AN ABSTRACT OF THE THESIS OF

ANDREW FREDERICK ROBINSON, JR. for the Ph. D.
(Name of Student) (Degree)

in BOTANY presented on May 2, 1969
(Major) (Date)

Title: DISTRIBUTION OF UNDERSTORY SPECIES IN RELATION TO MAXIMUM AND MINIMUM TREE INFLUENCE IN THE MONTANE FOREST OF THE CENTRAL OREGON CASCADES

Abstract approved: Redacted for Privacy
W. W. Chilcote

Twenty sites of uniform topography and soil were selected in the montane forest found on the East flank of the Central Oregon Cascades. These sites were located along a vegetational gradient composed of five plant communities: Abies/Pachistima, Pinus/Ceanothus, Pinus Arctostaphylos-Purshia, Pinus/Purshia/Festuca, and Juniperus Festuca. An attempt was made to relate the distributional pattern of understory species to six aspects of tree influence (overhead cover, amount of shade, daily differences in shading, seasonal differences in shading, amount of litter deposit, and species of tree depositing the litter) understory species' competition, and plot location. Cole's index and hierarchial classification analysis were statistical methods used to correlate the understory species' pattern to tree influence, understory species' competition, and plot location.

From frequency data of the 63 species analyzed by Cole's index, only two showed an inconsistent distributional pattern in relation to tree influence. Similarly, three distributional patterns were noted. (1) Species were distributed at random in the area of maximum tree influence regardless where the species occurred along the gradient. (2) Species were distributed at random in the area of minimum tree influence and were absent in the area of maximum tree influence regardless where the species occurred along the gradient. (3) Species at a point along the gradient were distributed at random in areas of maximum and minimum tree influence; but on more xeric plots the species were distributed similar to pattern 1, and on more mesic plots species were distributed similar to pattern 2. In pattern 3, the point along the gradient where the species were distributed at random to areas of maximum and minimum tree influence may suggest an optimum point along the gradient where the effect from tree layer influence is minimal. This point provides a basis for comparing the environmental tolerances of the species and ordinating the stands.

When the species' density data were analyzed by hierarchial classification to determine what factors of maximum and minimum tree influence effected the density distribution of the species, the following patterns were noted. Normally, species with highest densities in areas of maximum insolation or sparse litter were prominent on the xeric end of the gradient, and those species with maximum densities in areas of low insolation or deep litter were prominent on the mesic end of the gradient. Chamaephyte species sampled had highest densities in areas underneath the trees and usually near the mesic end of the gradient. Therophyte species sampled had highest densities in open areas usually near the xeric end of the gradient.

Thus, a theoretical model was constructed using data obtained from this structural analysis of internal distributional patterns of understory species. The distribution of the species is much wider according to the theoretical model than was actually found by constancy data, but the differences when statistically analyzed are not great enough to reject the model at the 1% significance level. The model suggests predictable patterns of species' distribution within the five community types and may reflect the relative stability of these species within the community types.

Distribution of Understory Species in Relation to Maximum and Minimum Tree Influence in the Montane Forest of the Central Oregon Cascades

by

Andrew Frederick Robinson, Jr.

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1969

APPROVED:

Redacted for Privacy

Professor of Botany

in charge of major

Redacted for Privacy

Head of Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented May 2, 1969

Typed by Muriel Davis for Andrew Frederick Robinson, Jr.

ACKNOWLEDGMENT

I wish to thank those who assisted me during the course of this study. I am especially grateful to my major professor, Dr. W.W. Chilcote, for his many hours of guidance, patience, and understanding which he generously devoted to helping me in this work.

I also appreicate the help of my editor, Mr. Preston Onstad, in polishing the final draft of the thesis.

To my wife, Mary Ann, for typing, reading of the manuscript, and patient understanding, I am everlastingly grateful.

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INTRODUCTION

One of the structural features common to most terrestrial plant communities is the vertical arrangement of plants into layers or strata. The layers in a forest may vary from as few as two in the northern forest, to four or five in the temperate forest, or to multiple layers in the tropical forest. Causes for this vertical arrangement are assumed to be related to the growth form (height and lateral spread potential) of the plant species capable of growing in the area, and the layered environments within these various strata which the various growth forms create. The degree of influence within and between the various layers which the plants exert is closely related to the degree in which the plant intercepts radiant energy. For this reason plant cover (the vertical projection of the aerial cover to the ground) is often used as a measure of dominance.

The influence of the dominant tree layer upon the lower strata is especially apparent in the montane forest which has developed on the East flank of the Central Oregon Cascades. Three prominent vertical layers (tree, shrub, and herb) characterize this forest. Horizontal spacing between the trees and shrubs is sufficient to provide openings in the lowermost herbaceous layer making it possible to assess to some degree the separate influence of the tree and shrub canopies upon this subordinate layer.

Daubenmire (1968 a), Johnson (1961), Dyrness (1966), West (1964), and Sherman (1969) have described some of the structural features of the montane forest as part of the coniferous forest of the Cascades. Similarly, Driscol (1964) has described some of the structural features of the Juniper woodlands of Central Oregon. However, no attempt has been made to analyze the internal structural patterns characteristic of the layers in any of these studies.

Preliminary investigations into the internal structural pattern of the layers of the Ponderosa pine forest were made by Robinson (1967). The purpose of the present study is to examine further the maximum and minimum influence of tree layers upon understory species distribution, and from this information construct a theoretical model which could be used to indicate where the species will probably occur and their possible future roles within the community.

Six aspects of forest crown influence upon the pattern development of understory species at particular points on the forest floor were measured: (1) the amount of tree cover directly overhead, (2) the degree to which direct insolation was intercepted by tree crowns in the vicinity, (3) the time of day the insolation was intercepted, (4) the time of year the insolation was intercepted, (5) the amount of litter deposited, and (6) the species of tree depositing the litter. In addition to tree influence, understory species' competition, and plot location were also taken into consideration. In the latter analysis, it was hoped that some insight might be obtained into the degree which crown canopy compensated for other aspects of the environment (particularly climate).

Through the analysis of distributional relationships of various species to crown influence, it is hoped that a better understanding of the structural development of the Montane forest, a considerable amount of information about ecological requirements of understory species, and perhaps some insight into the role tree influence exerts upon the development of understory specie's pattern might be obtained.

THE STUDY AREA

The study area is located on the Eastern flank of the Central Oregon Cascades within the montane forest zone (Oosting, 1948). A narrow strip of this forest which has been preserved for scenic purposes along Highway 20 and 126 was selected for study. This narrow strip ranged from Suttle Lake to beyond Sisters, Oregon (Figure 2).

The study area is part of a gentle sloping glacial outwash plain dotted with many cinder cones of which Black Butte is the largest. This plain is also marked by ridges which were formed by lava escaping from fissures at the base of the cinder and volcanic cones of the high Cascades. The study area itself drops gently from 3, 320 feet to 3, 200 feet from west to east in approximately 15 miles.

The rock substratum, quite simple and uniform, is composed mainly of andesite and olivine basaltic lavas of the higher Cascades which began activity in the lower Pliocene (Williams, 1953). The formation of cinder cones and their lava ridges occurred after the ice age (Williams, 1953).

Soils of the study area are immature, highly uniform in nature, and largely derived from volcanic sandypumice material (West, 1964). During the height of the ice age, glaciers extended down the mountain side 20 miles or more (Williams, 1953). At such time showers of hot ashes fell on the glaciers and caused torrents of mud and boulders to

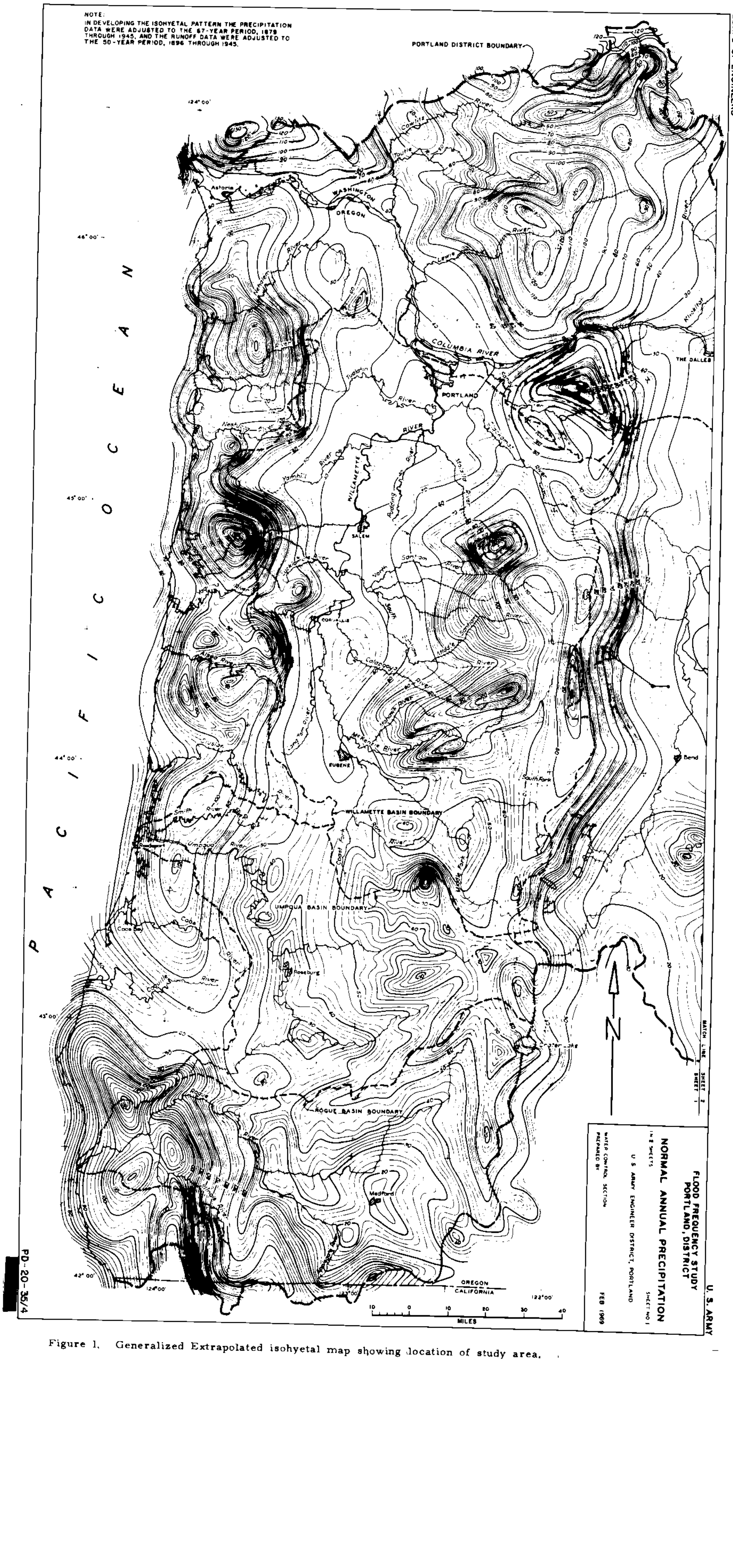


Figure 1. Generalized Extrapolated isohyetal map showing location of study area.

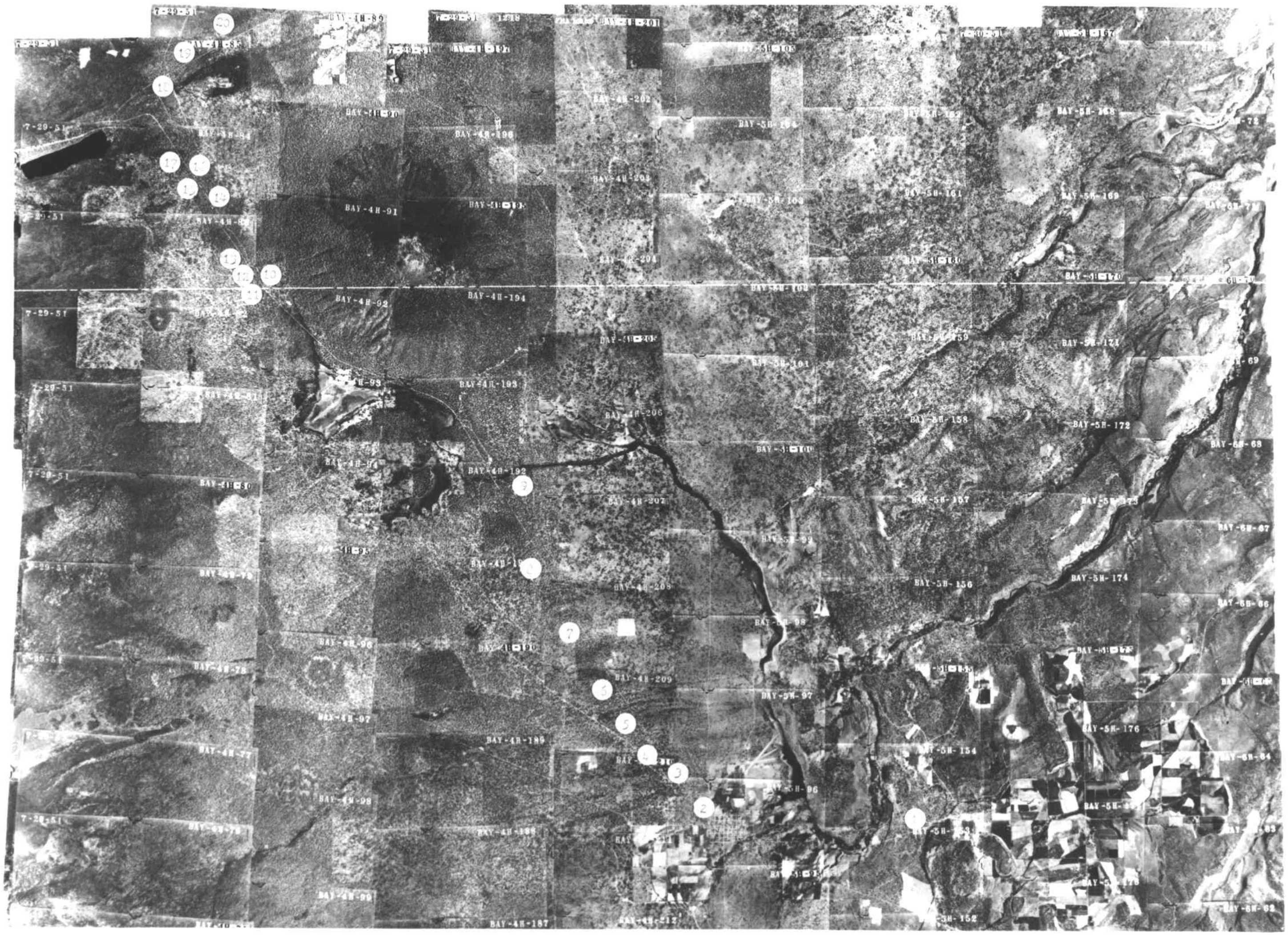


Figure 2. Aerial photograph index showing location of study area

sweep down and flood the plains below (Williams, 1953). However, most of the soil was derived from material deposited from glacial outwash during a pluvial period. Later other mantles of sandy pumice were deposited from nearby cinder cones such as Black Butte. Differences in soil depth over the area are therefore related to deposits of glacial outwash sediment over minor topographic relief, and to deposits of sandy pumice from the cinder cones.

In the study area 70% of the annual precipitation comes in late fall and winter (Wells, 1941). A sharp decrease in precipitation from the upper western boundary to the lower eastern boundary is noted from a generalized extrapolated isohyetal map of the area (Figure 1). A high percentage of moisture is removed by the high Cascades before the air reaches its crest. As the air descends the short eastern slope, it is warmed katabetically and the moisture holding capacity is increased, creating a "rain shadow." The highest average monthly temperatures occur in June, July, and August; and the lowest average monthly temperatures occur in December, January, and February (Figure 3). The highest temperature occurs during the season of lowest precipitation. It is not uncommon to find lows of 0 degrees F and highs of 95 degrees F at the Sisters station (West, 1964).

Disturbance from livestock grazing has been fairly light. The only part of the study area which may have been affected by livestock grazing occurs in the Sisters area, located near the old Santiam Toll

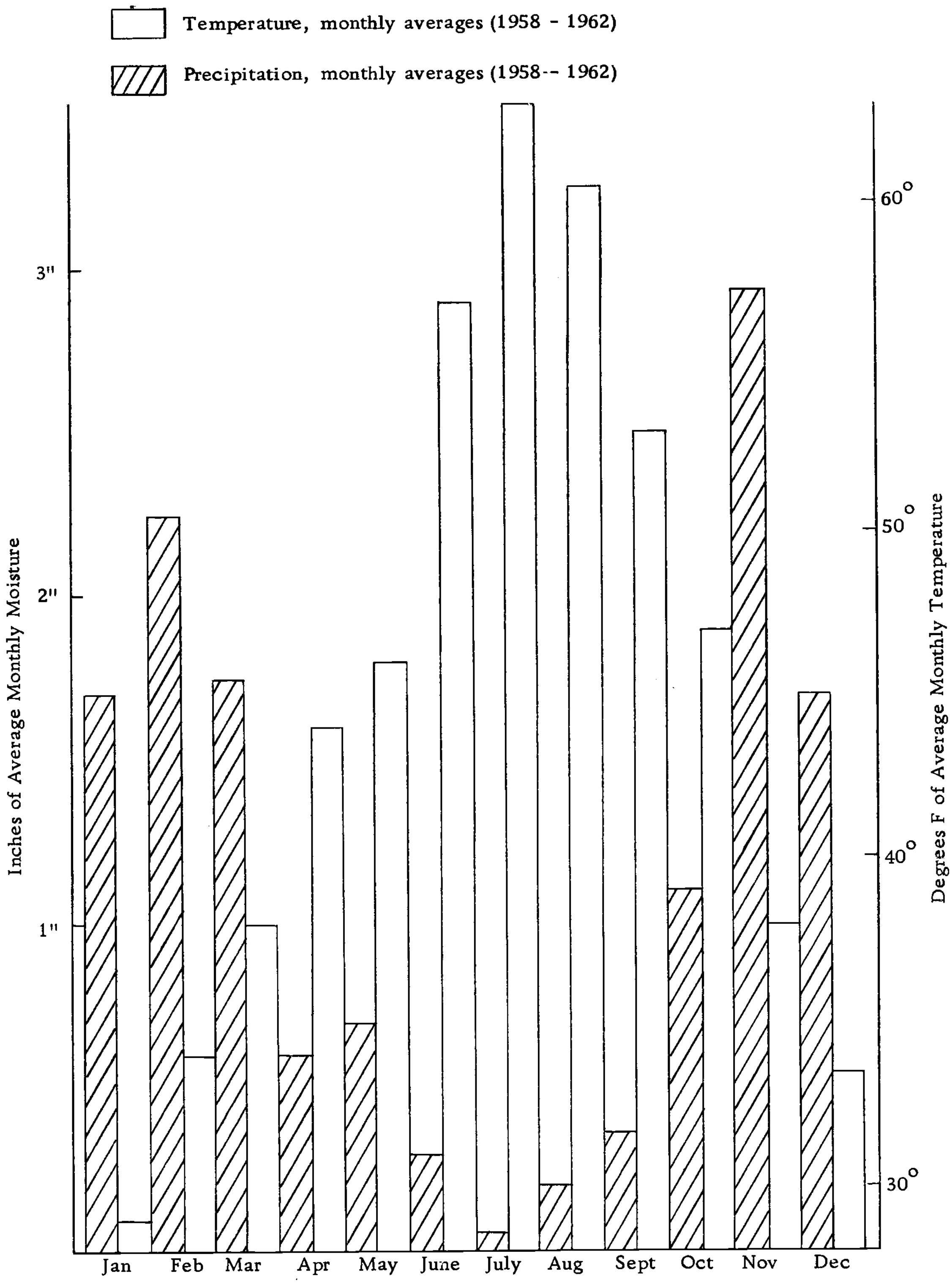


Figure 3. Average monthly temperatures and precipitation data from Sisters, Oregon (1958-1962).

road over which some livestock were driven around 1880 (Brogan, 1964). However, grazing pressures were reduced greatly when the area came under Forest Service control in 1905 (Brogan, 1964). No grazing has been permitted in this forest since 1940. Slight browsing of bitterbrush in the area indicates light use by mule deer.

Cutting in the scenic strip along the highway where the plots are located has been slight and confined to the removal of very old trees. Limited skidding and slash burning scars are evident.

Fire has played an important role in the history of the forest according to Soeriaatmadja (1965). Before 1900 the study area was open, park-like forests resulting from periodic ground fires. These fires were apparently more frequent on the xeric end of the gradient (Sherman, 1966). However, about 1905 the Forest Service commenced a fire control policy which effectively reduced the incidence of fire. Fire scarred stumps indicate that the most recent ground fires occurred on the mesic end of the gradient in 1935 (Sherman, 1966).

Fire has been one of the important factors influencing the distribution of vegetation along the gradient. Because of the frequent fires before 1900, the part of the gradient which Abies grandis would normally dominate is presently dominated by Pinus ponderosa. However, a marked reduction of fire has occurred since 1900, and thus Abies grandis is beginning to invade the area from higher refuges.

Thus the vegetation on the mesic end is undergoing long term succession (Daubenmire, 1968; Sherman, 1969; Dyrness, 1966).

Presently five communities are arranged in "zones" from the mesic to the xeric end of the gradient. These communities are similar to the Abies/Pachistima association (Daubenmire, 1968), Pinus/Ceanothus association (Dyrness, 1966), Pinus/Arctostaphylos-Purshia association (Dyrness, 1966), Pinus/Purshia/Festuca association (Dyrness, 1966), and Juniperus/Festuca association (Driscol, 1964).

