James R. Habeck

Department of Botany
University of Montana
Missoula, Montana

Mountain Hemlock Communities in Western Montana[1]

The principal objective of this report is to provide a basic description of the mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) communities in western Montana. Such a description has importance because this species reaches its easternmost range limits in western Montana, and is one of the rarest coniferous species in Montana. Throughout its botanical range, mountain hemlock is regarded as a highly shade-tolerant, climax species, and the nature of the communities such a climax species forms at its range limits is of additional interest. Its occurrence in western Montana is generally confined to the moist, upper slopes of the Bitterroot Mountains separating Idaho and Montana. Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are nearly constant associates of mountain hemlock in this region, with the three species occurring in various proportions.

Both subalpine fir and Engelmann spruce have rather wide distributional ranges in western North America, and both are commonly encountered at elevations above 5000 feet in the western Montana and northern Idaho area. Mountain hemlock, in contrast, has its main center of distribution in the Pacific Coastal mountains, ranging from central California to Alaska, but exhibits a peninsular extension into the Inland Empire region. The eastern range extension is well correlated with a similar eastward penetration of moist, Pacific Coast air masses that have been described in greater detail elsewhere (Kirkwood, 1922, 1928; Daubenmire, 1943; Benson, 1957; and Habeck, 1963).

With the exception of a few brief references by Kirkwood (1922), which report the occurrence of mountain hemlock in Montana, there have been no detailed treatments made of this community type in Montana. Forest communities composed of mountain hemlock, subalpine fir, and Engelmann spruce which occur in contiguous portions of northern Idaho have been treated by Daubenmire (1952, 1966) as a portion of more extensive analyses of the vegetation in that area.

Daubenmire's 1952 description and classification of the spruce-fir zone in northern Idaho includes information on the sociologic position of *Tsuga mertensiana* in this forest zone. At that time (1952), Daubenmire indicated that mountain hemlock could function as a minor climax species in the spruce-fir forests, as a climax co-dominant with subalpine fir and Engelmann spruce, or as a climax species capable of replacing all

[1] This study was supported by NSF Grant GB 2450.

other species. Common seral species in the spruce-fir zone were listed by Daubenmire and include *Pinus monticola, P. contorta, P. albicaulis, Larix occidentalis, Pseudotsuga menziesii,* and *Abies grandis.* Variation in the occurrence of these seral species is in part dependent upon whether specific communities occur at the lower, intermediate, or upper positions within the spruce-fir zone.

Daubenmire's most recent (1966) discussion and interpretation of the forest vegetation in northern Idaho encompasses the view that subalpine fir and Engelmann spruce are generally incapable of maintaining self-reproducing populations when in competition with *Tsuga mertensiana,* and consequently, climax communities co-dominated by hemlock, spruce, and fir are not likely to be formed. The only exception (Daubenmire, 1966, Fig. 2) would be in extremely narrow ecotones where mountain hemlock and subalpine fir reach their upper and lower limits on a moisture/elevational gradient.

Description of Study Area

The communities selected for detailed study are located directly within mountain hemlock's main range in Montana. The stands, with their locations, are shown in Figure 1. The elevations in this part of Montana are only moderate compared with other portions of the Bitterroot Mountains. Heights average about 6000 feet, and seldom do the mountain peaks exceed timberline. The somewhat lower elevations in northwestern Montana partially account for the eastern penetration of Pacific Coast air masses. Annual moisture in mountain hemlock habitats can only be estimated from several lower elevational stations in Montana and Idaho.

It is probable that the upper slopes receive between 45 and 50 inches annually, most of it in the form of snow. Short-term weather records from higher elevations indicate that annual moisture may be as high as 70 inches per year in certain areas of the Bitterroot Mountains. Figure 1 indicates the pattern of annual precipitation in western Montana (Maughan, 1941), and from these data it becomes evident that there is a very rapid reduction in annual moisture over a very short distance into Montana.

