/acre[a]	19,853	23,560	26,313	31,886	32,967	41,021
Average number of species/stand	30.1	25.8	31.4	24.4	23.2	22.0
Average number of trees/size class[b]						
4-10 inches dbh	72.4	57.6	38.8	38.4	29.8	25.2
11-20 inches dbh	7.6	22.0	40.6	38.0	45.4	30.4
21-30 inches dbh	0	0.4	0.6	3.6	4.6	17.2
Over 30 inches dbh	0	0	0	0	0.2	7.2

[a]Number of square inches per acre.
[b]Based on the 80 trees in each stand sample.

TABLE 4. Average quadrat frequency values for common understory species occurring within the stands of each successional gradient segment

Species	Gradient segments					
	I	II	III	IV	V	VI
Anaphalis margaritacea	2.0	0	0	0	0	0
Vaccinium myrtilloides	2.0	2.7	0	0	0	0
Campanula rotundifolia	4.0	1.0	0	0	0	0
Apocynum androsaemifolium	15.0	5.8	0	0	0	0
Vaccinium caespitosum	20.0	12.0	0	0	0	0
Juniperus communis	2.4	1.8	0.2	0	0	0
Vaccinium scoparium	8.0	6.0	5.0	2.7	0.2	0
Cornus canadensis	18.0	10.8	1.0	1.0	2.8	0
Spiraea betulifolia	49.0	40.8	10.0	13.7	5.0	0
Rosa gymnocarpa	12.0	25.0	6.8	9.2	4.5	0
Eleagnus canadensis	0.4	1.8	0.7	0.2	0.2	0
Symphoricarpos occidentalis	5.0	25.8	1.0	2.5	1.0	0
Fragaria braceata	27.0	24.2	8.5	1.8	4.3	0.2
Pteridium aquilinum	4.4	0.8	1.8	1.1	0.5	0.2
Xerophyllum tenax	44.2	42.5	15.0	11.0	0.2	0.2
Menziesia ferruginea	1.2	2.5	0.7	0.3	0.3	0.2
Berberis repens	7.0	26.7	3.5	2.5	4.3	0.3
Pachistima myrsinites	6.0	17.5	13.5	5.0	2.1	0.4
Rubus parviflorus	4.2	20.1	1.8	2.0	1.3	0.8
Lonicera utahensis	4.0	2.5	9.7	4.5	3.0	0.2
Aralia nudicaulis	2.0	31.0	0.2	5.3	16.8	5.1
Viola orbiculata	46.0	47.5	33.3	34.2	31.7	16.8
Chimaphila umbellata	38.0	36.7	50.8	35.0	40.8	5.8
Vaccinium membranaceum	33.0	41.7	50.1	26.7	19.5	1.5
Clintonia uniflora	21.0	48.3	57.5	64.2	64.2	24.1
Pyrola minor	2.2	2.6	7.0	2.0	3.4	1.7
Goodyera oblongifolia	4.2	6.8	24.0	21.7	35.0	7.5
Pyrola secunda	0.4	3.5	22.5	28.3	19.3	5.3
Smilacina stellata	0.4	20.8	5.2	10.8	12.5	6.0
Tiarella unifoliata	0.4	4.2	6.0	30.0	18.3	35.0
Pyrola asarifolia	0	0.8	11.6	9.3	3.6	1.8
Adenocaulon bicolor	0	2.5	3.3	9.2	12.7	12.5
Disporum trachycarpum	0	5.8	1.0	3.3	1.3	1.0
Acer glabrum	0	8.5	2.7	5.3	4.5	4.3
Osmorhiza occidentalis	0	19.3	4.3	6.0	5.8	2.7
Amelanchier alnifolia	0	27.7	5.3	6.1	1.9	0.3
Taxus brevifolia	0	0	4.0	3.0	1.0	22.7
Botrychium virginianum	0	0	0	2.6	1.0	1.0
Equisetum arvense	0	0	0	2.5	0.8	0.2
Phegopteris dryopteris	0	0	0	2.5	3.3	33.6
Holodiscus discolor	0	0	0	0	0.2	0
Circaea alpina	0	0	0	0	0.8	14.2
Athyrium filix-foemina	0	0	0	0	0.2	13.3
Listera convallarioides	0	0	0	0	0	9.2

climax stages. Average stand dominance doubles between pioneer and climax stages of forest development. A tabulation of the average number of species in each of the six successional segments reveals a gradual reduction in species diversity at later stages of succession. The shift in the distribution of trees within diameter size classes follows a predictable pattern.