The dominant tree species in the Abies grandis/Pachistima myrsinites community is Abies grandis. The characteristic shrub is Pachistima myrsinites, and the characteristic herbaceous species are Chimaphila umbellata var. occidentalis, Chimaphila menziesii, Hieracium albiflorum, Corallorhiza maculata, Linnaea borealis, Asarum caudatum, Osmorhiza obtusa, Rosa gymnocarpa, Anemone piperi, Pterospora andromedea, Pyrola bracteata, and Pyrola chlorantha.

The Pinus ponderosa/Ceanothus velutinus community is dominated by Pinus ponderosa which is seral to climax Abies grandis. The understory vegetation occurs in dense patches of Ceanothus velutinus between which are large openings relatively free of vegetation. Some characteristic herbaceous species are Chimaphila umbellata, Stipa occidentalis, Epilobium angustifolium, and Carex species.

The Pinus ponderosa/Arctostaphylos parryana var. pinetorum-Purshia tridentata community generally occurs on ridges of shallow soils. The dominant tree species is Pinus ponderosa. The shrub element is composed of Purshia tridentata, Arctostaphylos parryana var. pinetorum, Ceanothus velutinus, and Haplopappus bloomeri, while some characteristic herbaceous species are Epilobium angustifolium, Chimaphila umbellata, Viola purpurea, and Apocynum androsaemifolium var. pumilum.

Pinus ponderosa is the dominant tree species in the Pinus/Purshia tridentata/Festuca idahoensis community. The dominant understory shrub is Purshia tridentata, and the dominant herbaceous species is Festuca idahoensis. Other characteristic herbaceous species include Lupinus caudatus, Microsteris gracilis, Viola purpurea, Collinsia parviflora, and Antennaria geyeri.

Finally Juniperus occidentalis and Festuca idahoensis are the two dominant species in the Juniperus occidentalis/Festuca idahoensis community. Other grasses present include Agropyron spicatum, Koeleria cristata, and Poa secunda. In the shrub layer Purshia tridentata is a good indicator species, but Artemisia tridentata and Chrysothamnus viscidiflorus are also present.

METHODS

A vegetational survey was conducted along Highway 20 and 126 from Suttle Lake to beyond Sisters, Oregon, in order to ascertain where understory species were growing in relation to tree cover, and to select some plant species which might indicate microsites of high insolation or deep shade. The survey began on the mesic end of the gradient in the *Abies grandis*/*Pachistima myrsinites* community. Of the species found in this community, nine were selected which were thought to be particularly shade tolerant. Four of these species (*Pyrola chlorantha*, *Pyrola bracteata*, *Pterospora andromedea*, and *Chimaphila menziesii*) occurred only underneath trees. The other five species (*Clintonia uniflora*, *Rosa gymnocarpa*, *Osmorhiza obtusa*, *Symphoricarpos albus*, and *Chimaphila umbellata* var. *occidentalis*) occurred both underneath trees and out in the open. In more xeric communities the nine species occurred only underneath trees.

The second part of this vegetational survey began in the extreme xeric end of the gradient in the *Juniperus occidentalis*/*Festuca idahoensis* community. Of the species found in this community, ten were selected which were thought to be particularly tolerant to high insolation. Eight of these species occurred only in the open (*Gayophytum nuttallii*, *Microsteris gracilis*, *Eriogonum umbellatum*, *Madia minima*, *Cryptantha ambigua*, *Mimulus nanus*, *Leucocrinum* montanum, and Scutellaria nana). The other two species (Eriophyllum lanatum and Bromus tectorum) occurred both in the open and underneath trees. In more mesic communities, the ten species occurred only in the open.

Next, certain criteria were established for selection of stands. On the most mesic end of the gradient a reference stand was desired in the Abies grandis/Pachistima myrsinites community, while on the xeric end of the gradient a reference stand was desired in the Juniperus occidentalis/Festuca idahoensis community in order to sample extreme conditions. Between these two reference points, more stands were desired to study tree layer influence in the remaining communities along the gradient. Stands which showed recent signs of disturbance from grazing, fire, or logging were avoided.

Based on the above criteria, 20 stands were chosen. One stand was located in the Abies grandis/Pachistima myrsinites community; six stands were located in the Pinus ponderosa/Ceanothus velutinus community; five stands were located in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana community; seven stands were located in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis community, and one stand was located in the Juniperus occidentalis/Festuca idahoensis community. The exact location of the stands is shown in Figure 3.

Sampling Procedure

In order to study the influence of overstory species upon understory species, only the extremes in tree influence within each stand were sampled. The part designated as maximum tree influence was deepest shade, deepest litter, and 100% tree cover; while the minimum influence was least shade, least litter depth, and no overhead cover. To arrive at one of the measures of maximum and minimum tree influence, the range of insolation within the stand must be known. Furthermore, the importance of understory species as shown by frequency and density data should only be gathered from a representative sample of the entire stand.

Two 50 x 100 foot plots (macroplots) were so arranged that the most uniform representative vegetation of the stand could be sampled. Twelve 2 x 2 foot square grids (quadrats) were placed at 20 foot intervals along the sides of the macroplot (Figure 4). Each quadrat was composed of four 1 x 1 foot squares (microquadrat). Two macroplots were used to characterize the tree layer for each stand. Ninety-six microquadrats were used to characterize the importance of understory species. Twenty-four quadrats were used to characterize the range of litter depth, type of litter, and range of insolation.

To characterize the vegetation of the stand, phytosociological

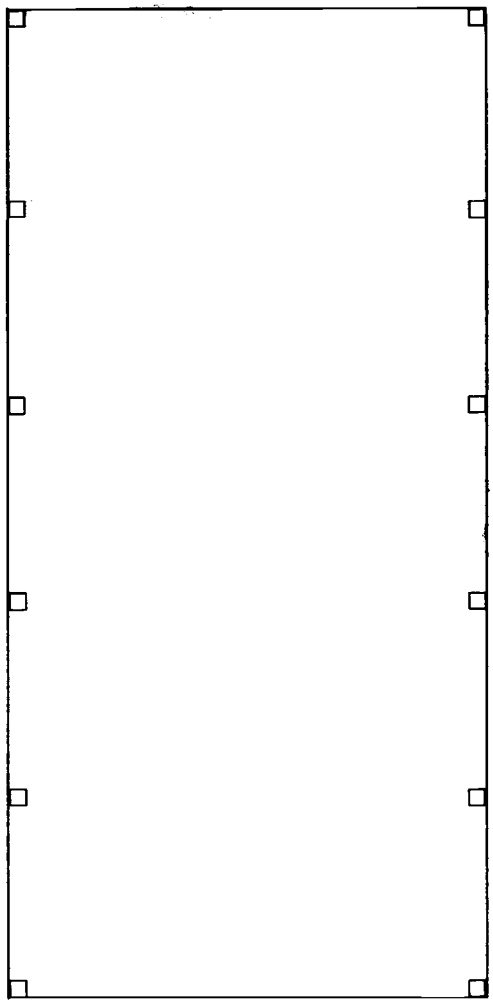


Figure 4. Schematic plan of Macroplot (scale 1" = 20')

data for the trees, shrubs, and herbs were obtained for each study plot. Number and diameter (breast high) data were recorded for the trees on both macroplots of each stand. All trees with a diameter of less than two inches were grouped into one class. Frequency and density data were recorded for the shrubs and herbs for the 96 microquadrats of each stand.

In order to gain some idea of the range of litter within the stand, the depth of litter for each of the 24 quadrats was estimated to the nearest 1/4 inch. If the litter was less than 1/4 inch, then cover estimates were taken using Braun-Blanquet cover classes (Braun-Blanquet, 1932).

A measure of the relative amount of shade each quadrat received was estimated using an insolation grid device described by Wagar (1964). The insolation grid takes into consideration the pattern of tree species, the apparent daily movement of the sun (elevation and azimuth changes), the seasonal changes in declination of the sun, and the increased energy of the sun as it rises in elevation during the day.

An insolation grid was constructed similar to Wagar's grid (Figure 5) which measures the total incoming insolation between the vernal equinox and the autumnal equinox but at a latitude of 44 degrees north. The insolation grid was placed in the center of each of the 24 quadrats and the percentage of direct insolation received was then

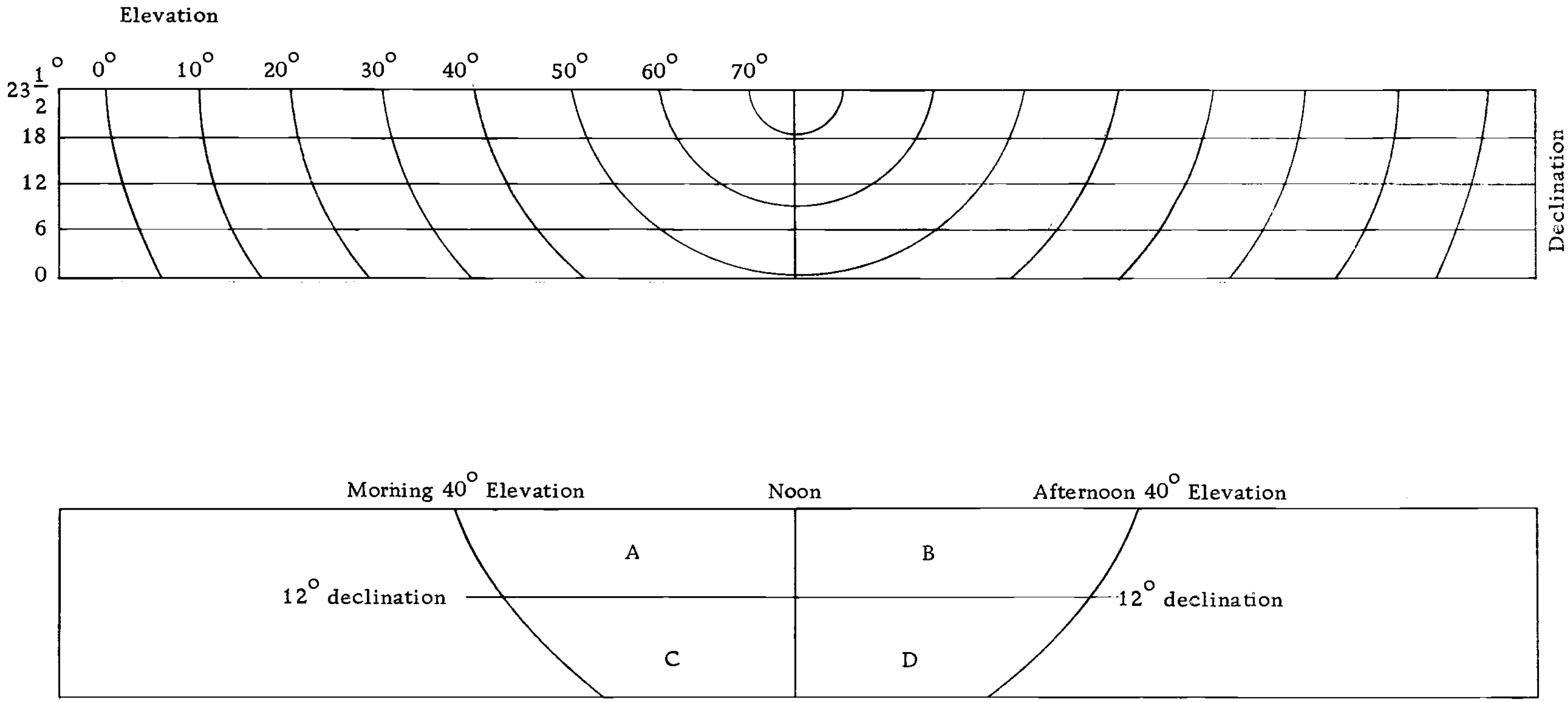


Figure 5. Figure showing division of insolation grid so that daily or seasonal differences in shade could be correlated with presence of species.

estimated. The insolation data ranged from 0 - 100% and was grouped into 20 insolation classes (Table II). Each quadrat was then assigned to one of these insolation classes. Next the range of insolation for the stand was plotted, and the extremes (generally the highest and lowest insolation class) were selected as a measure of maximum and minimum tree effect for each stand. These values are shown in Table I.

Those species which were selected as indicators of deep shade or high insolation by the original reconnaissance were used to help select the points of maximum and minimum tree influence within the stand. The insolation grid was then used to verify that the amount of insolation as shown by Table I for each stand was within acceptable limits. The influence from the shrub on lesser vegetation was reduced to mainly root influence, because area of minimum and maximum tree influence were devoid of mature shrubs other than seedlings. Thirty pairs of 2 x 2 foot quadrats were established in each of the stands. One of the pairs was located under maximum tree influence (minimum amount of insolation per plot and 100% overhead tree cover). The other was placed as close to this as possible but in an area of minimum tree influence (maximum amount of insolation per plot and no overhead tree cover). Criteria for picking the 30 paired sampling points were that insolation had to be greater or less than the limits shown in Table I. If the insolation was less than the amount shown

Table I. Frequency Distribution of Insolation Classes (0-90%) for the 24 Quadrats Sampled Within Each Stand Located Along the Environmental Gradient and Limits Selected to Study Maximum and Minimum Tree Influence.

	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr/ Pymy
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
90	12																			
85	4																			
80																				
75	4																			
70	4	4	8		4															
65	4	8	4	4	4															
60	12	8		4	12															
55		25	4	8	8															
50	8*	20*	8	4	8	4	4				4									
45	8	12	4	20	4	8	12				4									
40	8	4	25*	20*	8	4	20	8	4		4	8	4							
35	4		8	8	25*	33*	20*	8	8	4	8	4	8		4		8			
30	8	4	8	12	4	4	8	33*	8	4	12	8	12	4	8	12	4	8		
25			12	8	8	12	8	20	33*	16	12	12	16	12	16	12	8	4		
20	8	4	8	4	4	20	16	12	16	33*	25*	25*	20*	25	25	25	8	8	8	
15	8	8	8	4	8	12	4	8	12	20	12	8	25	25*	37*	25*	20	20	8	
10							4	8	12	16	8	20	4	16	4	8	8*	16*	25	20
5										4	8	12	4	16	4	4	25	20	16*	20
0																12	16	20	33	60*

Minimum Tree Influence

Maximum Tree Influence

* = median insolation range for 24 quadrats sampled within each stand.

in Table I, the point had to have 100% tree cover. If the insolation was greater than the amount shown in Table I, the point had to have no tree cover. Thus 30 paired points were selected and sampled within each stand.

First the amount of insolation was estimated with the insolation grid, and each quadrat was assigned to one of the insolation classes (Table II). Next the seasonal differences in the distribution of direct insolation above and below the 12 degree declination line were recorded. This was accomplished by recording the seasonal location of unshaded dots on the plastic templates of the insolation grid. In Figure 5, the area above the 12 degree declination line and between the 40 degree declination points were labeled A and B, and the area below the 12 degree declination line and between the 40 degree elevation points were labeled sectors C and D. Differences due to seasonal distribution of direct insolation could be determined by recording the number of unshaded dots in sectors A and B and comparing this total with the total number of unshaded dots recorded in sectors C and D. Finally, the daily differences in the distribution of direct insolation right or left of the noon elevation point were recorded. This was accomplished by recording the daily location of unshaded dots on the plastic template of the insolation grid. In Figure 5, the area between the morning 40 degree and noon elevation point is labeled sectors A and C, and the area between the afternoon 40 degree and noon elevation point is labeled sectors B and D. Differences due to daily distribution of direct insolation could be determined by recording the number of unshaded dots in sectors A and C and comparing this total with the total number of unshaded dots recorded in sectors B and D.

After the amount of insolation and the number of dots per sector were recorded per sample point, the depth of litter if over 1/4 inch, the cover of litter if less than 1/4 inch, and the kind of litter (*Pinus ponderosa*, *Juniperus occidentalis*, *Pseudotsuga menziesii*, *Abies grandis*, *Libocedrus decurrens*, or *Castanopsis chrysophylla*) were recorded for each quadrat.

Next the density and frequency of all the species found on the square foot microquadrat were recorded. A crude estimate of interspecific competition was assessed by placing each square foot microquadrat in one of three categories. These categories included (1) no plants present, (2) one species present, and (3) more than one species present.

Analysis of Data

Stands and species were ordinated using constancy data gathered from the macroplots. Based on this ordination the density and frequency data were recorded for each plot in separate tables (Appendix Tables 1 and 2). These tables were used to group the stands so that the insolation range, litter depth range, frequency, constancy, and density data of the various species of each community could be characterized.

Frequency data gathered from 120 microquadrats under maximum tree influence and 120 microquadrats in the open (30 pairs of quadrats) were analyzed by Cole's index of interspecific association (Cole, 1949). Cole's index was used to determine if a significant correlation existed between maximum or minimum tree influence and the occurrence of the species. The significance level chosen was .5%. Any species occurring in less than three stands was not analyzed. Likewise the different species of the genus Sitanion were not easily identifiable in the field and thus were not analyzed. The same situation applied to the species of Carex and Stipa.

After noting significant correlations between maximum or minimum tree influence and the distribution of a species in the understory, hierarchial classification (Li, 1964) was then used to determine if any of the eight factors measured (plot location, tree cover, amount of insolation, amount of litter, kind of litter, presence or absence of interspecific competition, seasonal difference in shade, and daily difference in shade) showed a significant correlation with the occurrence of the species. One of the disadvantages of the hierarchial classification analysis is that the factors must be arranged from increasing to decreasing relative effect of the factor upon the individual species, whereas in linear regression analysis this is not necessary (Li, 1964). In linear regression analysis the influence of the factors upon the species must be linear, whereas in hierarchial analysis the influence may be linear or curvilinear. In nature, the influence of a factor upon species density is generally accepted as nonlinear (Greig-Smith, 1957). Thus hierarchial classification was chosen as the method of analysis, and the significance level chosen was .5%. Furthermore, since the correct sequence of the eight study factors was not known, an arbitrary arrangement had to be assumed (Table II). If a species was not present within a stand, the stand was not used in the specie's hierarchial analysis.

The 16 categories for evaluating insolation according to seasonal effect are listed in Table II. These 16 categories are based upon the distribution of the unshaded dots above and below the 12 degree declination line (sectors A, B, C, and D of Figure 5). The area above the 12 degree declination line corresponds to dates from the 1st of May to the 1st of August. The area below the 12 degree declination line corresponds to the dates from the 21st of March to the 1st of May and from the 1st of August to the 21st of September. The 16 categories take into consideration the relative number of unshaded dots above the 12 degree declination line and the total number of unshaded dots between the 40 degree elevation points (sectors A, B, C, and D of Figure 5). The classes based on the relative number of dots above the 12 degree declination line are 100% above, greater than 75%, 60%,

Table II. Explanation of Eight Factors Used in the Hierarchial Classification Analysis and Symbols Used in Graphs

Factor	Description of and symbols used in figures
Plot location (A)	20 plots were located along the gradient with plot number 1 beginning on the most xeric end and plot number 20 ending on the most mesic end of gradient.
Cover (B)	100% tree cover (△) No tree cover (□). Species showing random distribution to 100% tree cover and no tree cover (○).
Amount of insoltion (C)	Divided into 20 insolation classes. 0%, 5%, 10%, 15%, 20%, 25%, 30%, 35%, 40%, 45%, 50%, 55%, 60%, 65%, 70%, 75%, 80%, 85%, 90% and 95% .
Amount of Litter (D)	Litter divided at 1/4 inch intervals from 1/4 inch to 4 inches. (1/4", 1/2", 3/4", 1", 1-1/4", 1-1/2", 1-3/4", 2", 2-1/4", 2-1/2", 2-3/4", 3", 3-1/4" and 3-1/2". Less than 1/4" designated amount of litter by cover - = no litter x = sparsely or very sparsely covered 1 = more than sparsely covered but less than 5% 2 = at least 5% of area covered by litter 3 = 25% - 50% of area covered by litter 4 = 50% - 75% of area covered by litter 5 = more than 75% of area covered by litter
Type of litter (E)	Juniperus occidentallis, Pinus ponderosa, Libocedrus decurrens, Abies grandis, Pseudotsuga menziesii and Castanopsis chrysophylla.
Competition (F)	Presence = more than one species found in the square foot plot (P = 2 or more ♁) Absence = no species found or only one species found in square foot plot. (N = 1, 0 = none ⫰)
Seasonal Insolation (G)	(see below)

Seasonal Insolation (G)	Sectors insolation found in	Amount of insolation in sections ABC&D	Rel. % of insol. above 12 degree declination	Designation
	A &/or B / 0	44-31%	100%	A2
		30-16%	100%	A3
		15-1 %	100%	A4
	A &/or B / C &/or D	62-46%	75%	B175
			60%	B160
		45-31%	75%	B275
			50%	B250
			less than 50%	B2<50

Table II (continued).

Factor	Description of and symbols used in figures			
(continued) Seasonal insolation (G)	Sectors insolation found in	Amount of insolation in sectors ABC&D	Rel. % of insol. above 12 degree declination	Designation
	A &/or B / C &/or D	30-16%	75%	B375
			50%	B350
			less than 50%	B3<50
		15-2%	75%	B475
			50%	B450
			less than 50%	B4<50
	0 / C &/or D	18-1%	0%	D4
	0 / 0	0%	0%	none

Factor	Sectors insolation found in	Amount of insolation in sectors ABC&D	Designation
Daily insolation differences (H)	A &/or C/0 (morning)	31-16%	M
		15-1%	Mt
	A &/or C/B &/or D (noon)	62-46%	N1
		45-20%	N2
		19-1%	Nt
	0/B &/or D (afternoon)	31-16%	A
		15-1%	At
	0/0	0%	none

50%, less than 50%, 0% above but some unshaded dots below, and no unshaded dots above or below the 12 degree declination line. The total number of unshaded dots (amount of direct insolation) ranged from 0 to 62 between the 40 degree elevation points. This range was then divided into four classes.