The distribution and abundance in mountain hemlock is closely related to this moisture pattern. Mountain hemlock is commonly encountered in areas with annual moisture above 40 inches; in such areas, the hemlock occupies a variety of slopes and exposures. Further eastward, with moisture reduction, hemlock becomes restricted to higher elevations and to generally northern exposures. At its extreme eastern range limits, on the upper slopes of the Continental Divide, the hemlock forms poorly defined communities consisting of a few individual trees on north-facing rock outcrops.

Methods

Field Methods. During the summer of 1964, after extensive examination of mountain hemlock communities throughout western Montana, 15 stands were selected for detailed sampling; their locations are shown in Figure 1. The communities selected represent a wide range of sites, compositions, and stand ages. As is true throughout the forested regions of western Montana, the mountain hemlock forests typically reflect a history of past fire disturbance. The area of current hemlock abundance was nearly uniformly destroyed by the great 1910 fire that swept over the northern Idaho and western Montana region. Many hemlock communities have a more recent history of cutting and domestic grazing, but stands with these disturbances were not included in the investigation.

The trees and saplings in each stand were sampled by the quarter method (Cottam and Curtis, 1956), with 20 points sampled in each stand. Trees were defined as individuals with diameters of 4″ DBH or more; saplings with diameters between 1 and 4″ DBH. The understory vegetation, including tree seedlings, was sampled at each point with a meter square quadrat. Plant nomenclature used in this study follows Davis (1952).

Laboratory Methods. The field data were used to calculate importance values for each tree species in each stand. The importance value is a summation of the relative density, relative frequency, and relative dominance values. An importance value for saplings was also calculated by summing the relative density and frequency values. Absolute densities for both trees and saplings were also computed. The understory quadrat data were summarized as percentage frequency.