Average quadrat frequency values were determined for the common vascular species within each of the successional segments (Table 4). The species demonstrate numerous patterns of arrangement along the successional gradient and it is clear that a vegetational continuum exists. Some species or groups of species are restricted to one or another of the gradient segments. Species such as *Anaphalis margaritacea, Vaccinium myrtilloides, V. caespitosum,* and *Apocynum androsaemifolium* are generally restricted to the pioneer, *Pinus contorta*-dominated communities. Other species, including *Holodiscus discolor, Circaea alpina, Athyrium filix-foemina,* and *Listera convallaroides,* are characteristically restricted to communities that are climax. *Xerophyllum tenax* and *Vaccinium membranaceum,* two common understory species in the communities of the spruce-fir zone in western Montana, achieve very high frequency values in the pioneer and seral communities in the cedar-hemlock zone in Glacier Park, but then become rare as these communities reach old age. This same behavior is demonstrated by *Spiraea betulifolia, Fragaria bracteata,* and *Amelanchier alnifolia,* which are common understory components in the drier, *Pseudotsuga menziesii* communities in western Montana. Under the dense canopy created by cedar and hemlock only a few understory species really thrive, and even these are often restricted to the occasional islands of sunlight that reach the forest floor. Large portions of the understory in climax stands are completely devoid of herbs and shrubs, and quadrat frequency values become a function of the distribution of sunspots. Of the 31 species encountered in the communities summarized in gradient segment VI, only four achieve average frequency values over 20%. *Tiarella unifoliata* attained the highest average frequency in the hemlock-dominated communities, but its value (35%) is relatively small when compared with abundance levels attained by other species in other gradient segments.

CEDAR-HEMLOCK AND SPRUCE-FIR ECOTONAL COMMUNITIES

Generally above 3,500 ft (1,150 m) both *Abies lasiocarpa* and *Picea engelmannii* become increasingly more abundant. *Thuja plicata* and *Tsuga heterophylla* are both encountered up to elevations of 4,000 ft (1,315 m). Thus a zone of overlap exists where all four of these major tree species occur together. Stand data are summarized for a series of stands sampled between 3,500 and 4,000 ft (Table 5). These stands are arbitrarily arranged in order of increasing importance values for *Abies lasiocarpa;* it is merely a coincidence that this ordering matches closely with an elevational gradient. None of these stands can be classed as pioneer, and many of them are actually old-aged stands. The arrangement in no way represents a successional gradient.

Within this transitional zone climax stands composed of various proportions of *Abies lasiocarpa, Picea engelmannii, Thuja plicata,* and *Tsuga heterophylla* are likely to exist in some habitats, although at elevations above 3,800 ft (1,250 m)

TABLE 5. Community data from 10 stands occurring within the cedar-hemlock and spruce-fir overlap zone between 3,500 and 4,000 ft (1,150–1,315 m) (stands are arranged in order of increasing importance values of *Abies lasiocarpa*)

Species	Importance values									
	1	2	3	4	5	6	7	8	9	10
Abies lasiocarpa	35	38	39	48	49	60	63	84	123	137
Betula papyrifera	4	0	0	4	15	9	40	0	0	0
Larix occidentalis	50	0	0	16	70	14	0	71	26	60
Picea engelmannii	46	67	89	108	47	44	155	108	144	90
Pinus contorta	24	0	0	0	4	0	0	9	0	0
P. monticola	121	0	16	64	56	136	27	11	0	9
Pseudotsuga menziesii	13	10	10	24	56	37	7	17	7	0
Thuja plicata	0	98	34	7	0	0	8	0	0	0
Tsuga heterophylla	7	87	112	29	3	0	0	0	0	0
Elevation (ft)	3,550	3,600	3,550	3,610	3,625	3,750	3,800	3,850	3,900	4,000
	Sapling importance values									
Abies lasiocarpa	110	8	38	123	119	123	125	165	121	113
Picea engelmannii	48	12	8	47	23	0	11	35	79	87
Thuja plicata	0	67	38	5	0	0	0	0	0	0
Tsuga heterophylla	0	113	116	25	4	0	64	0	0	0
Tree density (number/acre)	251	258	222	194	259	148	222	239	149	351
Sapling density	315	90	82	142	252	151	90	538	86	379
Diameter size classes	Number of trees in each size class									
4-10 inches dbh	50	35	41	25	43	40	24	42	34	62
11-20 inches dbh	29	26	26	25	35	35	36	32	35	11
21-30 inches dbh	1	11	8	24	2	5	18	6	8	7
Over 30 inches dbh	0	8	5	6	0	0	2	0	3	0