The eight categories for evaluating insolation according to daily effect are listed in Table II. These eight categories are based on the distribution of the unshaded dots right and left of the noon elevation point and between the 40 degree elevation points (sectors A, B, C, and D of Figure 5). The area to the left of the noon elevation point corresponds to morning insolation, and the area to the right of the noon elevation point corresponds to afternoon insolation. The eight categories take into consideration the area of the insolation grid where the unshaded dots were located and the total number of unshaded dots found between the 40 degree elevation points (sectors A, B, C, and D of Figure 5). The classes based on the location of dots are (1) all of the unshaded dots found only in the morning (sectors A and/or C); (2) unshaded dots found in the morning and afternoon (sectors A and/or C, and B and/or D); (3) unshaded dots found only in afternoon (sectors B and/or D); (4) no unshaded dots found in any sectors. The total number of unshaded dots (amount of direct insolation) ranged from 0 to 62 between the 40 degree elevation points. This range was then divided into three classes (Table II).

Finally, the area of highest density for the species within the gradient was determined according only to those factors found significant by the hierarchial classification analysis. The square foot micro-quadrats were sorted into groups where a single group was composed of similar levels for each significant factor. Next, the confidence interval was determined for the density of the species for the entire gradient (Li, 1964). The groups were then analyzed to find the level of maximum density of the species. After determining the area of maximum species density within the gradient, these densities were plotted on tables with two or more axes depending upon how many factors showed a significant correlation with species density distribution.

RESULTS

The ordination of the stands is shown by the constancy and frequency distribution (Appendix 1) and density distribution (Appendix 2) of trees, shrubs, and herbs. Using these data the gradient was divided into five communities: Juniperus occidentalis/Festuca idahoensis; Pinus ponderosa/Purshia tridentata/Festuca idahoensis; Pinus ponderosa/Arctostaphylos parryana var. pinetorum-Purshia tridentata; Pinus ponderosa/Ceanothus velutinus; and Abies grandis/ Pachistima myrsinites. These communities are closely similar to associations described by Daubenmire (1968), Dyrness (1966), and Driscol (1964). Appendix 1 and 2 are composed of 15 species' groups based upon the distribution of the species in relation to the five communities. Species of these groups may be found within one community or in more than one community (two, three, four, or five communities). The species of any group suggest similar environmental tolerances. Species of groups 1 and 2 generally tend to show a wide tolerance range, whereas a narrow tolerance range is indicated by the species of groups 5, 9, 12, 14, and 15.

Changes in Tree Species Composition

The density in size class distribution of tree species' composition for the five communities located along the gradient are shown in

Table III. Average Number of Tree Species by Size Class (diameter breast high) per 10,000 Square Feet for Each of the Five Communities.

Communities and Species		Size Class (DBH in inches)									
		0-2	2-4	4-6	6-8	8-12	12-18	18-24	24-30	30-36	36-48
Juniperus/Festuca											
Pinus ponderosa	c	6.00		1.00	2.00						
Juniperus occidentalis	C	11.00	11.00	15.00	6.00	2.00	2.00				
Pinus/Purshia/Festuca											
Pinus ponderosa	C	20.57	.14	1.28	.42	2.00	2.71	4.28	3.00	.28	.14
Juniperus occidentalis	s	1.28	.71	.42	.57	.14	.14				
Pinus/Arctostaphylos-Purshia											
Abies grandis	c		.20			.20	.20				
Pseudotsuga menziesii	c		.20								
Pinus ponderosa	C	258.40	.60	.80	1.20	1.60	2.60	3.80	3.60	2.20	.80
Juniperus occidentalis	s	.20									
Pinus/Ceanothus											
Abies grandis	C	2.83	.16	.33	1.00	1.33	.83	.16	.16		
Libocedrus decurrens	c	4.33	.16								
Pseudotsuga menziesii	c	1.50	.33	1.00	1.00	1.00	.33		..16		
Pinus ponderosa	S	230.33		.33	.16	1.00	2.66	2.83	3.66	2.83	.83
Abies/Pachistima											
Pinus monticola	s	1.00									
Abies grandis	C	72.00	2.00	27.00	5.00	3.00	1.00				
Pseudotsuga menziesii	c	1.00		1.00		2.00	5.00	6.00	4.00		2.00
Pinus ponderosa	s										1.00

C = major climax c = minor climax
S = major seral s = minor seral

Table III. From this data the tree species for each community were designated to one of four successional categories: major climax (C), minor climax (c), major seral (S) and minor seral (s). Generally the tree species were found in more than two communities. However, in more xeric communities the tree species was normally climax, but in more mesic communities the species was normally seral. For example, Pinus ponderosa was a minor climax tree species in the Juniperus/Festuca community, a major climax species in the Pinus/ Purshia/Festuca and Pinus/Arctostaphylos-Purshia communities, a major seral species in the Pinus/ Ceanothus community, and a minor seral species in the Abies/Pachistima community.

Patterns of Insolation and Litter Along the Gradient

Frequency distribution of insolation classes (0 - 95%) for the 24 quadrats sampled within each stand located along the environmental gradient is illustrated in Table I. Table I is composed of an insolation axis that ranges from 0 - 90% and a stand axis in which stands are arranged in sequence of increased moisture. The highest insolation classes generally occurred on the xeric end and the lowest insolation classes usually occurred on the mesic end of the gradient. The widest insolation range generally occurred on the xeric end, while the narrowest insolation range usually occurred on the mesic end of the gradient.

Frequency distribution of litter classes (bare ground to 4" in depth) for the 24 quadrats sampled within each stand is illustrated in Table IV. Generally, the amount of litter increased gradually as plot location became more mesic. The widest litter range generally occurred on the xeric end, while the narrowest litter range usually occurred on the mesic end of the gradient.

Insolation and litter class medians and range limits for the five communities are illustrated in Figure 6. These median values were determined by combining all of the insolation and litter class data from all of the plots belonging to a community as designated by the original ordination (Appendix 1 and 2). Likewise the range limits were determined for each community from insolation and litter class extremes. The figure shows the relationships between the communities for insolation and litter class medians and range limits. Although range extremes decrease markedly in more mesic communities, the median values for all of the communities except the *Juniperus/Festuca* community are grouped near the mesic end of the gradient. Median values for the *Juniperus/Festuca* community are found near the xeric end of the gradient.

Description of the Area Sampled for Minimum Tree Influence

Characterization of the eight factors sampled (plot location, tree cover, amount of insolation, amount of litter, type of litter,

Table IV. Frequency Distribution of Litter Classes (bare ground to 4 inches in depth) for the 24 Quadrates Sampled within Each Stand Located Along the Environmental Gradient.

		Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr/ Pymy
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0"	-	.41																			
0"	x	.29	.16	.08	.20	.12															
0"	1		.08																		
0"	2	.08	.08			.08															
0"	3		.20	.04	.08	.04	.08	.04				.08									
0"	4		.16		.08	.04	.04	.12		.04	.16	.08									
0"	5			.16	.25	.33		.20		.29	.33	.16	.16	.33	.04		.16	.08	.04		
1/4"	5		.08				.08	.04	.12	.12	.20		.33	.29		.20		.16			
1/2"	5	.08	.04	.16	.12	.12	.37	.04	.33	.16	.25	.16	.16	.08	.08	.04	.04		.25	.12	.08
3/4"	5						.04		.04												.04
1"	5	.08	.08	.33	.12	.25	.20	.12	.50	.12		.20	.33	.12	.58	.16	.25	.16	.37	.54	.33
1-1/2"	5			.04			.04	.20		.04		.08			.20	.12	.08		.12		.04
1-3/4"	5																				
2"	5	.04	.08	.16	.12		.08	.20		.20	.04	.20		.12	.04	.25	.45	.45	.16	.25	.16
2-1/4"	5																				
2-1/2"	5															.08		.04			.04
2-3/4"	5																				
3"	5															.08		.04			.04
3-1/2"	5																				.04
4"	5																				.16

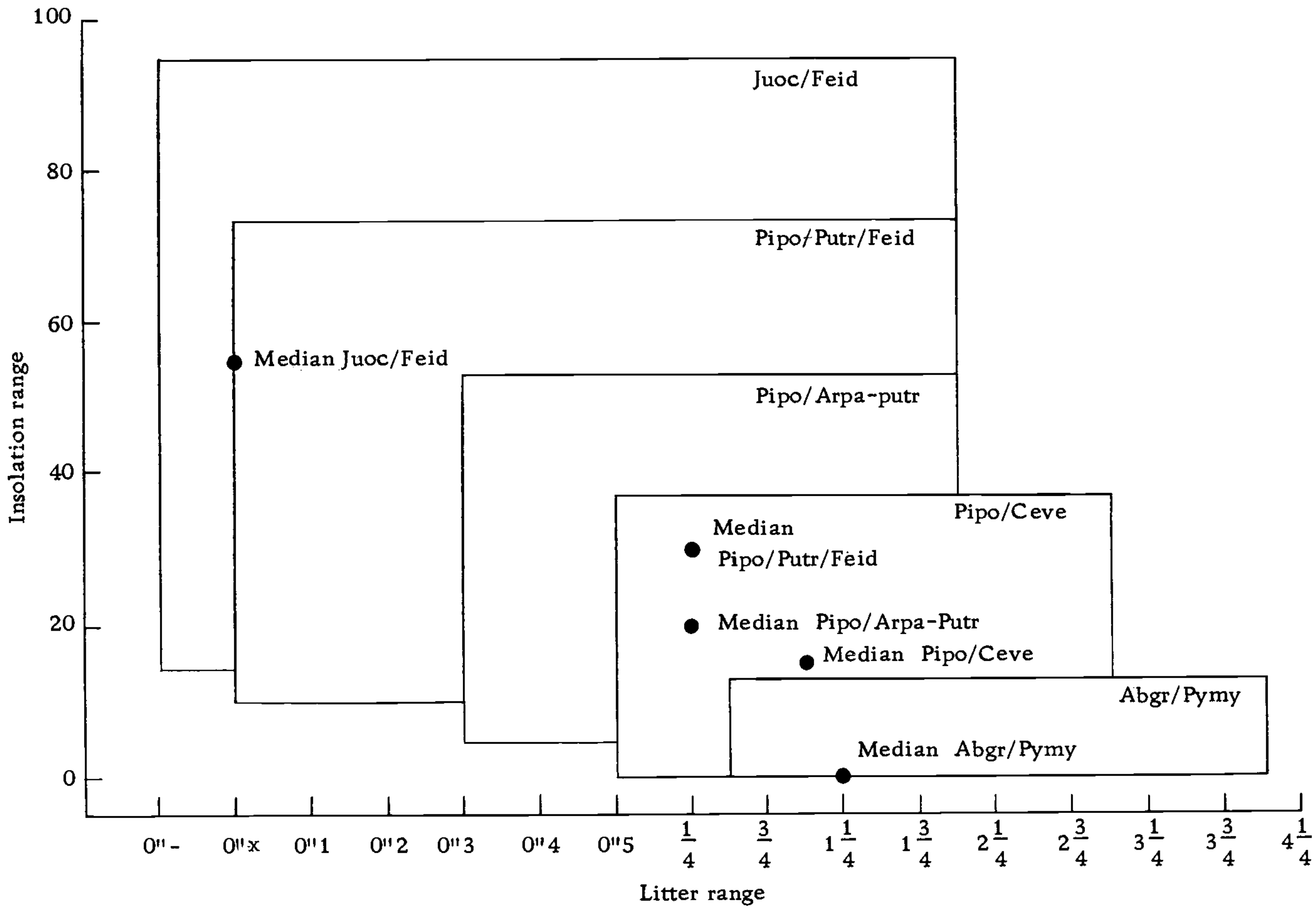


Figure 6. Insolation, litter medians, and range limits for the five plant communities occurring along the environmental gradient.

species' competition, seasonal insolation differences, and daily insolation differences) for minimum tree influence is illustrated in Appendix 3. Area sampled for minimum tree influence had no overhead tree cover and high insolation values. On the right side of Appendix 3, the table is divided into 20 columns that correspond to the geographic position of the 20 plots (Factor A). These plots are arranged with the most xeric plot on the left and the most mesic plot on the right. The seven columns on the left side of the table correspond to the other factors measured. These seven columns are arranged in the same order as used in the hierarchial factor analysis. Each of these seven columns is subdivided into classes. The classes for each factor are described in Table II. These classes are arranged hierarchially starting with tree cover on the left side of the table. On the right side of the table, frequency distribution of the microquadrats within the plots is tabulated. For example, the first entry at the top of the table indicates 6% of the microquadrats of plot #1 occurred in the open, received 95 - 99% direct insolation, had no litter (0"-), had species' competition present (P), had most of the insolation coming from the 1st of May to the 1st of August (B160), and had most of the insolation during the noon period (N1) of the day.

Under minimum tree influence (open) the amount of insolation ranged from 10 to 95%. In general, as was the case of the entire plot, the amount of direct insolation decreased as the amount of litter increased. Insolation usually was greater in xeric plots and decreased as plot location became more mesic. Litter usually was sparse on xeric plots and increased as plot location became more mesic. The range in the amount of litter was narrowest at insolation or plot location extremes; and in the central part of the gradient where insolation was moderate, the litter range was quite wide.

The type of litter found along the gradient is related to the dominance of the species, plot location, and amount of insolation. Litter from Pseudotsuga menziesii and Abies grandis occurred normally on the mesic end of the gradient where insolation was low. Litter from Juniperus occidentalis occurred on the xeric end of the gradient where the amount of insolation was moderate to high. Pinus ponderosa occurred generally throughout the gradient where insolation was of moderate intensity.

Species' "competition" shows no correlation with the amount of insolation. Thus most of the microquadrats throughout the gradient have an equal probability of having more than one species (P), only one species (N), or no species (O) present.

Seasonal insolation affect was determined by the distribution of the unshaded dots above and below the 12 degree declination line and between the 40 degree elevation points (sector A, B, C, and D of Figure 5). As the total amount of insolation increased, a reduction was also generally seen for the amount of insolation within the 40 degree elevation points. Likewise, as the amount of insolation (factor C) decreased, the relative amount of insolation above the 12 degree declination line (factor G) also decreased, except when all of the insolation was above the 12 degree declination line (seasonal category A). In seasonal category A, the total amount of insolation was generally less than 15%.

Daily insolation affect was determined by the distribution of the unshaded dots right and left of the noon elevation point and between the 40 degree elevation points (sectors A, B, C, and D of Figure 5). The area left of the noon aximuth corresponds to morning insolation, and the area right of the noon azimuth corresponds to afternoon insolation. Generally, as the total amount of insolation decreased within the 40 degree elevation points, a reduction was also seen for the amount of insolation. Usually morning (M) and afternoon (A) insolation occurred in low insolation classes, while noon insolation (N) occurred in low to high insolation classes.

Description of Sample Area for Maximum Tree Influence

Characterization of the eight factors sampled (plot location, tree cover, amount of insolation, amount of litter, type of litter, species' competition, seasonal insolation differences, and daily insolation differences) for maximum tree influence is illustrated in Appendix 3[1/]. Area sampled for maximum tree influence had 100%

[1/] See page 34 for explanation of Appendix 3.

overhead tree cover and very low insolation values. The eight factors were subdivided into classes which are described in Table II. Under maximum tree influence, insolation ranged from a minimum of 0% to a maximum of 19%. Normally, the frequency of lower insolation classes was highest on the mesic end, while the frequency of higher insolation classes was highest on the xeric end of the gradient.

The amount of litter ranged from 75% cover (0"-5) to a maximum depth of 3" (3"-5). Deepest litter was generally found on the mesic end of the gradient and decreased as plot location became more xeric. Litter from Pseudotsuga menziesii and Abies grandis occurred mostly on the mesic end of the gradient, while litter from Juniperus occidentalis occurred mainly on the xeric end of the gradient. Litter from Pinus ponderosa occurred generally throughout the central portion of the gradient.

In general, sampling points had approximately the same probability of having all three conditions of species' "competition:" two or more species present (P), only one species present (N), and no species present (O) in the quadrat.

Seasonal insolation distribution generally showed more variation underneath maximum tree influence than in the open. All four classes of seasonal insolation were sampled in most insolation classes: (1) where insolation was both above and below the 12 degree declination line (B4), (2) where insolation was found only above the

12 degree declination line (A4), (3) where insolation was found only below the 12 degree declination line (D), and (4) where no insolation was found above or below the 12 degree declination line (none or full shade). Conditions A4 and full shade usually increased in frequency underneath the tree in lower insolation classes or deeper litter. Condition full shade similarly had a high frequency under Abies grandis.

Generally, daily differences in direct insolation also showed more variation underneath the tree than out in the open. All four classes of daily insolation were sampled in all insolation classes: morning (Mt), noon (Nt), afternoon (At), and no insolation within the 40 degree elevation points (full shade). No apparent differences in daily insolation were found which could be correlated with the amount of insolation, amount of litter, and type of litter.

Cole's Index Analysis

The correlation of maximum and minimum tree influence with frequency of understory species within plots as determined by Cole's index is shown in Figure 7. Figure 7 is composed of 63 individual graphs that represent 63 out of the 104 species found along the gradient (Appendix 1 or 2). Each individual graph is composed of two axes: the vertical axis; composed of Cole's index values that range from +75 to a -100; and the horizontal axis, composed of the stands arranged in sequence from the xeric to mesic end of the gradient.

Maximum tree influence is shown by a triangle, and minimum tree influence is shown by a square in each individual graph. The vertical position of these two symbols (square and triangle) determines if a positive or negative correlation existed between the kind of tree influence and the distribution of the species within a stand. Very seldom was the positive value significant, and thus the vertical position of the square or triangle was plotted at the random point (0). If both the positive and negative values were not significant, a circle was plotted at the random point (0). A positive association value is one where the species occurred more often than would be expected on an equal probability basis. A negative association value is one where the species occurred less frequently than would be expected on an equal probability basis. Random distribution values are those where the species occur as often as would be predicted on an equal probability basis. A positive correlation strongly suggests that the area is compatible with the requirements of the species. However, a negative correlation strongly suggests that the area is not compatible with the requirements of the species. Since life forms may be related in some degree to the ecology of the species, the 63 species of Figure 7 were subdivided into seven groups based on the life forms: Phanerophyte, Chamaephyte, Geophyte, Proto-hemicryptophyte, Partial and

Rosette-Hemicryptophyte, Grasslike Hemicryptophyte and Thereophyte (Appendix 5). For example, Chrysothamnus viscidiflorous shows a non-significant positive association value to tree cover (Plot 1) and the open (Plot 6), a random association value to both the open and tree cover (Plots 3 and 5), and a significant negative association value to the open (Plot 1) and tree cover (Plot 6).

Of the 63 species analyzed, only Collinsia parviflora and Lathyrus lanszwertii ssp. aridus showed an inconsistent distributional pattern in relation to tree influence. The other 61 species fit into one of three patterns: (1) the area most compatible with the requirements of the species occurred only underneath the trees regardless where the species occurred along the gradient; (2) the area most compatible with the requirements of the species occurred only out in the open regardless where the species occurred along the gradients, and (3) the area most compatible with the requirements of the species occurred only underneath the trees on xeric stands, underneath the trees and out in the open on more mesic stands, and only out in the open on the most mesic stands.

A total of ten species fit pattern one. Two species, Chimaphila menziesii and Pterospora andromedea may be used to illustrate this pattern. All of the plants of these two species were found underneath trees, and none were found out in the open. All of the life forms in the table have some representative species in pattern one except the Phanerophyte and Therophyte groups.

Eighteen species fit pattern two. Leucrocrinum montanum and Gayophytum nuttallii illustrate this pattern. These plants occurred only in the open rather than underneath the trees. The Geophyte, Proto-Hemicryptophyte, Partial or Rosette Hemicryptophyte, and Therophyte life form groups had representative species in pattern two.

Purshia tridentata, Lomatium simplex, and Achillea millefolium are three of the 35 species which may be used to illustrate pattern three. These plants occurred mainly under the trees in the xeric end of the gradient. As plot location became more mesic, these plants occurred less frequently underneath the trees and more frequently out in the open. All the life forms have representative species in pattern three.

The point along the gradient where the species were distributed at random to areas of maximum and minimum tree influence may suggest an optimum point along the gradient where the effect from tree layer influence is minimum. This point may also provide a basis of comparison for the environmental tolerances of the species. In patterns one and two, this position along the gradient where the species were distributed at random in relation to tree influence did not occur. However, if the gradient was extended to include more mesic and xeric stands, then possibly this equal frequency distribution pattern could occur. Therefore, it is possible that all three patterns are actually parts of pattern three.