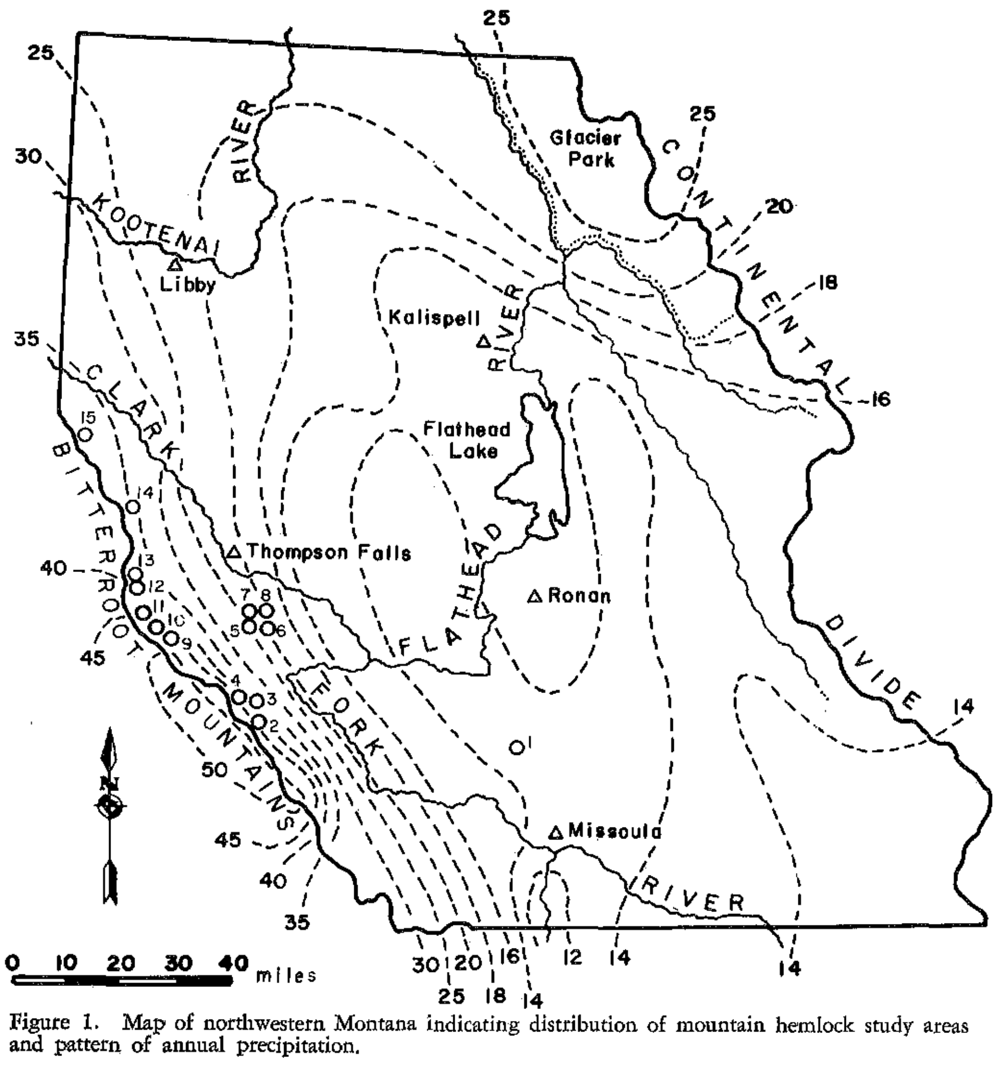

Figure 1. Map of northwestern Montana indicating distribution of mountain hemlock study areas and pattern of annual precipitation.

The basic approach used in the analysis of the community data involves an arrangement of the stands in order of increasing importance values for *Tsuga mertensiana.* This ordering of the communities closely corresponds to an arrangement of the 15 stands along the primary axis of an ordination based on the technique described by Bray and Curtis (1957). The relatively low number of stands involved, combined with the rather low floristic diversity in these forest stands, contributed to a low degree of stand separation on both the secondary and tertiary axes of the constructed ordination. Stand ordering, on the primary axis, was discovered to be highly correlated with mountain hemlock importance values, and it was decided to arrange the communities on the basis of these latter values.

Results

Within the 15 stands studied, a total of 10 tree species was recorded. These are, with the number of stands of occurrence indicated, as follows: *Tsuga mertensiana* (15), *Abies lasiocarpa* (15), *Picea engelmannii* (15), *Pinus contorta* (14), *Pinus monticola* (11), *Larix occidentalis* (8), *Pinus albicaulis* (6), *Pseudotsuga menziesii* (3), *Abies grandis* (2), and *Thuja plicata* (1).

A summary of importance values for each tree species in each stand is presented in Table 1. A summary of sapling importance values is provided in Table 2. As the importance values of *Tsuga mertensiana* trees increase, there is a gradual reduction of the importance values for all other tree species. The importance values for *Abies lasiocarpa* and *Picea engelmannii* actually show both high and low values in those stands where mountain hemlock values are below 135 per cent. Subalpine fir's values in this part of the ordination appear, in part, to be inversely related to the importance values of *Pinus contorta.* The field data, combined with extensive observations in Montana

Table 1. Summary of importance values for each tree species in each stand. The 15 stands in this table have been arranged in order of increasing importance values for *Tsuga mertensiana* (Tm). An *x* is placed in those stands where a species was recorded as present only. Symbols for species listed in this table are as follows: Al, *Abies lasiocarpa;* Pe, *Picea engelmannii;* Pc, *Pinus contorta;* Lo, *Larix occidentalis;* Pm, *Pinus monticola;* Pa, *P. albicaulis;* Psm, *Pseudotsuga menziesii;* Ag, *Abies grandis;* Tp, *Thuja plicata.*