the dominance or potential dominance of *Abies* and *Picea* is clearly evident. It is likely that many of these ecotonal stands originated as either *Pinus contorta* and/or *Larix occidentalis* communities following fire, with successional replacement involving *Pinus monticola* and *Pseudotsuga menziesii*. These latter two species show a shift from roles as major seral species at elevations below 3,700 ft (1,214 m) to minor seral species above this height. *Picea engelmannii* displays increasing importance in stands located above 3,600 ft (1,180 m).

It is problematic whether spruce will maintain its dominance in communities such as stands 7, 8, and 9 (Table 5), but an interpretation of the sapling importance values indicates that *Abies lasiocarpa* is likely to attain dominance in the communities currently dominated by *Picea engelmannii*. Daubenmire (1966, Fig. 2) assigns Engelmann spruce a seral role in the spruce-fir zone in northern Idaho and indicates that spruce is not capable of maintaining self-reproducing populations when in direct competition with *Abies lasiocarpa*. Such a conclusion is not well supported by studies of spruce-fir communities in Glacier Park or other portions of western Montana. Current information better supports the view that *Picea engelmanii* can often attain dominance in seral communities in the spruce-fir zone and may persist as a minor climax species in the older, *Abies lasiocarpa*-dominated stands.

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ECOLOGY OF *PICEA CHIHUAHUANA* MARTINEZ

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Abstract. *Picea chihuahuana* probably arrived in North America during Cretaceous or earlier times. The physiography, climate, and forest geography of its present range in the Sierra Madre Occidental of Mexico are described. The forests are cool montane temperate rather than boreal. In the station examined, *P. chihuahuana* was distributed only on fresh and moist sites. Growth rates both in height and diameter on moist sites exceeded those on the fresh. The culmination point for diameter growth was at 85 years. The mean specific gravity was .347, and differences due to site were not significant. The moist site soils supporting *P. chihuahuana* differed from the fresh site soils only in having lower pH, Ca, and K levels. Since the sites were closely associated and the parent materials identical, it is assumed that these differences were due to differences in moisture regime. The foliar nutrient concentration of N, P, and K decreased with increasing needle age except that P and K increased markedly in the oldest needles. Conversely, Ca increased with advancing needle age but decreased in the oldest needles. *P. chihuahuana* shows a remarkable tolerance for high Ca concentration. The associated vegetation of the *P. chihuahuana* stand was measured on both fresh and moist sites, and significant differences between the plant assemblages of these sites were found. Its present range and pattern of regeneration indicate that *P. chihuahuana* may not long escape extinction.

Introduction

The genus *Picea* is among the most important of the world's arboreal genera, contributing to the economy of several northern countries. A good deal is known about many of the commoner species, but much remains to be learned regarding some of the minor species. Studies of the peripheral species may provide information on the history and tolerances of the genus as a whole, as well as the attributes of the species themselves, their associates, and their environmental factors. This study is directed towards these ends. The field work was carried out in August 1963. While the present study presents data from only one of the known stations, discussions with a number of forest engineers on whose lands the other stations are located have confirmed the descriptions presented here, particularly with regard to competing ground vegetation, regeneration, tree dimensions, stand composition, and distribution. Recent confirmation has also been received from Hans Nienstaedt concerning one of the main stands in Chihuahua (*personal communication*).

Before 1942 representatives of *Picea* were not known to occur in Mexico. *P. chihuahuana* was found in that year by Sr. Rigoberto Dueñas in the State of Chihuahua in northwestern Mexico. It was identified as a new species and described by the late, distinguished Mexican taxonomist, Maximino Martínez (1942). Subsequently, the species was found at a few other stations in Chihuahua and Durango, where it is called by its scientific name *Picea,* pronounced "Pissere" in Mexican Spanish. The fact that it was discovered so recently is, however, indicative of its rarity and general inaccessibility.

In 1961 a second Mexican species, *P. mexicana* Martínez, was discovered in the mountains of Coahuila and Nuevo Leon by Ing. Manual Enríquez Quintana and subsequently collected by Ing. Jésus Vásquez Soto of the Instituto Nacional de Investigaciones Forestales. This species, de-