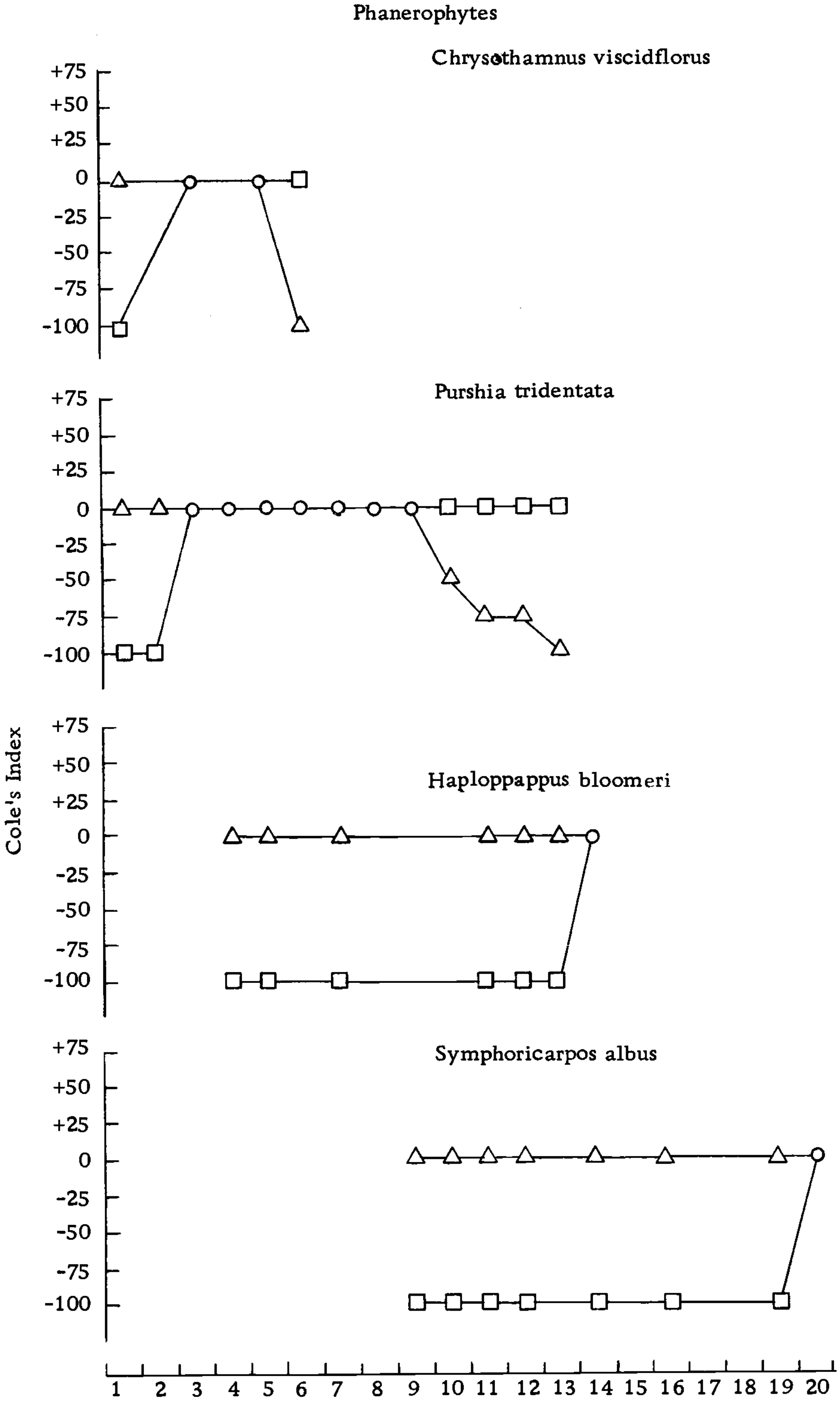
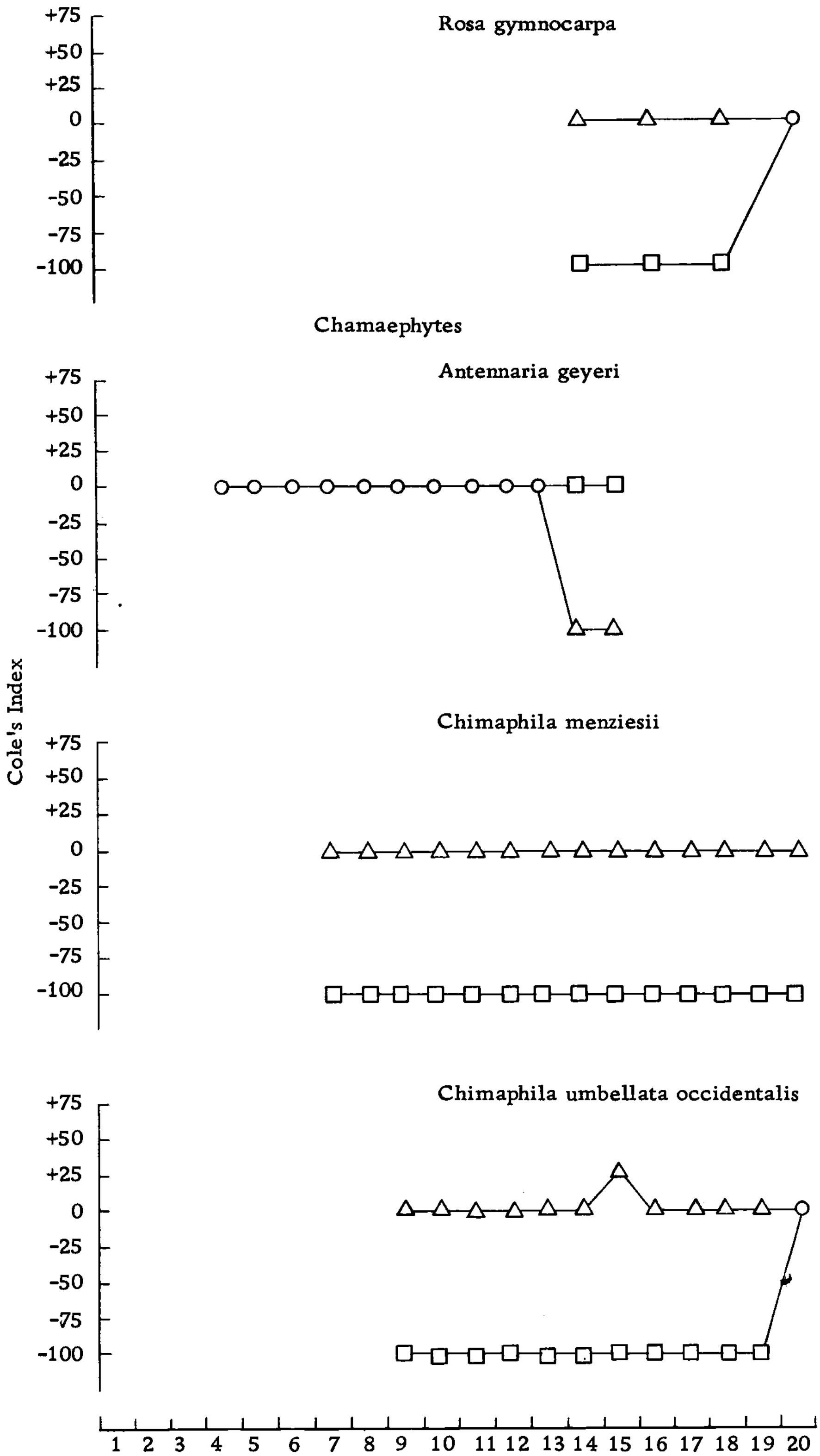


Figure 7. The effect of maximum and minimum tree influence upon understory species distribution as determined by Cole's index (significance level = .5%)



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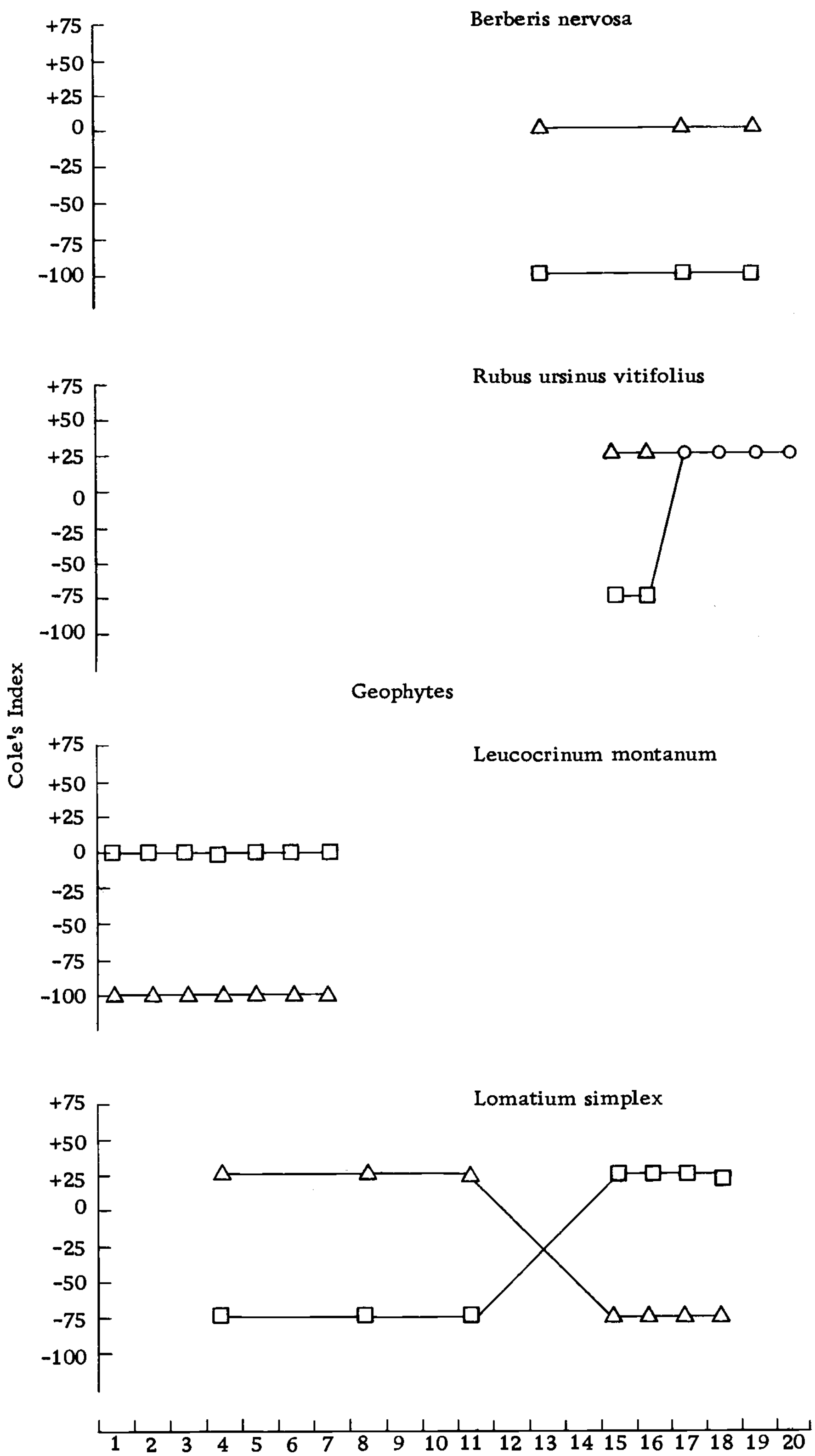

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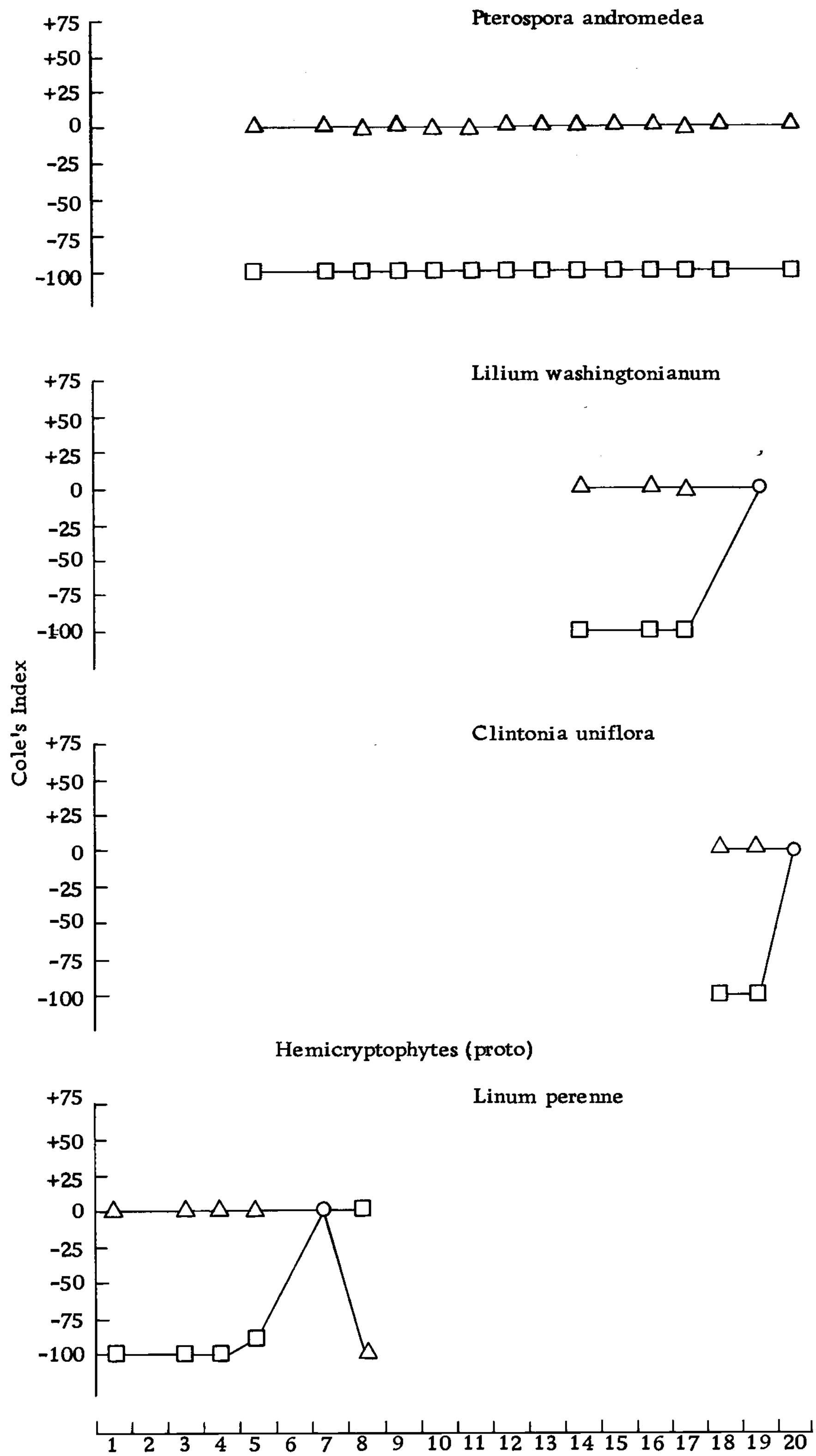

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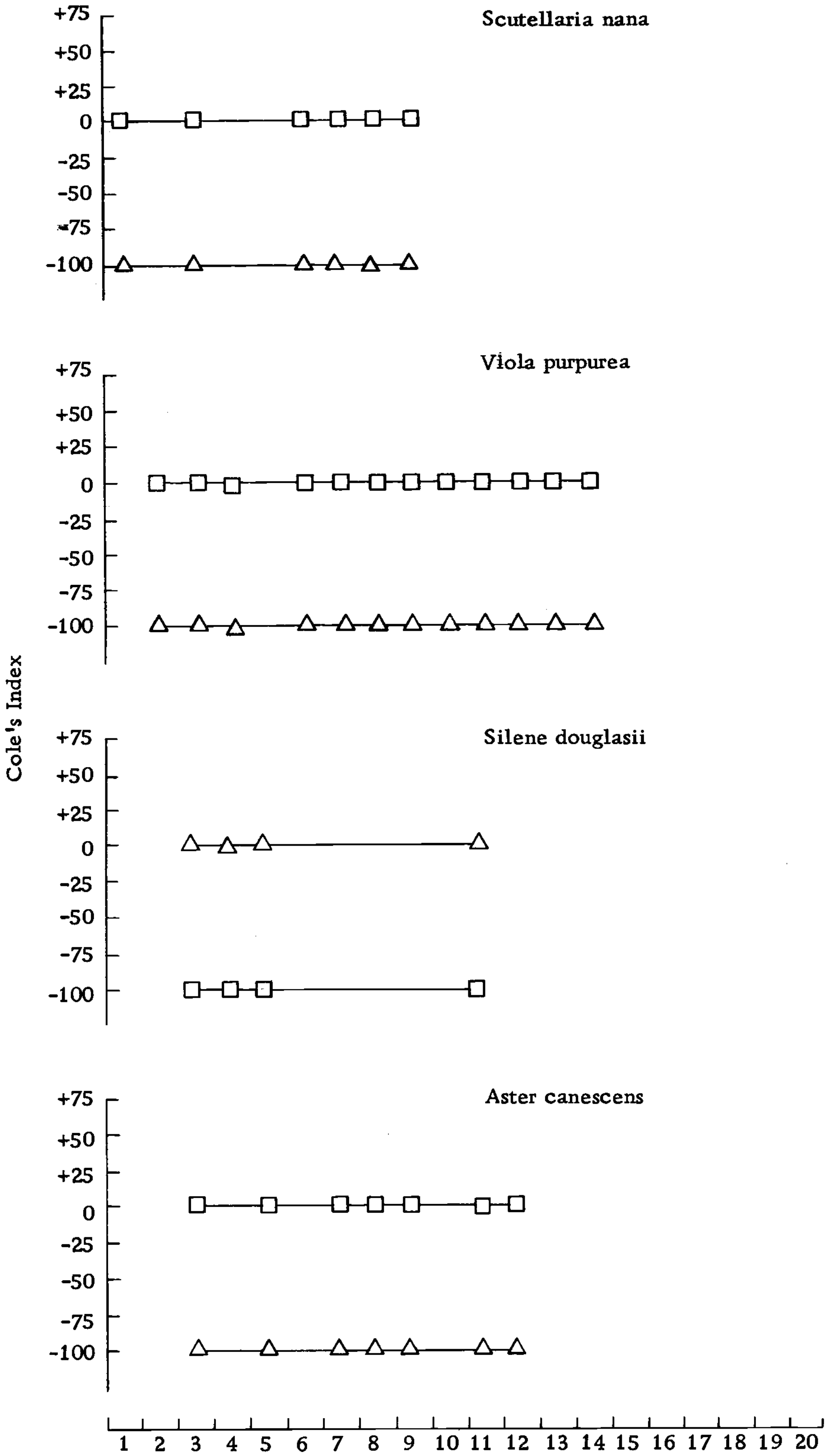

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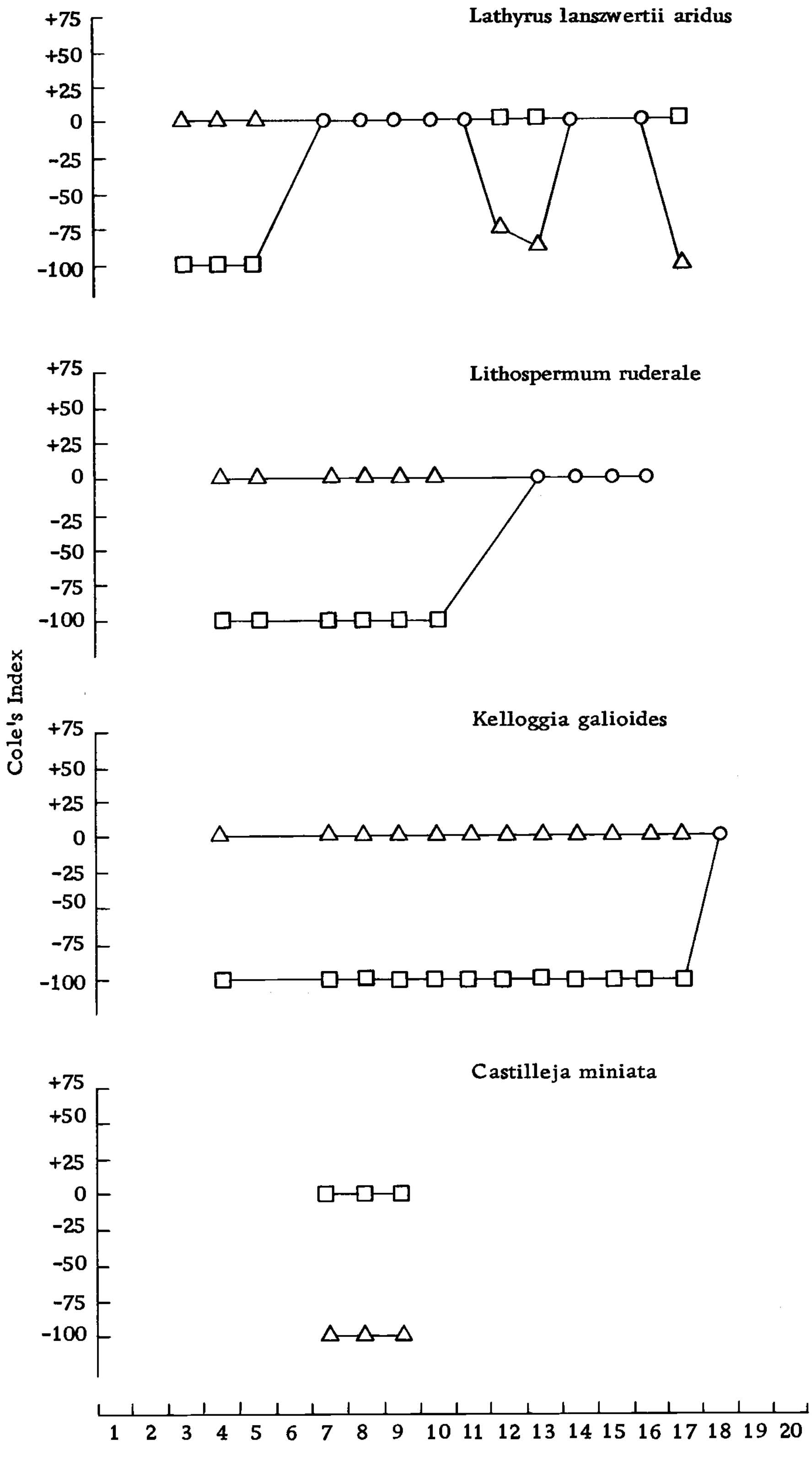