Stand	Tm	Al	Pe	Pc	Lo	Pm	Pa	Psm	Ag	Tp
11	40.5	25.2	44.6	90.6	6.1	82.8		x	10.0	
8	60.7	104.4	46.0	6.9	35.1	x		46.9		
9	68.8	60.1	31.3	71.6		58.8			9.4	
1	97.4	132.7	3.9	49.0			17.0			
12	97.8	155.8	13.9	8.9		17.2	6.3			
14	119.8	55.7	x	38.9	73.3	12.3				
7	127.8	102.7	25.9	x	23.7	11.4		8.5		
4	135.6	103.4	21.9	33.6	5.5	x				
5	175.5	51.9	13.3	27.5	31.8		x			
2	185.5	71.4	29.0	6.8		x	7.3			x
6	204.8	80.8	x	x	14.4					
3	207.3	57.9	24.9	4.6	x		5.3			
13	209.9	49.7	x	27.9		6.4	6.1			
10	221.9	24.9	24.5	28.7		x				
15	257.2	29.7	13.1			x				

Table 2. Summary of importance values for tree saplings in each stand. The ordering of the stands and the symbols for species are the same as shown in Table 1.

Stand	Tm	Al	Pe	Pc	Lo	Pm	Pa	Ag
11	28.3	141.9	13.0	0	0	5.6	0	11.2
8	55.5	140.2	4.3	0	0	0	0	0
9	17.0	140.0	17.1	5.6	0	20.3	0	0
1	42.8	112.8	7.4	28.3	0	0	8.7	0
12	108.3	79.4	0	6.8	0	0	5.5	0
14	100.7	36.2	0	9.6	39.5	14.0	0	0
7	82.3	113.8	3.9	0	0	0	0	0
4	55.4	108.8	28.2	0	0	0	7.6	0
5	81.2	81.7	25.5	11.6	0	0	0	0
2	102.5	72.5	25.0	0	0	0	0	0
6	101.5	98.5	0	0	0	0	0	0
3	69.4	122.4	0	4.1	0	4.1	0	0
13	110.1	61.6	0	13.3	0	0	15.0	0
10	88.2	111.8	0	0	0	0	0	0
15	39.2	151.7	9.1	0	0	0	0	0

and Idaho, support the idea that considerable variability exists among the seral stands which are developing toward a mountain hemlock climax. Following fire disturbance, some sites are immediately invaded by dense *Pinus contorta* populations, and with time, this species is replaced by such species as *Pinus monticola, P. albicaulis, Abies lasiocarpa,* and *Picea engelmannii,* in various combinations. On other occasions, lodgepole pine is nearly absent in forest re-establishment, with initial invasion made by *Abies lasiocarpa* and *Picea engelmannii.* Occasional observations were made of instances where initial invasion following disturbance involved the direct return of *Tsuga mertensiana.* Succession, therefore, does not follow a single, predictable pattern in its early stages.

Successional patterns, in mountain hemlock communities, seem, in part, to be influenced by elevational factors in western Montana. The 15 stands range from 5100 to 6700 feet (Table 3), with an average elevation of about 5600 feet. Site exposures are also variable among the stands. Seral species such as *Pinus monticola, Larix occidentalis,* and *Pseudotsuga menziesii* attain their highest importance values among the hemlock communities located at elevations below 5600 feet. These same species are generally minor seral species or are absent at higher elevations. Both *Pinus contorta* and *Picea engelmannii* function as major seral species throughout the elevational range of *Tsuga mertensiana,* with *Abies lasiocarpa* seemingly playing a very complex role in stand development.

Although the data reveal that most of the species associated with *Tsuga mertensiana* become markedly reduced in number or entirely replaced as the stands become older, it appears that *Abies lasiocarpa* retains some ability to reproduce itself in hemlock-dominated stands. An examination of the sapling data in Tables 2 and 3 indicates this species' ability to generate sizable sapling populations. The conversion of fir saplings to tree-sized individuals, however, is another matter. Throughout all of the stands studied there is a remarkably low percentage of tree-sized firs (over 4" DBH) compared with the number of sapling-sized individuals in the understory. Many of the saplings of *Abies lasiocarpa* exist in a severely suppressed condition, with individuals 1-2 inches DBH

Table 3. Summary of stand elevation and exposure, tree diameter size-class data, and tree and sapling densities for *Tsuga mertensiana* and *Abies lasiocarpa.* Diameter size-class data (DBH) are based on the 80 trees included in each stand sample. The ordering of the stands is the same as in Table 1.