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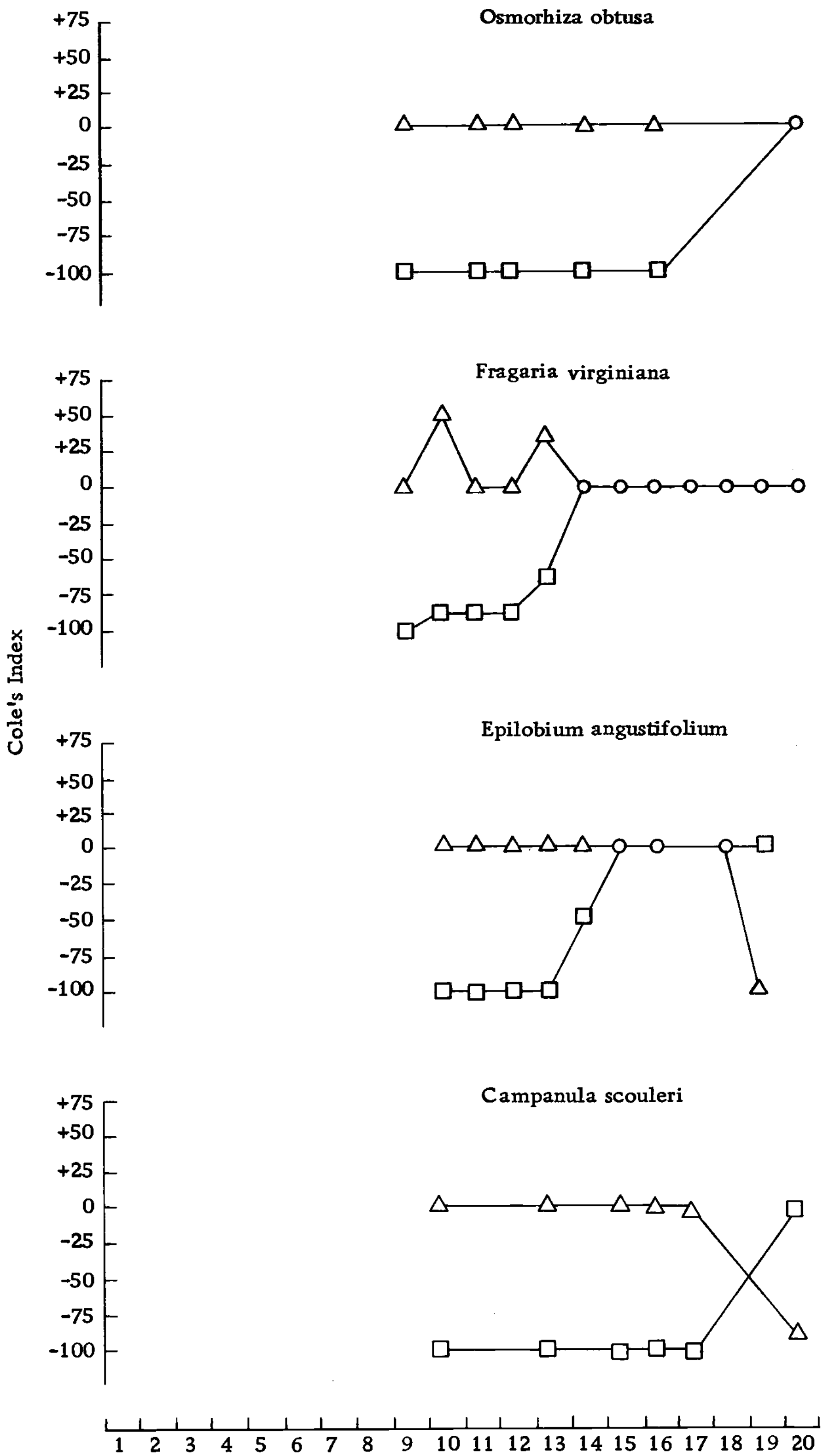

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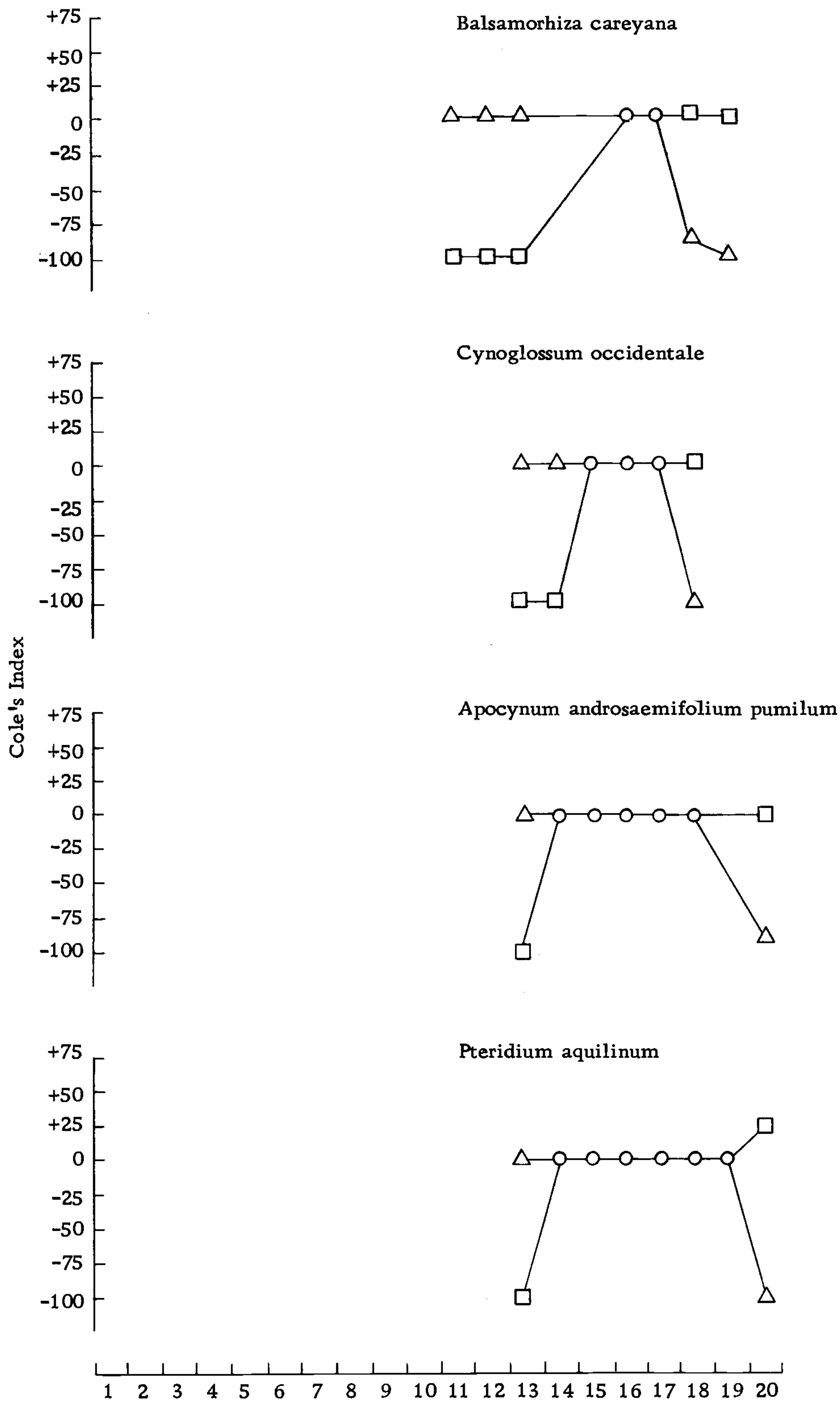

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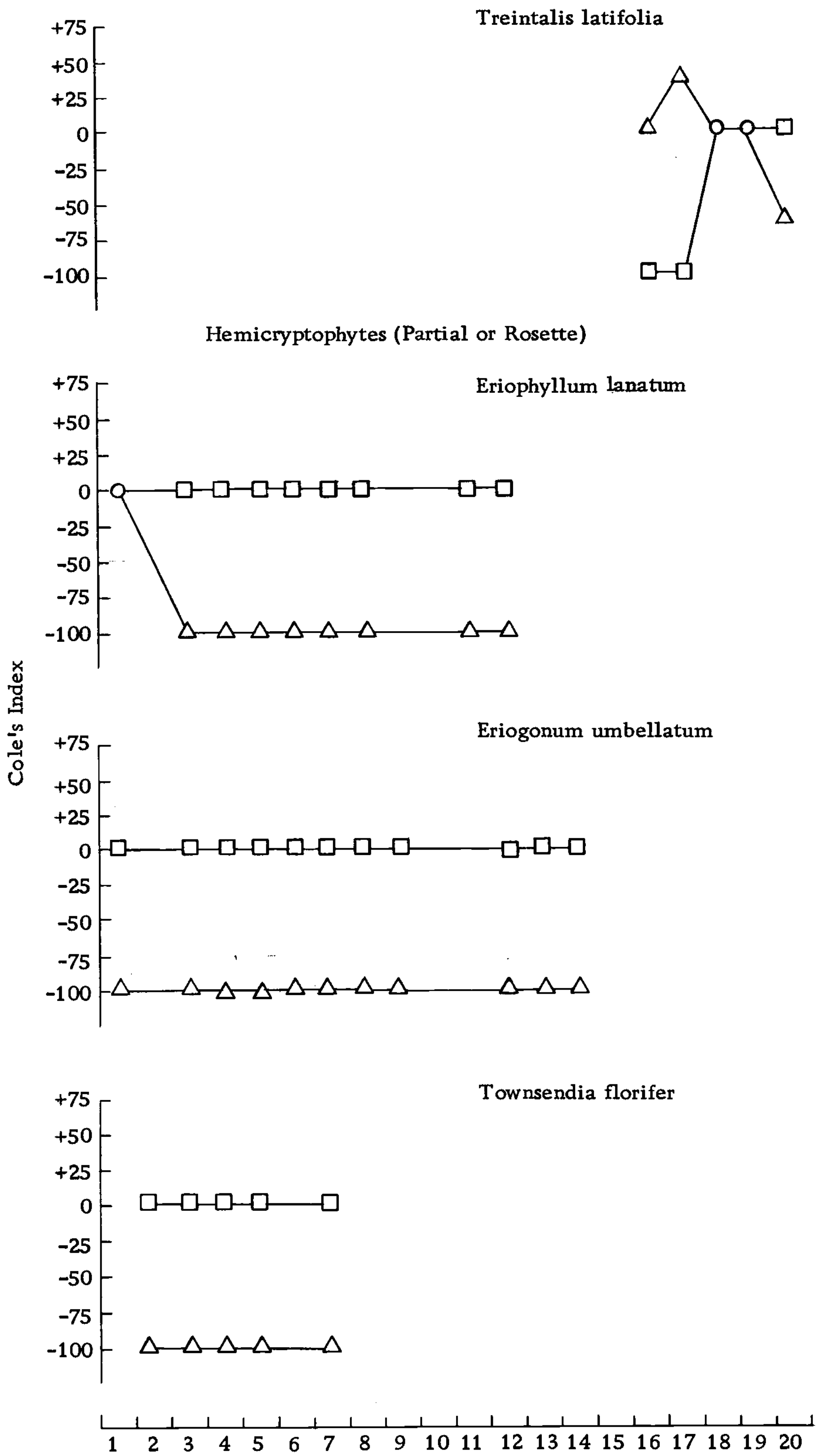

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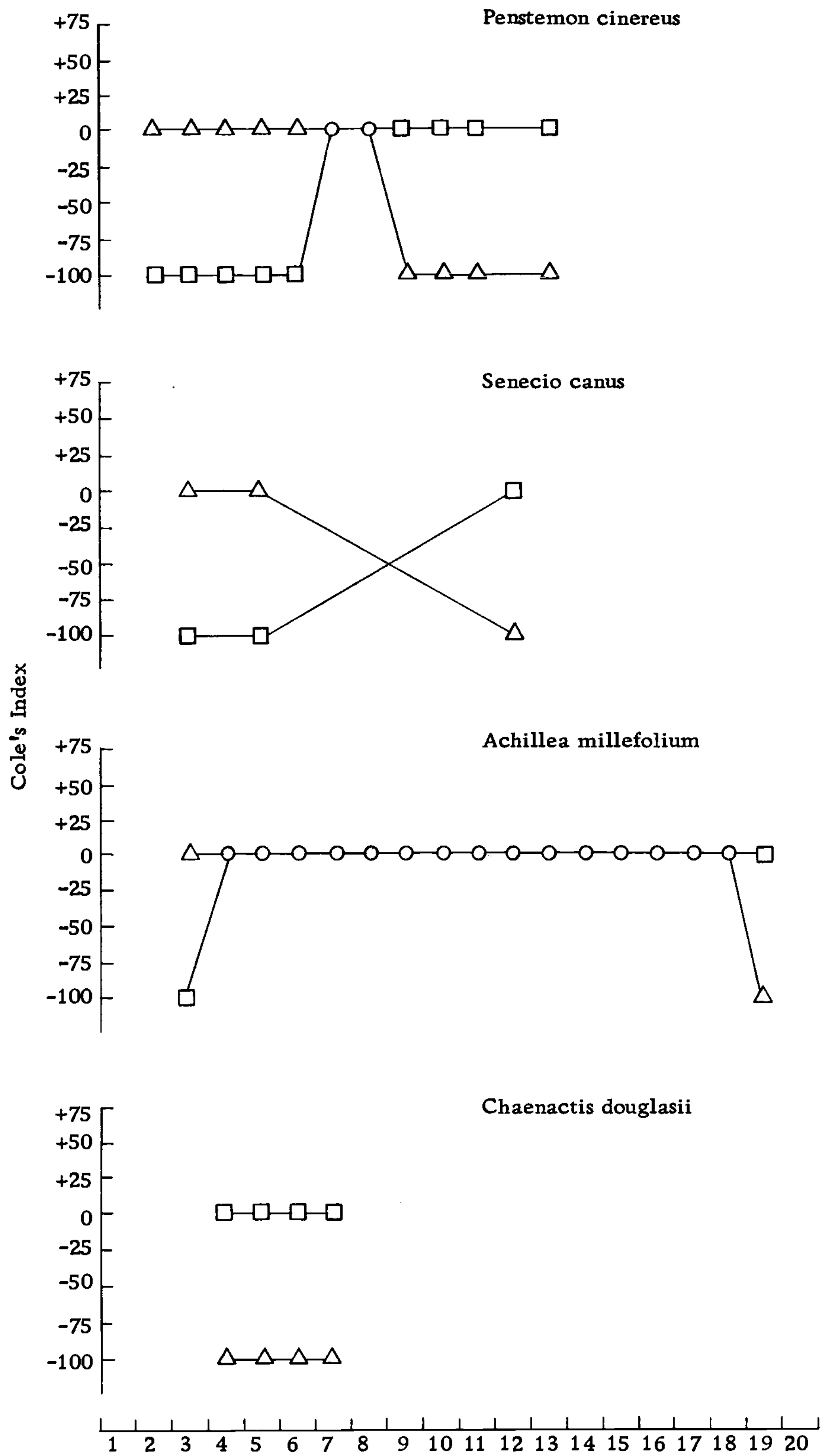

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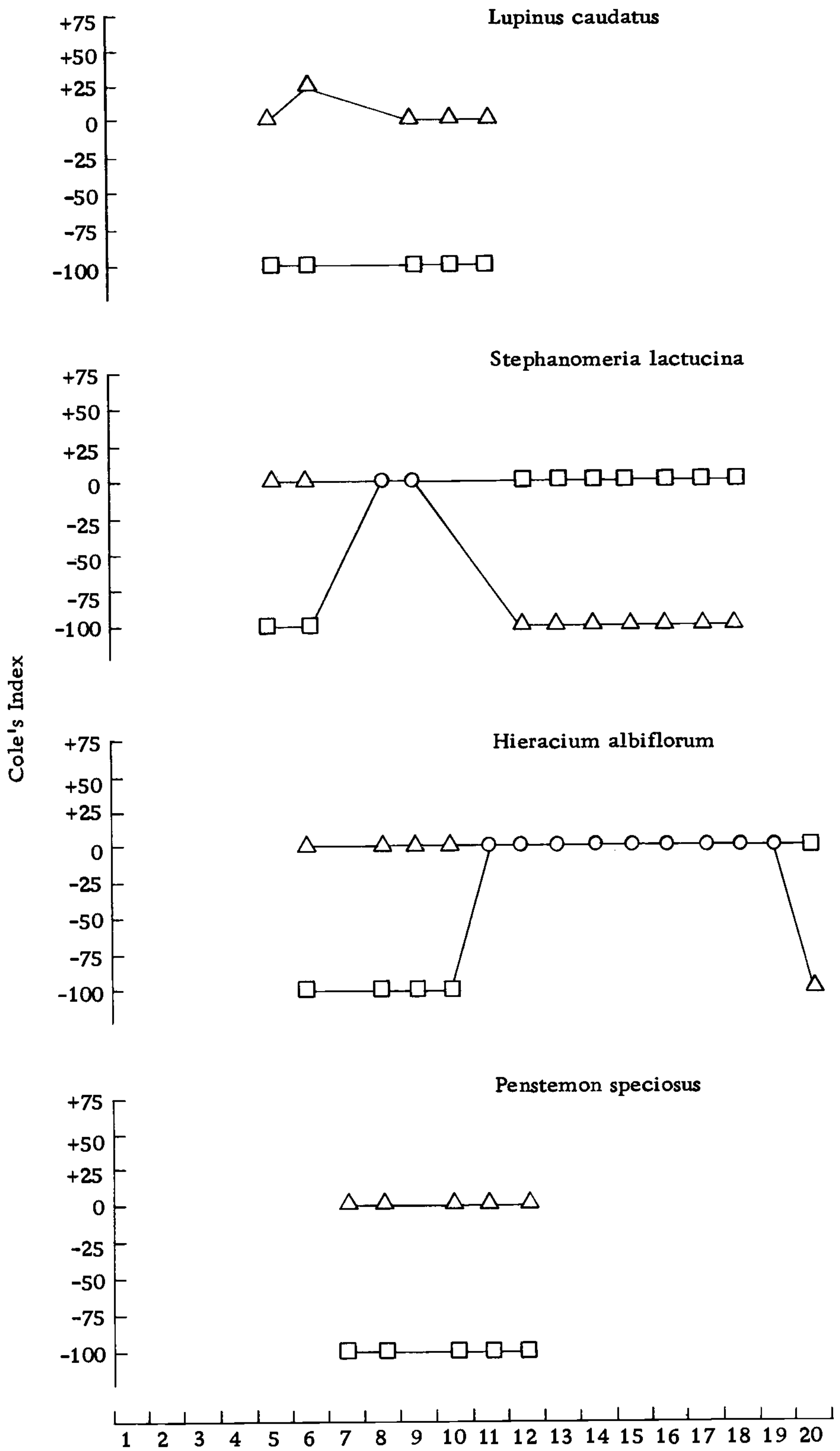

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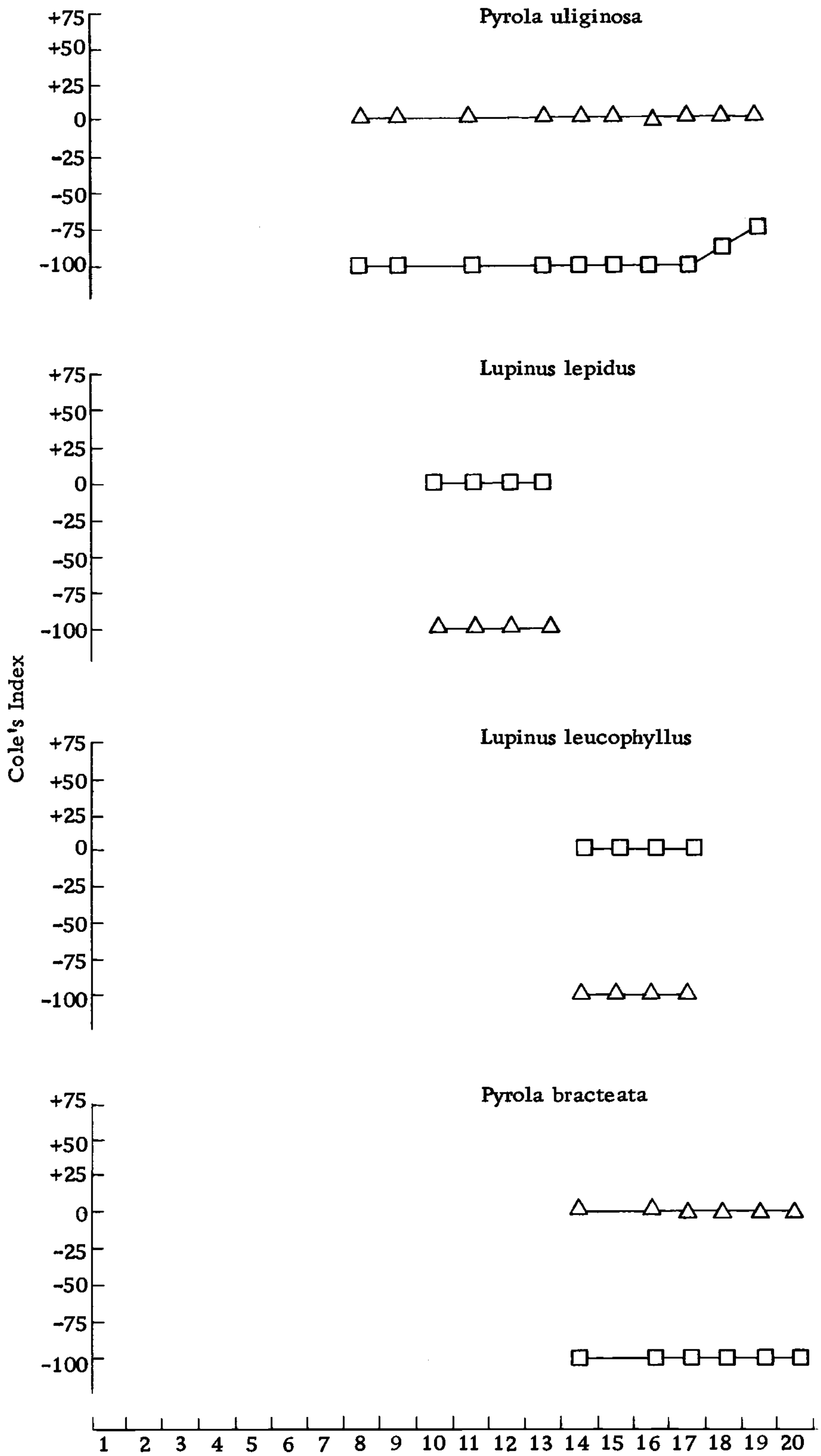

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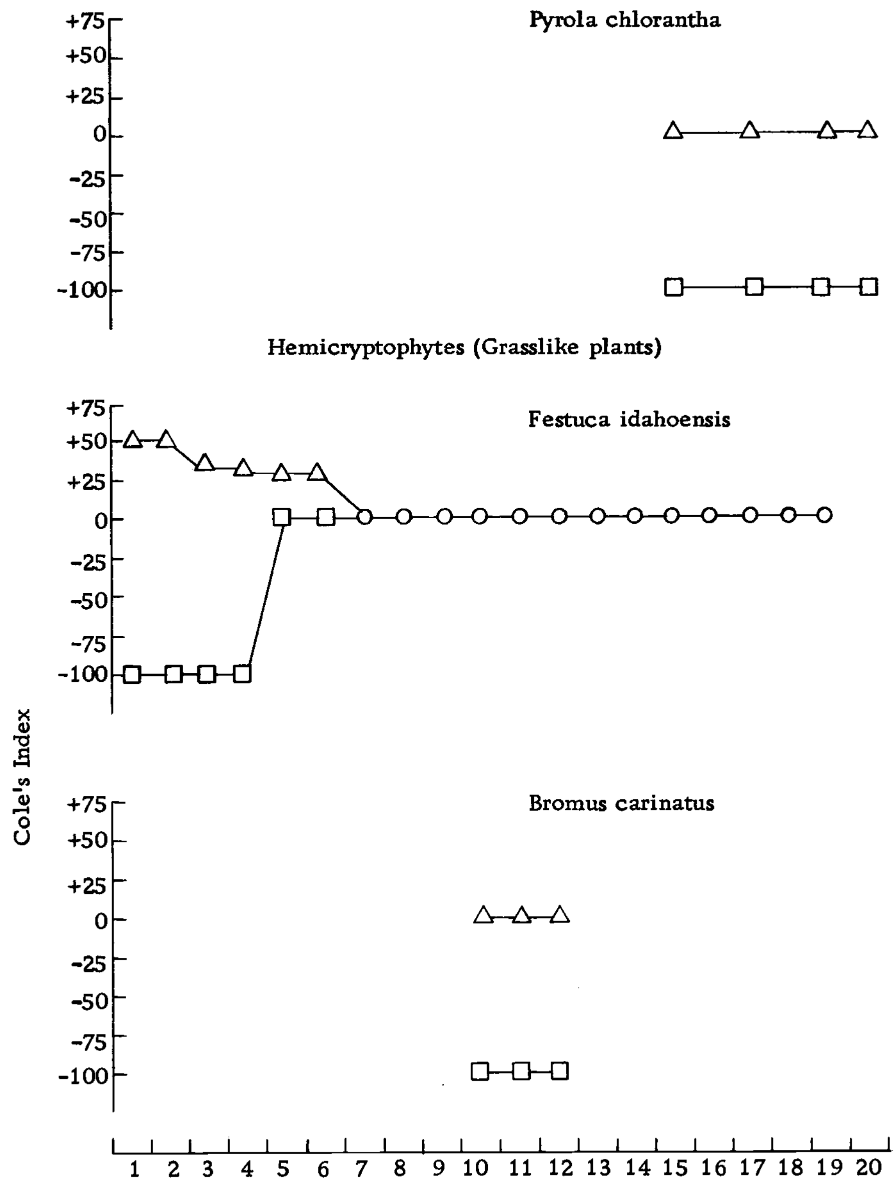

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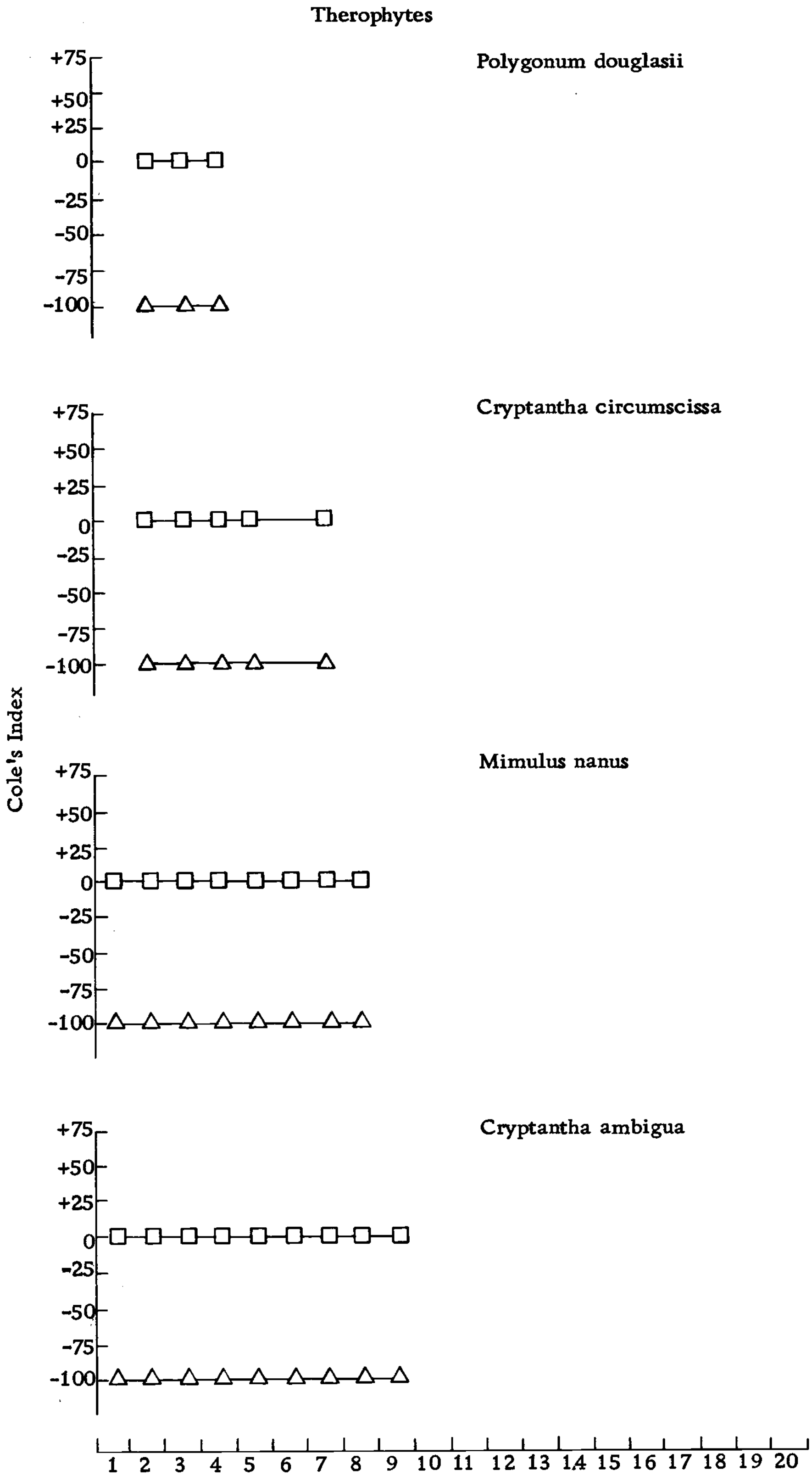

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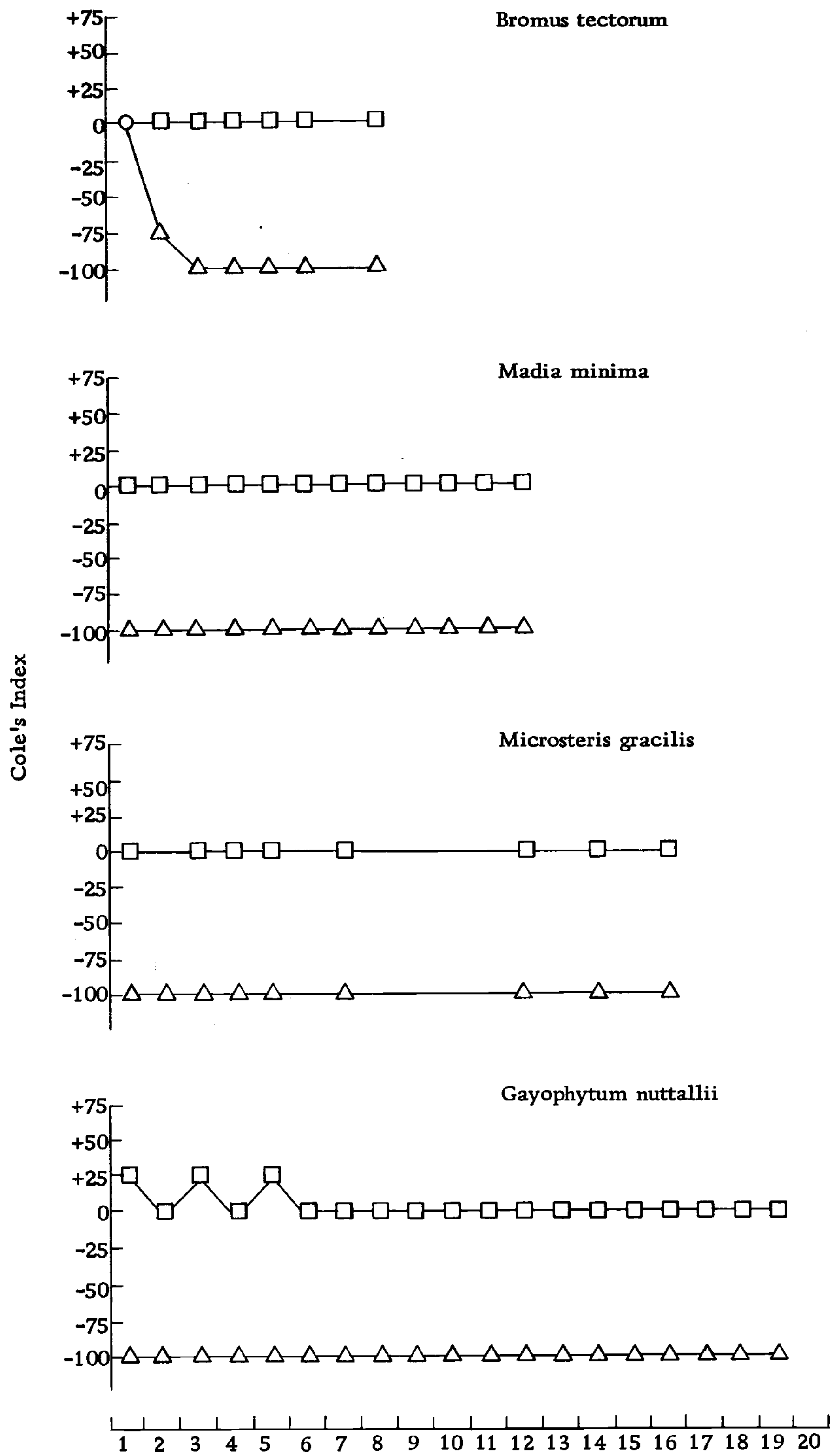

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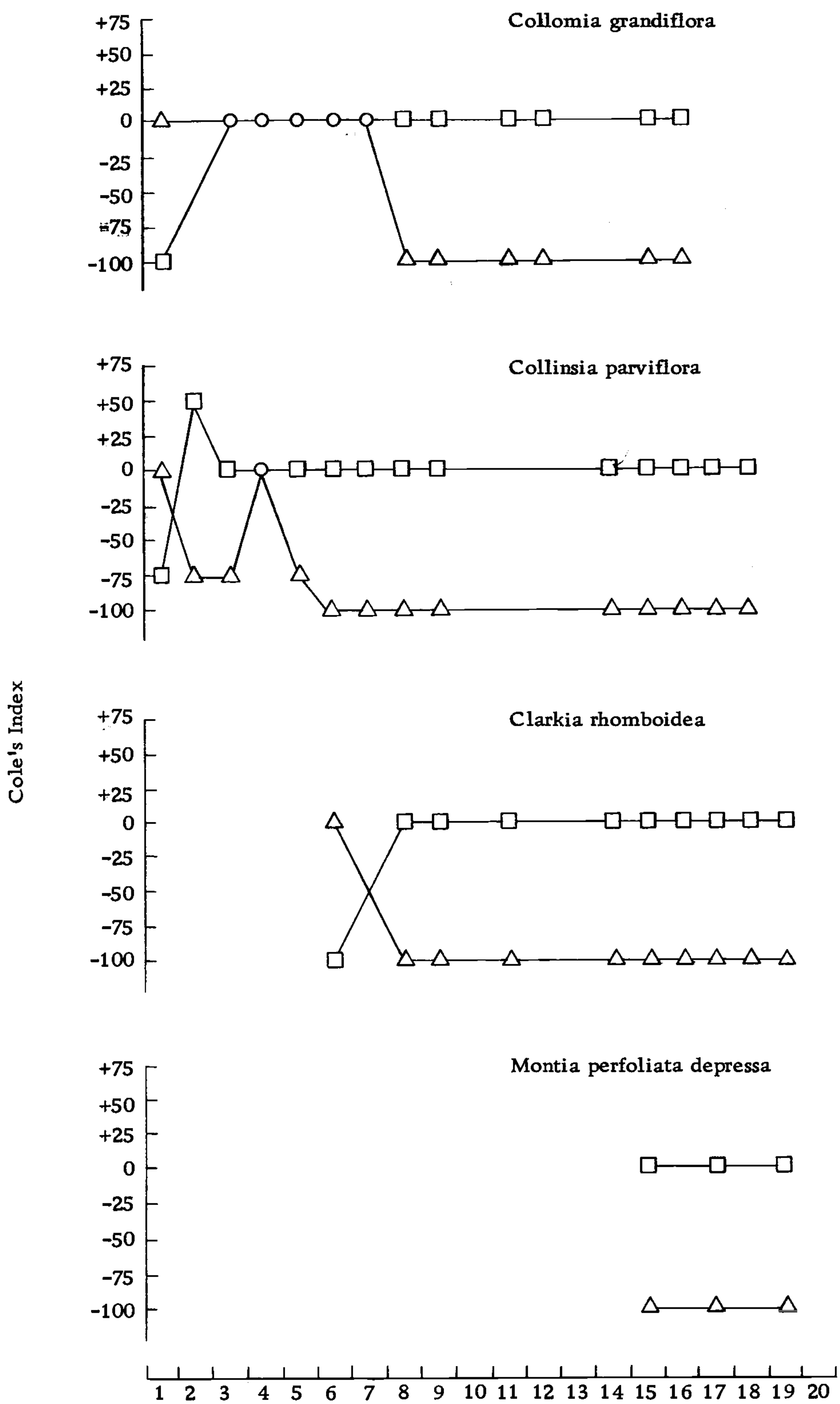

Figure 7. (continued)

Hierarchial Classification Analysis

Since a significant correlation was found between understory species' distribution and maximum or minimum tree influence, a more detailed analysis of the factors within these two main categories was undertaken. The influence of some of the factors affecting the distribution of understory species were examined by this detailed hierarchial classification analysis. The eight factors measured and analyzed were plot location (factor A), tree cover (factor B), amount of insolation (factor C), amount of litter (factor D), type of litter (factor E), presence or absence of species' competition (factor F), seasonal differences in direct insolation (factor G), and daily differences in direct insolation (factor H). Table II describes these factors in more detail, and Appendix 3 gives the distribution of these factors along the gradient.

The factors which showed a significant correlation with the understory species' density distribution are shown in Table V. The numerical values indicate how many times greater the variation was for that factor than would be expected in a normal population. These numerical values are the quotients of the F statistic computed by hierarchial analysis from field data which is then divided by the corresponding F statistic which is found in the .5% tables (Li, 1964). The quotients which are greater than one were considered significant and listed in the table. Those quotients less than one were not considered significant and were disregarded. The factors and species were ordinated so that those species which were influenced by the same factors were found generally in the same part of the table, and those species which had no significant factors in common were located in different parts of the table. Festuca idahoensis shows a value of 10.05 to tree cover (B) in the upper left corner of Table V. This numerical value indicates that the density variation in relation to tree cover is ten times greater than would be expected if tree cover effect had no influence upon the distribution of Festuca idahoensis. Examples of species found in the same part of the table are Chimaphila umbellata var. occidentalis, Campanula scouleri, Festuca idahoensis, and Kelloggia galioides which all show a significant correlation with type of litter (factor E), daily differences in direct insolation (factor H), and tree cover (factor B). Examples of species found in different parts of the table are Rubus ursinus which showed a significant correlation only with type of litter, and Microsteria gracilis which showed a significant correlation only with amount of litter.

Significant differences in density were contributed by tree cover for 47 species, by amount of litter for 25 species, by seasonal differences in insolation for 17 species, by daily differences in direct insolation for 16 species, by the amount of direct insolation for 15 species, by species' competition for 14 species, and by the type of litter for 11 species. None of the species which were tested by the hierarchial analysis showed a significant difference in density for plot location (factor A), amount and type of litter (factors D and E), or seasonal and daily differences in direct insolation (factors G and H).

In order for the significant factors of a species to show continuous patterns in Table V, a minimum of four factor arrangements had to be used to satisfy this requirement for all 63 species. These four arrangements are designated on the table as groups 1 through 4. In general, most of the species were influenced by daily differences in direct insolation, tree cover, and species' competition in group 1; species' competition, tree cover, and seasonal differences in direct insolation in group 2; amount of litter, and tree cover in group 3; and amount of insolation, tree cover, and seasonal differences in direct insolation in group 4. Tree cover showed a significant correlation to most of the species in all four groups. Group 3 is composed mostly of mesic species, whereas the other groups are not composed of species from any particular part of the gradient.

In order to determine if a correlation existed between the type of significant hierarchial factors and the position of the species along the gradient, the species were divided into two groups based on the distribution of Abies grandis. The percentage of species of the two groups that show significant differences in density to a particular hierarchial factor is shown in Table VI. Species associated with

Table V. Significant Values[1] for Understory Species as Determined by Hierarchial Classification

Species	E Type of Litter	H Insol. Daily Diff.	B Cover	F Compe-tition	C Amt. of Insol.	G Insol. Seas. Diff.	D Amt. of Litter	A Plots
GROUP 1								
Chimaphila menziesii	1.66	1.99	4.01	1.85	1.14	.	.	.
Chimphila umbellata	5.23	3.13	7.11					
Campanula scouleri	7.19	6.89	3.09					
Festuca idahoensis	2.25	2.78	10.05					
Kelloggia galioides	2.41	4.19	6.06					
Rubus ursinus	2.69							
Eriogonum umbellatum		1.60	10.02	2.67	1.06			
Pyrola bracteata		4.65	4.69	3.12				
Bromus carinatus		1.04	5.62					
Fragaria virginiana platypetala		3.36	12.78					
Lupinus caudatus		1.85	13.11					
Chrysothamnus viscidiflorus		1.35						
Senecio canus			2.30	1.04	1.44			
Silene douglasii			1.19	1.10	1.29			
Rosa gymnocarpa			36.91	2.13				
Chaenactis douglasii			1.11	2.97				
Pyrola uliginosa			4.34	4.30				
Lupinus leucophyllus			1.04	15.00				
Balsamorhiza careyana			4.12					
Lilium washingtonianum			2.40					
Lupinus lepidus			1.24					
Pterospora andromeda			3.74					
Aster canescens				1.79				
Cynoglossum occidentale				1.57				
Montia perfoliata depressa						1.16	1.28	
Collomia grandiflora						3.42	4.80	
Castilleja miniata						1.05	5.58	
Achillea millefolium lanulosa						1.19	1.84	
Microsteris gracilis							4.91	
Haplopappus bloomeri								
Clintonia uniflora								

	H	C	D	F	B	G	E	A
GROUP 2								
Lomatium simplex	2.10	1.50						
Apocynum androsaemifolium			2.01	4.91				
Gayophytum nuttalii				3.72	4.12	5.42		
Stephanomeria lactucina				1.56	1.59	2.18		

(continued)

Table V (continued)

Species	F	H	D	B	G	C	E	A
GROUP 3								
Scutellaria nana	2.52	1.77	1.08	2.44				
Penstemon cinereus		1.28	5.12	4.57				
Penstemon speciosus		5.00	2.63	4.63				
Clarkia rhomboidea		1.29	13.00					
Viola purpurea			7.50	2.03	2.40	1.08		
Purshia tridentata			1.30	1.96	2.90			
Lathyrus lanszwertii			143.29	1.34	3.02			
Bromus tectorum			68.19	2.33	1.007			
Collinsia parviflora			80.54	5.60	2.01			
Antennaria geyeri			12.23	1.77				
Eriophyllum lanatum			1.86	2.66				
Osmorhiza obtusa			1.12	7.61				
Townsendia florifer			2.73	1.08				
Cryptantha ambigua			40.34	6.80				
Polygonum douglasii			38.11	1.30				
Mimulus nanus				1.49	1.07	1.51		
Epilobium angustifolium					1.60	3.04	2.92	
Berberis nervosa						1.96	3.61	

Species	H	D	C	B	G	E	F	A
Group 4								
Lithospermum ruderale	11.11	3.61	1.27	1.52				
Leucocrinum montanum		6.25	1.19	1.23				
Madia minima		10.60	1.12	1.24				
Cryptantha circumscissa		9.39	1.04					
Pteridium aquilinum			1.11	1.60				
Trientalis latifolia			1.14	1.12				
Symphoricarpos albus				12.58	3.08	4.74		
Hieracium albiflorum				1.08	1.10	4.24		
Pyrola chlorantha				2.67	5.88	6.99		
Linum perenne				1.96	2.01			

[1] Values are derived by dividing the F statistic computed by hierarchial analysis from field data by a corresponding F statistic which is found in the .5% F Table (Li).