Stand	Elevation and exposure	Diameter Size classes* I	II	III	IV	Tree and sapling densities/acre *Tsuga mertensiana* Trees	Saplings	*Abies lasiocarpa* Trees	Saplings
11	5100 S	8	66	6	0	22	8	14	84
8	5600 N	43	24	11	2	43	55	174	201
9	5200 E	24	50	6	0	33	6	35	98
1	6700 N	71	9	0	0	64	189	96	702
12	5760 —	46	37	0	0	152	717	272	450
14	5100 S	62	16	2	0	118	494	42	127
7	5560 W	53	24	3	0	239	248	165	428
4	5580 S	58	22	0	0	228	236	196	623
5	5500 SE	41	37	2	0	269	395	72	419
2	5600 W	45	34	1	0	241	122	73	69
6	5550 NW	53	26	1	0	459	763	148	763
3	5600 W	62	17	1	0	383	357	117	758
13	5750 —	64	16	0	0	365	398	63	188
10	5900 E	22	57	1	0	244	96	20	144
15	5400 W	8	50	22	0	158	20	13	139

* I = 4-10″, II = 11-20″, III = 21-30″, IV = Over 30″.

not uncommonly 70 to 90 years old. Mountain hemlock saplings of the same size, in the same communities, are generally one-half to one-third this age. It is, therefore, difficult to assess completely the status of *Abies lasiocarpa* in mountain hemlock communities. Subalpine fir's persistence in old-aged mountain hemlock communities is a reality; however, its competitive ability is reduced in the presence of hemlock. The ability of subalpine fir to withstand suppression for long periods accounts for the numerous seedlings and saplings in the understory of hemlock stands, but the vast majority of these small trees never achieve tree-sized proportions beneath a canopy of mountain hemlock. Occasional openings in the hemlock canopy allow a few firs to make a greater growth response and reach the upper canopy layer, but even on these occasions the fir saplings are often in direct competition with rapidly growing hemlock saplings.

The occurrence of *Abies grandis* and *Thuja plicata* in several of the stands sampled is of additional interest. Both of these species occur more commonly at much lower elevations in this same region; however, there is a zone of overlap between the upper limits of grand fir and western redcedar, and the lower limits of mountain hemlock. The zone of overlap, between these three species, is not narrow. The moist, upper ravines on the Idaho/Montana border, at 5000 feet, support communities composed of both spruce-fir and redcedar-western hemlock zone elements. The lowest mountain hemlock stands sampled occur at 5100 feet, although the lower limit noted for *Tsuga mertensiana* in Montana, a few miles from the state line, is at 3700 feet, in a ravine habitat.

Table 4 summarizes the quadrat frequency values for seedlings of major tree species as well as eight of the most common understory species encountered in the hemlock stands. Various proportions of four species typically compose the understories of the hemlock communities. These are *Xerophyllum tenax, Vaccinium membranaceum, V.*

Table 4. Summary of quadrat frequency data for seedlings of major tree species and common understory species. Symbols used are as follows: Tm, *Tsuga mertensiana*; Al, *Abies lasiocarpa*; Pe, *Picea engelmannii*; Vm, *Vaccinium membranaceum*; Vs, *V. scoparium*; Xt, *Xerophyllum tenax*; Mf, *Menziesia ferruginea*; Cu, *Chimaphila umbellata;* Go, *Goodyera oblongifolia*; Ps, *Pyrola secunda*; Pm, *Pachistima myrsinites.*