Abies grandis occurred in the upper part of the gradient (groups 10, 11, 12, 13, 14, and 15 of Appendix 1 or 2). Species not associated with Abies grandis occurred in the lower part of the gradient (groups 4, 5, and 9 of Appendix 1 or 2). Type of litter (factor E) and daily differences in direct insolation (factor H) showed a significant difference only to the species associated with Abies grandis. The highest percentage of the species which showed a significant correlation to tree cover (factor B), amount of insolation (factor C), amount of litter (factor D), and seasonal differences in direct insolation (factor G) were species not associated with Abies grandis.

The percentage of species of a certain life form (Phanerophyte, Chamaephyte, Hemicryptophyte, Geophyte, and Therophyte) which showed significant differences in density to hierarchial factors is shown in Table VII. The percentage value listed for each factor is the quotient of the number of species of a particular life form which show a significant correlation to that factor divided by the total number of species that belong to that life form. Significant differences in density were contributed by tree cover (factor B) for most of the Phanerophyte, Hemicryptophyte, and Geophyte species; by type of litter (factor E) for most of the Chamaephyte species, and by amount of litter (factor D), for most of the Therophyte species. Factors which did not show significant differences in density to a particular life form were plot location for all life forms, amount of insolation

Table VI. Percentage of Species in Upper and Lower Parts of the Environmental Gradient which Show Significant Correlation to Hierarchial Factors.

Species Groups	A Plots	B Cover	C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Compe-tition	G Insol. Seas. Diff.	H Insol. Daily Diff.
Species found only in part of gradient where Abies grandis is present (20 species)[1]		.60	.20	.15	.30	.20	.25	.15
Species found only in part of gradient where Abies grandis is absent (7 species)[2]		.85	.42	.57		.14	.42	

1 = composed of species from Groups 10, 11, 12, 13, 14 and 15. (Appendix I or 2.)

2 = composed of species from Groups 4, 5 and 9 (Appendix 1 or 2).

Table VII. Percentage of Species of a Particular Life Form which Shows Significant Correlations to Hierarchial Factors.

Life - Form	A Plots	B Cover	C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Compe-tition	G Insol. Seas. Diff.	H Insol. Daily Diff.
Phanerophytes (5 species)		.60		.20	.20	.20	.40	.20
Chamaephytes (5 species)		.60	.40	.14	.80	.14		.40
Hemicryptophytes (36 species)		.83	.22	.33	.16	.33	.25	.36
Geophytes (5 species)		.60	.40	.20				.20
Therophytes (12 species)		.58	.25	.83		.08	.08	.08

for Phanerophyte forms, type of litter for Geophyte and Therophyte forms, and seasonal differences in direct insolation for Chamaephyte and Geophyte forms.

The species which had the highest correlation with a particular factor as determined by hierarchial classification analysis is shown in Figures 8 through 14. The numerical values show how many times greater the variation was for that factor than would be expected on an equal probability basis. This numerical value suggests the level of importance of the factor in relation to that species. High values mean the factor is more important than factors with lower values. Thus these values are arranged in order of importance from left to right with the highest on the left and the lowest value on the right. For example, in the lower right corner of Figure 7 Champhila menziesii shows 4 times more variation for tree cover (B), 2 times more variation for daily difference in direct insolation (H), 1.85 times more variation for species' competition (F), 1.66 times more variation for type of litter (E), and 1.14 times more variation for amount of insolation (C) than would be expected if these factors did not affect the distribution of the species. Thus, in hierarchial classification analysis the factors should be arranged in the following order to analyze their affect upon the distribution of Chimaphila menziesii: factors B, H, F, E, and C. Highest signficant differences in density were contributed by tree cover for 19 species (Figure 8), by amount

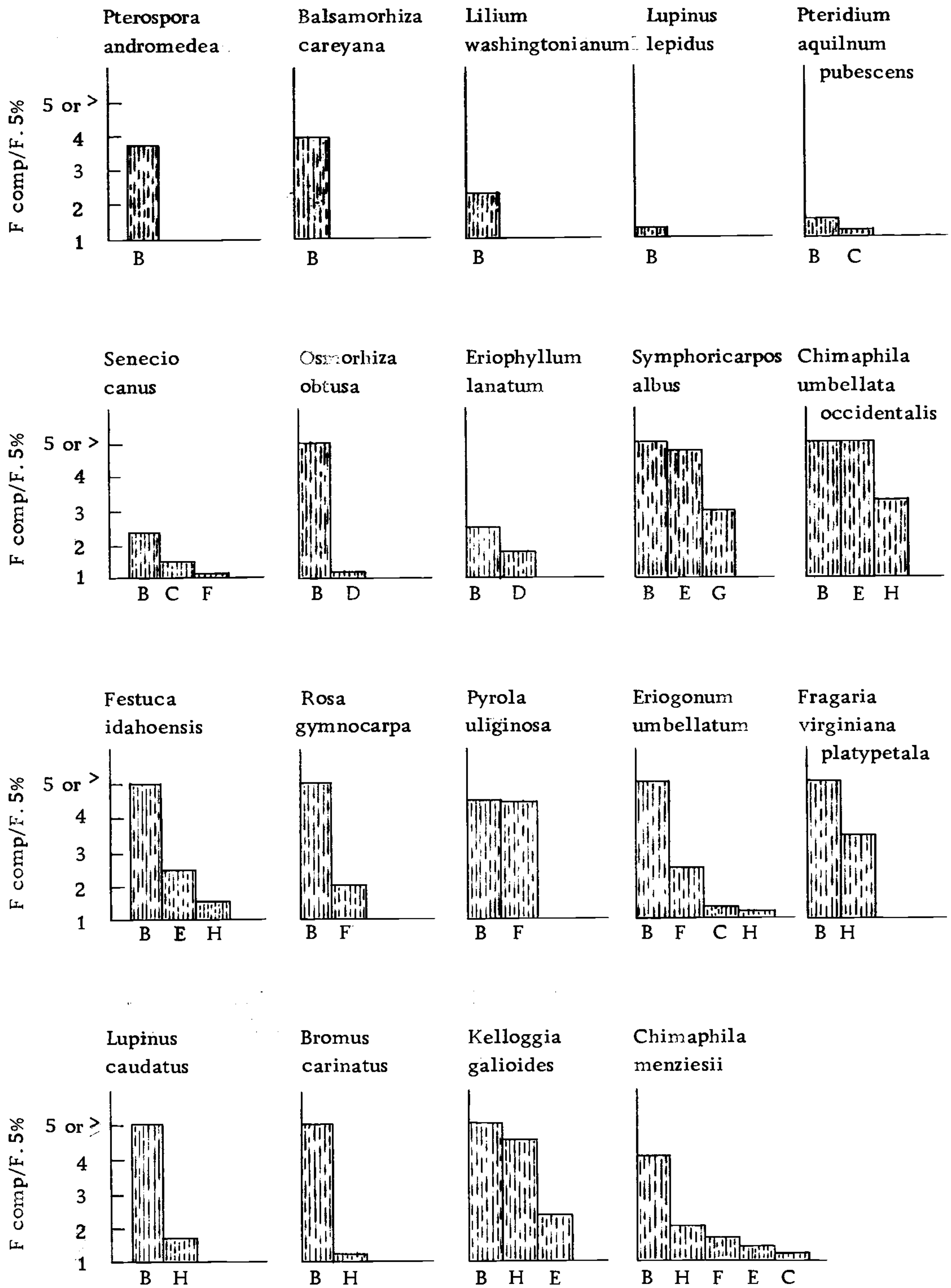

Figure 8. Species which show highest correlation with factor B (cover) as determined by hierarchial classification.

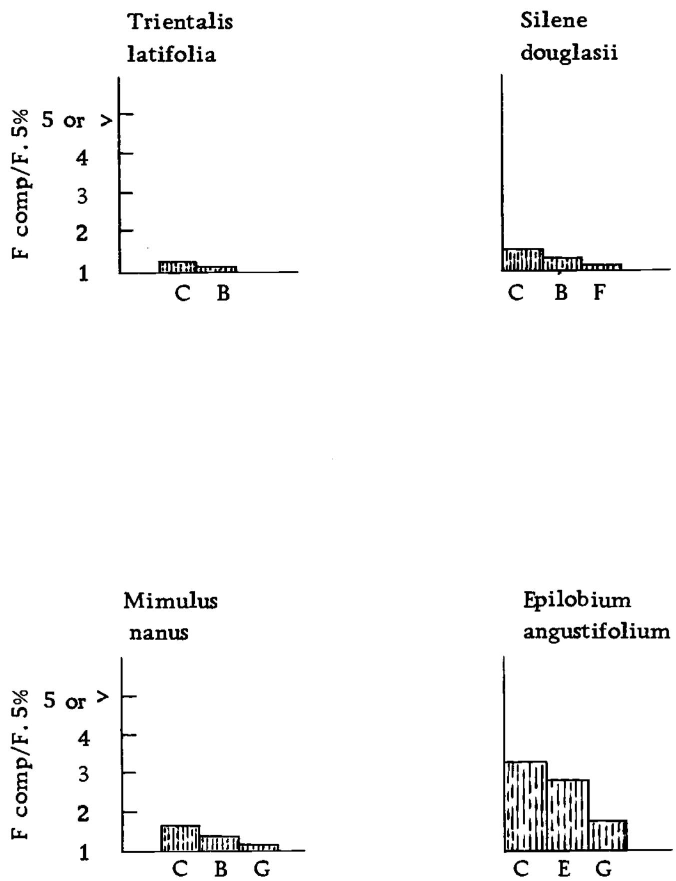

Figure 9. Species which show highest correlation with factor C (Amt. of insol.) as determined by hierarachial class.

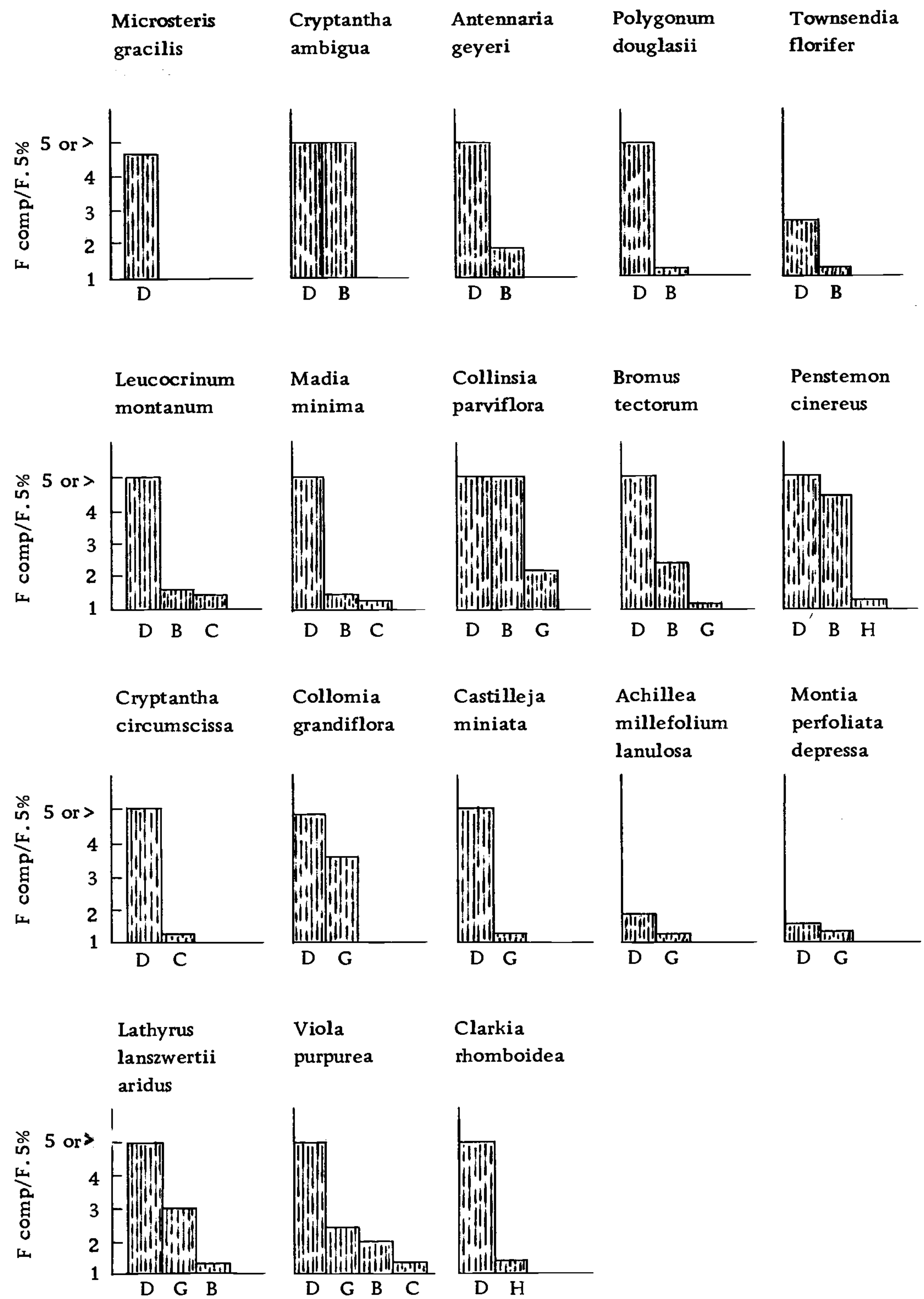

Figure 10. Species which show highest correlation with factor D (Amt. of litter) as determined by hierarachial classification.

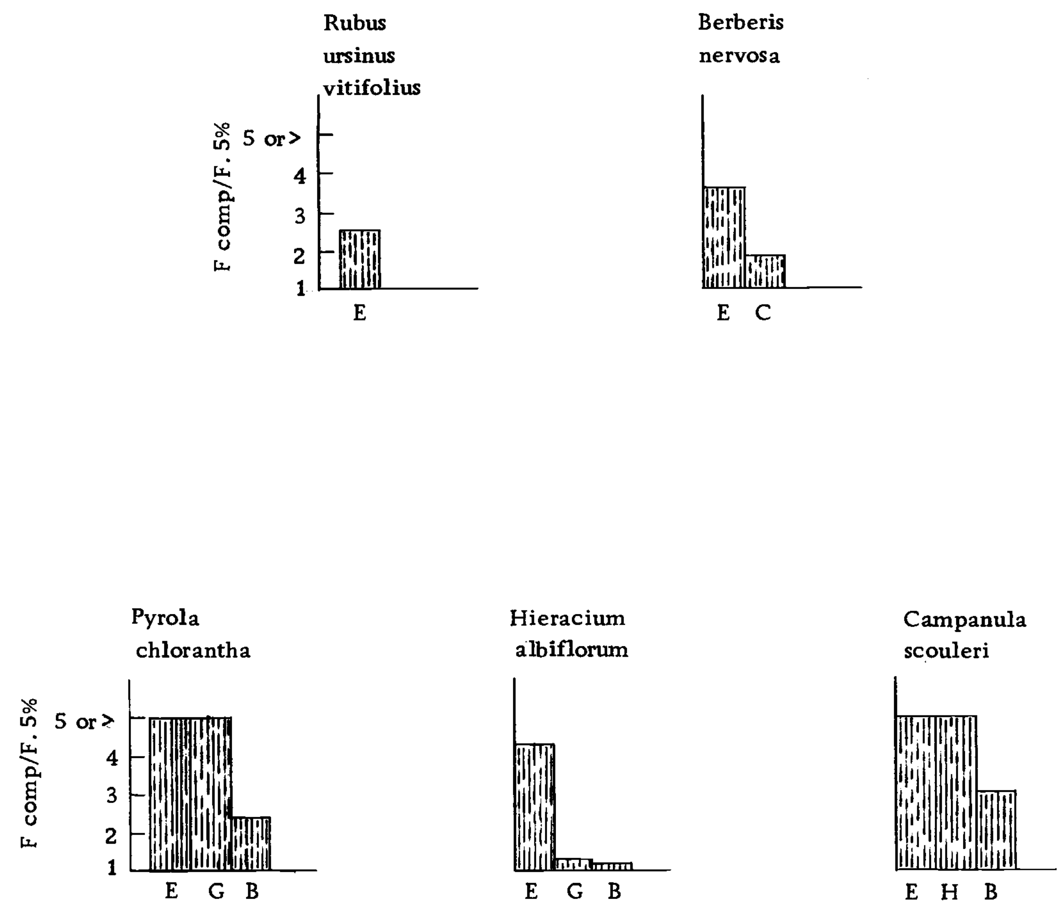

Figure 11. Species which show highest correlation with factor E (type of litter) as determined by hierarachial classification.

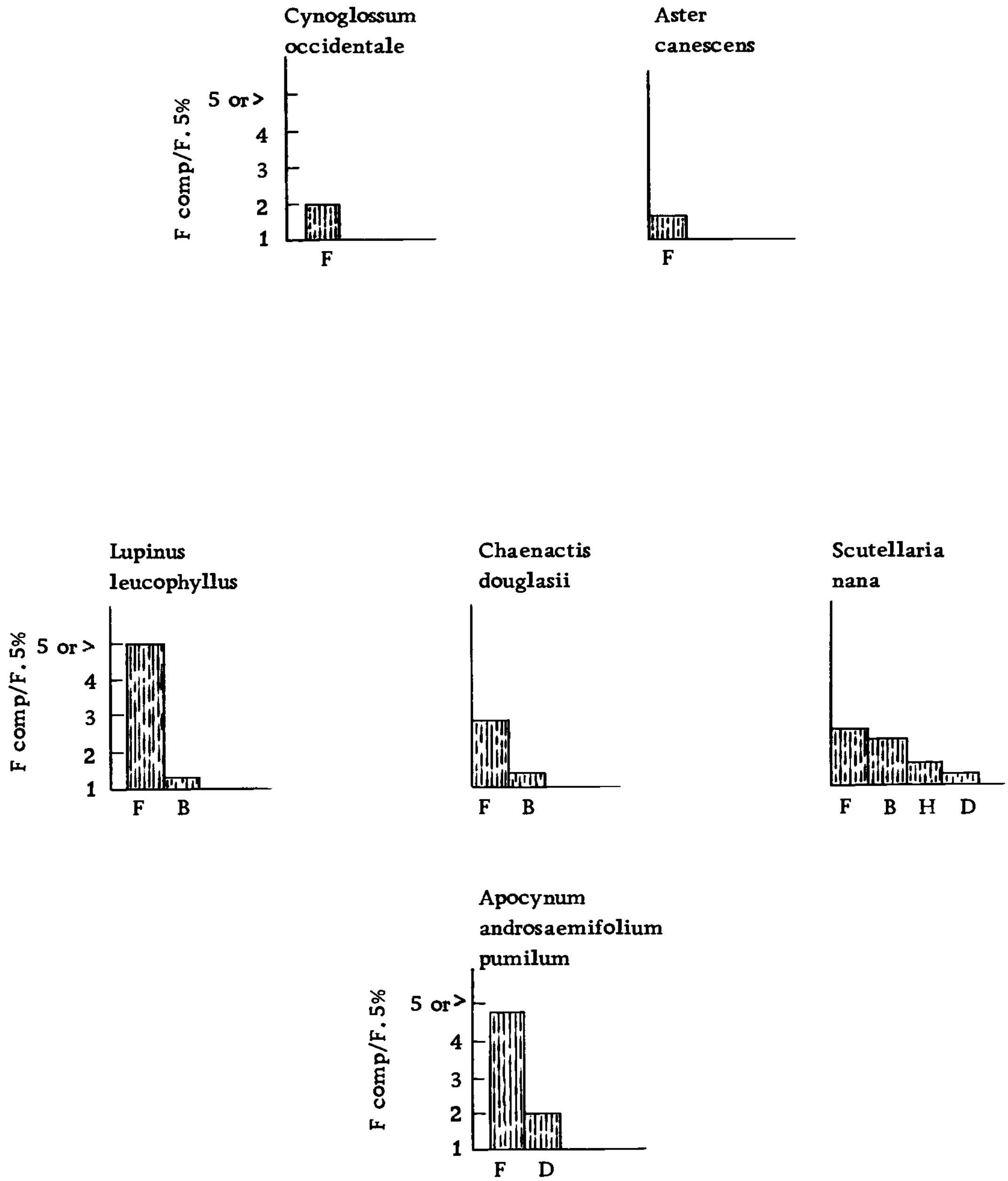

Figure 12. Species which show highest correlation with factor F (competition) as determined by hierarachial classification.

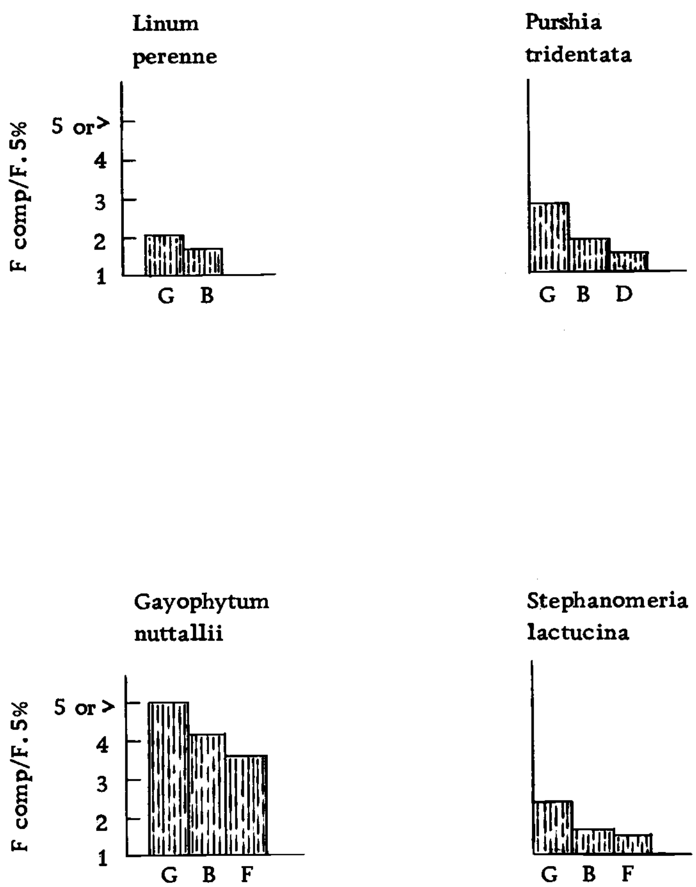

Figure 13. Species which show highest correlation with factor G (Seasonal sun distribution) as determined by hierarachial classification.