	Tree seedlings			Understory species							
Stand	Tm	Al	Pe	Xt	Vm	Vs	Mf	Cu	Go	Ps	Pm
11	0	5	0	85	95	0	20	5	5	0	0
8	0	10	0	80	70	0	20	20	0	50	40
9	5	5	0	80	95	0	25	5	0	10	0
1	30	80	0	75	35	100	5	0	0	10	0
12	5	40	0	100	15	90	25	0	5	0	0
14	15	0	0	85	35	100	25	0	0	0	0
7	0	15	0	75	70	40	35	20	10	20	0
4	0	20	0	95	85	15	50	15	5	30	0
5	15	15	0	80	75	15	15	25	0	0	0
2	0	40	5	65	60	0	85	0	5	20	0
6	40	20	0	95	50	45	65	0	0	0	0
3	0	20	0	100	85	0	10	30	0	35	0
13	0	5	0	100	40	95	0	0	0	0	0
10	5	15	0	100	95	25	25	0	0	0	0
15	5	5	0	20	90	20	90	0	0	0	0

scoparium, and *Menziesia ferruginea.* The latter three shrub species generally form a dense understory cover which allows little light penetration to the soil surface. Other groundlayer species are uncommon; a total of only 37 herbaceous and shrub species were observed in the entire 15 stands, and only seven of these were present in three or more of the stands. Based on quadrat data, *Xerophyllum tenax* dominates the understories of nine stands, *Menziesia ferruginea* dominates the understory of two communities, as do *Vaccinium membranaceum* and *V. scoparium.* Often the percentages among these understory species do not greatly differ, and the impression one gets in observing these understories is that dominance is generally shared by two or more of these species.

The data in Table 4 reveal an interesting relationship between *Vaccinium scoparium* and *V. membranaceum.* There are no instances where both species achieve high values in the same stands, and typically, in stands where *Vaccinium membranaceum* is common, *V. scoparium* is either absent or present in low amounts. This disassociation of the two *Vaccinium* species appears to be well correlated with elevational factors. Stands within which *V. scoparium* reaches its highest values (above 90%) are at the highest elevations included in the study (above 5700 feet); within these same stands *V. membranaceum* achieves its lowest frequency values.

Discussion

Although *Tsuga mertensiana* demonstrates a marked reduction in its distribution as it reaches its eastern range limits in western Montana, it gives evidence of maintaining itself as a shade-tolerant, climax species in the easternmost habitats within which it occurs. In all of the communities studied or observed in western Montana, it has become clear that if available moisture is sufficient to allow the existence of mountain hemlock, it will establish some type of self-regenerating population. Isolated mountain hemlock communities, occurring in upper ravines or on exposed ridgetops as far east as Missoula, are characterized by low numbers of individuals, sometimes as few as 20-30 trees over 4 inches DBH on sites only fractions of an acre in size. Nevertheless, these small communities give indication of stability by the presence of some individuals in all age and size classes.

It is suspected that the Pacific Coast floristic elements in former times showed a much greater range extension into western Montana than is reflected by current botanical ranges. Easternmost occurrences of *Tsuga mertensiana,* and other Pacific Coast species such as *Thuja plicata, Tsuga heterophylla, Abies grandis,* and *Taxus brevifolia,* occur as small, disjunct, relict populations some distance from areas where these species show general, widespread distributions. Often associated with these tree species are herbs and shrubs which are also members of the Pacific Coast flora. It is probable that macroclimatic changes have occurred in the northern Rocky Mountains, and have been responsible for a degree of withdrawal of the Pacific Coast floristic peninsula from Montana. Such a possibility requires further investigation.

In the extreme western portions of Montana, in the upper reaches of the Bitterroot Mountains, where a majority of the hemlock communities were studied, the favorable moisture conditions allow *Tsuga mertensiana* to invade successfully the *Picea-Abies* forest zone. The data collected in this study indicate that in these moist regions of Montana, mountain hemlock can generally achieve stand dominance when in competition with *Abies lasiocarpa, Picea engelmannii,* and other species. This attainment of dominance, however, does not necessarily imply that the hemlock is capable of replacing subalpine fir entirely, nor do the data indicate that this does happen. In the absence of *Tsuga mertensiana, Abies lasiocarpa* is capable of developing climax communities as witnessed by its sociologic behavior elsewhere in the Bitterroot Mountains and other mountainous areas throughout western Montana. The joint occurrence of mountain hemlock and subalpine fir should be interpreted as a change in the fir's status from that of a major climax species to that of a minor climax species.

The retention by *Abies lasiocarpa* of some ability to reproduce itself in the mountain hemlock-dominated communities in western Montana may be the result of an onset of suboptimum moisture conditions just a short distance within the state as indicated by Figure 1. Even with its high shade tolerance, the dependency of mountain hemlock on a relatively high moisture supply may well limit its ability to displace completely *Abies lasiocarpa.* In describing the sociologic roles of *Tsuga mertensiana* and *Abies lasiocarpa* in northern Idaho, Daubenmire (1966, Fig. 2) indicated that joint occurrence of these two species in climax communities would be confined to a very narrow zone of overlap on a moisture/elevational gradient. It is likely that, as annual moisture becomes reduced with a vertical decrease in elevation on the west slope of the Bitterroot Mountains in Idaho, a zone is reached where moisture limits mountain hemlock's capacity to replace completely subalpine fir, and consequently stable communities of both species exist. In western Montana, a comparable moisture reduction takes place along a longitudinal gradient, beginning at the crest of the Bitterroots and extending eastward. If annual moisture is a limiting factor for mountain hemlock development, as it seems to be, then a result of suboptimum moisture conditions in much of western Montana would be the development of a rather wide zone of overlap where both *Tsuga mer-*

tensiana and *Abies lasiocarpa* can occur jointly. Consequently, mountain hemlock not only shows a gradual reduction in its abundance and distribution as it reaches its easternmost range limits, but it evidently loses some of its ability to replace completely all other associated species.

A description of forest succession in mountain hemlock communities in western Montana is made difficult because numerous variables are involved. Community reestablishment following disturbance can involve various combinations of pioneer or seral species, including *Pinus contorta, P. monticola, Pseudotsuga menziesii,* and *Larix occidentalis.* Most of these latter species function as major seral species at elevations below 5600 feet, and as minor seral species at higher elevations. These same species are characteristically more abundant in secondary forests within the *Thjua plicata-Tsuga heterophylla* zone at much lower elevations in northern Idaho and western Montana. Mountain hemlock communities developing after disturbance at elevations above 5600 feet are most often composed of various combinations of *Pinus contorta, Picea engelmannii, Abies lasiocarpa,* and *Tsuga mertensiana.* Due to numerous chance factors that are involved in community reestablishment, it is generally not possible to construct and describe a simple linear pattern which portrays successional replacement. The data collected, combined with field observations, indicate that *Tsuga mertensiana,* regardless of the exact composition of pioneer stands, will eventually attain stand dominance in a major part of its distributional range in western Montana.

Literature Cited

Benson, L. 1957. Plant classification. D. C. Heath and Co., Boston. 688 p.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monog., 27:325-349.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology, 37(3): 451-460.

Daubenmire, R. F. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev., 9: 325-393.

———. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monog., 22: 301-330.

———. 1966. Vegetation: identification of typal communities. Science, January 21, 1966, Vol. 151, No. 3708, pp. 291-298.

Davis, R. J. 1952. Flora of Idaho. Wm. C. Brown Co., Publ., Dubuque, Iowa. 828 p.

Habeck, J. R. 1963. The composition of several climax forest communities in the Lake McDonald area of Glacier National Park. Mont. Acad. Sci., 23: 37-44.

Kirkwood, J. E. 1922. Forest distribution in the northern Rocky Mountains. Univ. of Montana Press. Series No. 2, Bull. No. 247. 180 p.

———. 1928. Botanical exploration in the Rocky Mountains - Lolo Trail. Sci. Monthly, 26: 315-328.

Maughan, W. E. 1941. Climate of Montana. Climate and Man, Yearbook of Agriculture. pp. 955-966.

Accepted for publication May 3, 1967.