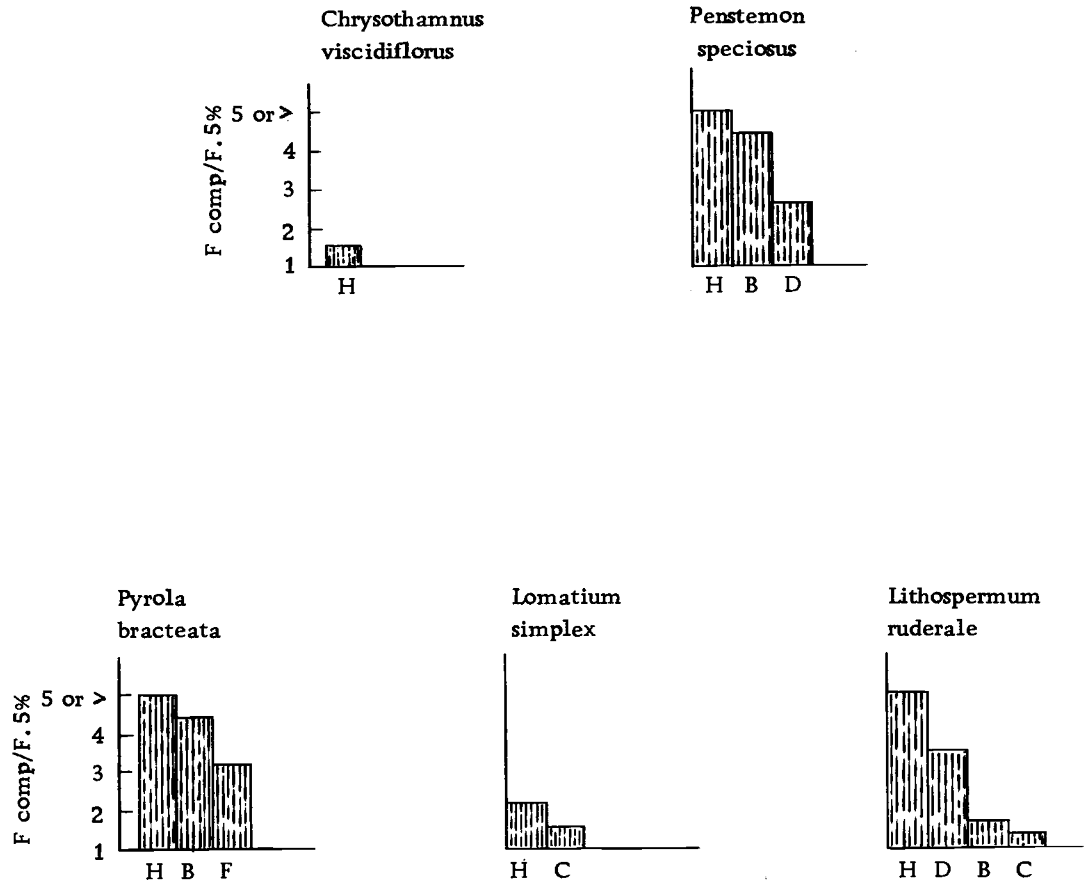

Figure 14. Species which show highest correlation with factor H (Daily sun distribution) as determined by hierarachial classification.

of insolation for 4 species (Figure 9), by amount of litter for 18 species (Figure 10), by type of litter for 5 species (Figure 11), by species' competition for 6 species (Figure 12), by seasonal differences in direct insolation for 4 species (Figure 13), and by daily differences in direct insolation for 5 species (Figure 14). By relating the importance of the factor to the statistic found in Figures 8 through 14, an idea of factor arrangement might be obtained. The most important hierarchial factor would be those with the highest statistic, and the least important factor would be those with the lowest statistic. Thus, most of the 63 species have their own hierarchial factor arrangement, and very few species have identically the same.

Maximum Density of the Species

After determining which hierarchial factor(s) shows a significant correlation with the species, a next step was to determine the area of highest density for the species within the gradient according only to those factors found significant by hierarchial classification analysis. This was accomplished by sorting the square foot microquadrats into goups composed of similar levels for each of the factors that were significant. The groups were then analyzed to find the level of maximum density of the species. Appendix 4 shows the density distribution of the species in relation to their important factors, and Figures 15-19 are composed of two or more axes depending upon the

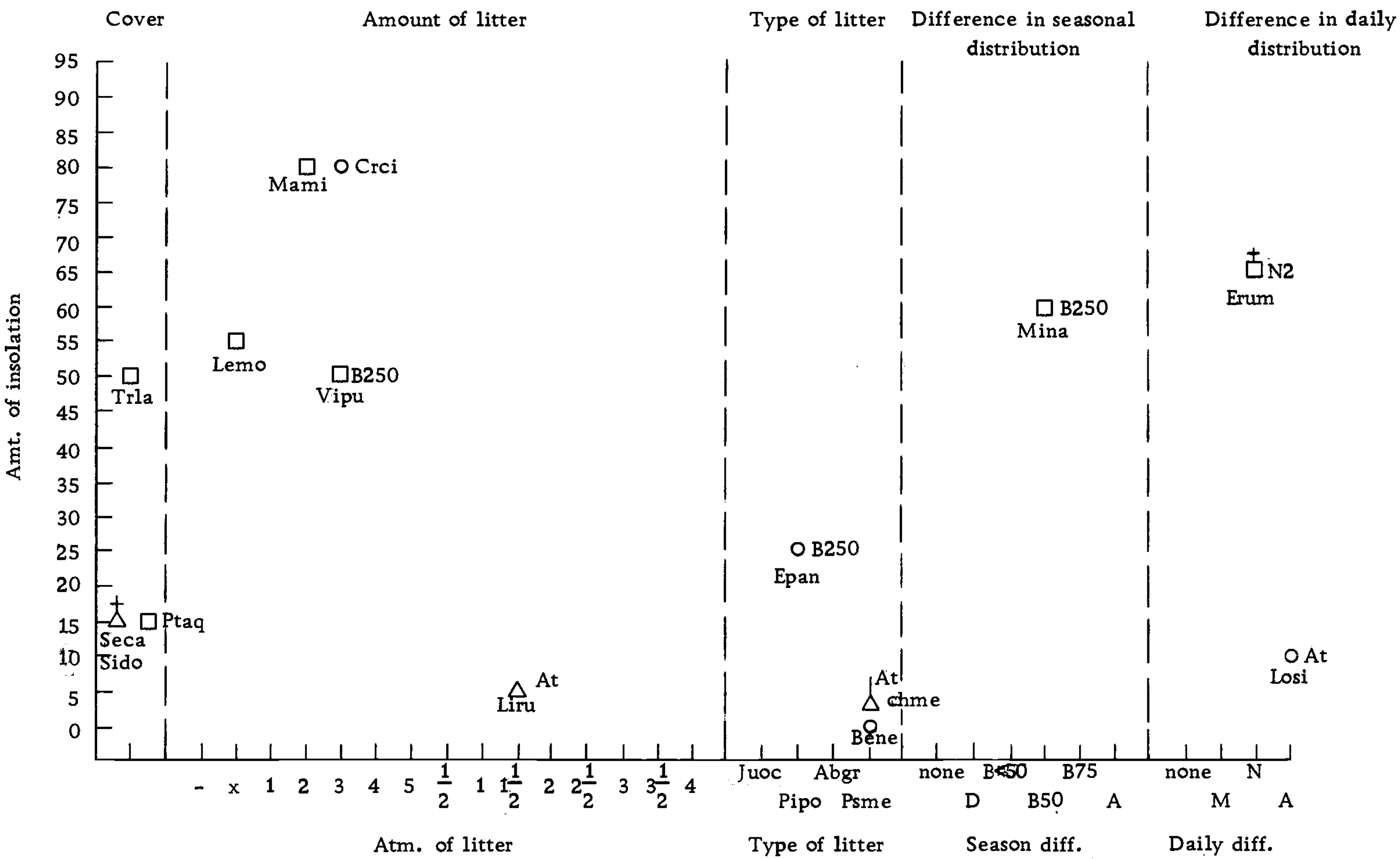

Figure 15. Maximum density of species in relation to amount of insolation, and/or cover, and/or amount of liter, and/or type of liter, and/or competition, and/or differences in seasonal distribution of direct insolation, and/or differences in daily distribution of direct insolation.

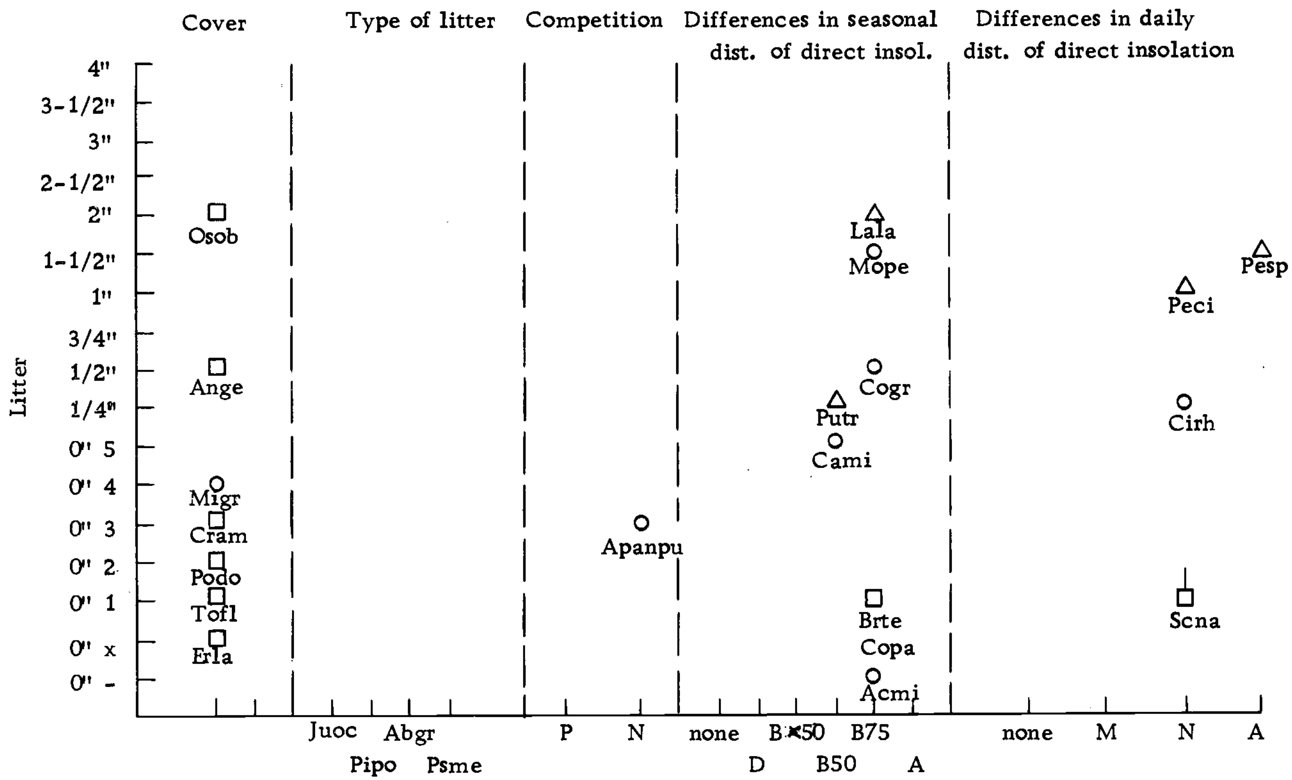

Figure 16. Maximum density of species in relation to amount of litter, and/or cover, and/or type of litter, and/or competition, and/or differences in seasonal distribution of direct insolation, and/or differences in daily distribution of direct insolation.

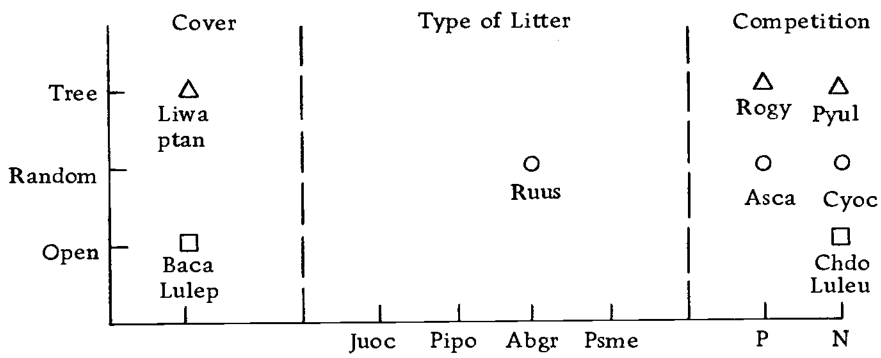

Figure 17. Maximum density of species in relation to cover, and/or type of litter, and/or competition.

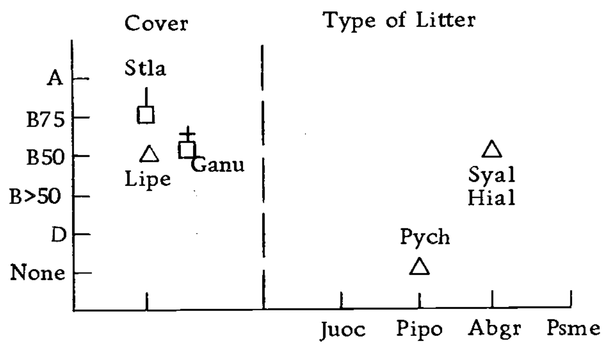

Figure 18. Maximum density of species in relation to differences in seasonal distribution of direct insolation, and/or cover, and/or type of litter.

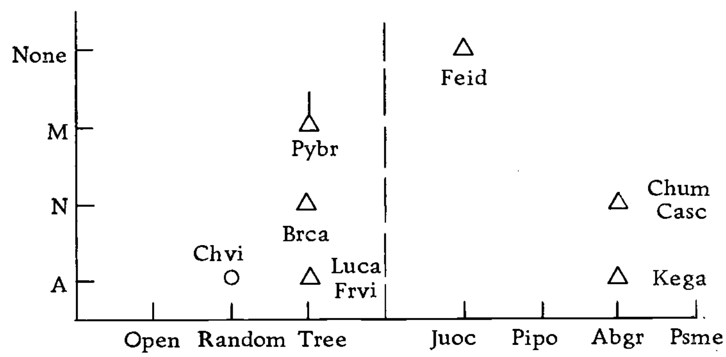

Figure 19. Maximum density of species in relation to differences in daily distribution of direct insolation, and/or cover, and/or type of litter.

number of factors which showed a significant difference in density to the species.

Those species (Madia minima, Cryptantha circumscissa, Leucocrinum montanum, and Viola purpurea) which showed significant difference in density to insolation in high insolation ranges (80% or greater) generally occurred on the xeric end of the gradient, and those species (Pteridium aquilinum, Lithospermum ruderale, Chimaphila menziesii, and Berberis nervosa) which showed significant differences to low insolation generally occurred on the mesic end of the gradient. In regard to litter depth, species (Lithospermum ruderale, Osmorhiza obtusa, Montia perfoliata, and Penstemon speciosus) that showed a maximum density for deep litter generally occurred on the mesic end of the gradient, and species (Eriophyllum lanatum, Townsendia florifer, Bromus tectorum, and Scutellaria nana) which showed maximum density to sparse litter generally occurred on the xeric end of the gradient. Chamaephyte species generally showed maximum density to area underneath the tree usually near the mesic end of the gradient. Therophyte species generally showed maximum density to open area usually near the xeric end of the gradient.

Theoretical Model

A theoretical model showing possible species' distribution is given in Table VIII. The theoretical model is composed of two parts:

Table VIII. Theoretical Model of Species Distribution and Actual Constancy[1] Distribution for the Five Communities Found Along the Gradient

Species	Juoc/Feid		Pipo/Putr/Feid		Pipo/Arpa-Putr		Pipo/Ceve		Abgr/Pymy
<u>Wide Ranging Xeric Species</u>									
Madia minima	OM	1.00	O	1.00	O	.80			
Mimulus nanus	OM	1.00	OM	1.00					
Leucocrinum montanum	OM	1.00	OM	1.00					
Scutellaria nana	OM	1.00	OM	.57	O	.16			
Eriogonum umbellatum	OM	1.00	OM	.85	O	.60	O	.16	
Gayophytum nuttallii	OM	1.00	OM	1.00	O	1.00	O	1.00	
Cryptantha ambigua	OM	1.00	OM	1.00	OM	.20			
Microsteris gracilis	OM	1.00	OM	.57	OM	.40	O	.33	
Cryptantha circumscissa	M		O	.71					
Townsendia florifer	M		OM	.71					
Polygonum douglasii	M		OM	.42					
Chaenactic douglasii	M		OM	.57					
Viola purpurea	M		OM	.85	OM	1.00	O	.16	
Castilleja miniata	M		OM	.42	OM	.21	M		
Aster canescens	M		OM	.71	OM	.60	M		
Lupinus lepidus	M		M		OM	.80	M		M
Montia perfoliata	M		M		M		OM	.50	M
Lupinus leucophyllus			M		M		OM	.66	M
<u>Juoc/Feid</u>									
Eriophyllum lanatum	RM	1.00	O	.85	O	.40			
Bromus tectórum	RM	1.00	OM	.85					
<u>Pipo/Putr/Feid</u>									
Penstemon cinereus	M		RM	1.00	OM	.80	OM	1.00	M
Clarkia rhomboidea	M		RM	.57	OM	.40	OM	1.00	
Stephanomeria lactucina	M		RM	.42	RM	.80	OM	.83	M
Antennaria geyeri	M		RM	.85	RM	1.00	OM	.16	M
Achillea millefolium	M	1.00	R	1.00	R	1.00	R	1.00	
Lathyrus lanszwertii	M		RM	.71	RM	1.00	R	.66	

Table VIII (continued).

Species	Juoc/Feid		Pipo/Putr/Feid		Pipo/Arpa-Putr		Pipo/Ceve		Abgr/Pymy	
Pipo/Putr/Feid (continued)										
Linum perenne	TM	1.00	RM	.71						
Collinsia parviflora	TM	1.00	RM	1.00	O	.20	O	1.00		
Chrysothamnus viscidiflorus	TM	1.00	RM	.57		.20				
Purshia tridentata	TM	1.00	RM	1.00	OM	1.00				
Collomia grandiflora	TM	1.00	RM	.85	OM	.60	OM	.33	M	
Festuca idahoensis	TM	1.00	RM	1.00	RM	1.00	RM	1.00		
Pipo/Arpa-Putr										
Senecia canus	M		TM	.42	OM	.20	M			
Lomatium simplex			TM	.42	RM	.20	OM	1.00	M	
Lithospermum ruderale			TM	.71	RM	.80	RM	.50	M	
Hieracium albiflorum			TM	.42	RM	1.00	RM	1.00	OM	1.00
Pipo/Ceve										
Lilium washingtonianum	M		M		M		RM	1.00	M	
Trientalis latifolia	M		M		M		R	.66	O	1.00
Apocynum androsaemifolium	M		M		TM	.20	R	1.00	O	1.00
Kelloggia galioides			TM	.42	TM	1.00	RM	1.00	M	
Cynoglossum occidentale			M		TM	.20	RM	.83	M	
Balsamorhiza careyana	M		M		TM	.60	RM	.83	M	
Epilobium angustifolium	M		M		TM	.80	RM	1.00		
Pteridium aquilinum	M		M		TM	.20	RM	1.00	O	1.00
Campanula scouleri			M		TM	.40	RM	.83	OM	1.00
Fragaria virginiana	M		M	.14	TM	1.00	RM	1.00	RM	1.00
Rubus ursinus							RM	.83	RM	1.00
Absr/Pymy										
Chimaphila umbellata				.14	TM	1.00	TM	1.00	RM	1.00
Osmorhiza obtusa	M		M		TM	.80	TM	.33	RM	1.00
Symphoricarpos albus			M		TM	1.00	TM	.50	RM	1.00
Rosa gymnocarpa	M		M		M		TM	.66	RM	1.00

Table VIII (continued)

Species	Juoc/Feid	Pipo/Putr/Feid		Pipo/Arpa-Putr		Pipo/Ceve		Abgr/Pymy	
<u>Wide Ranging Mesic Species</u>									
Silene douglasii	M	TM	.42	TM	.20	M		M	
Penstemon speciosus	M	TM	.28	TM	.60	M		M	
Lupinus caudatus	M	TM	.42	TM	.60	M		M	
Bromus carinatus	M	M		TM	.60	M		M	1.00
Pyrola uliginosa		TM	.14	TM	1.00	TM	1.00	M	
Berberis nervosa				T	.20	TM	.66	M	
Chimaphila menziesii		T	.28	T	1.00	TM	1.00	TM	1.00
Pterospora andromedea	M	TM	.28	TM	1.00	TM	.83	TM	1.00
Pyrola bracteata	M	M		M		TM	.83	TM	1.00
Pyrola chlorantha	M	M		M		TM	.50	TM	1.00

R = the area most compatible with species requirements both underneath the tree and out in the open.

O = the area most compatible with species requirements out in the open.

T = the area most compatible with species requirements underneath the tree.

M = the possibility of a condition occurring within the community (niche) that fits the requirements of the specie as determined by hierarchial classification analysis and maximum density analysis.

[1] Constancy data = based on number of plots for each community (Juoc = 1, Pipo/Putr/Feid = 7, Pipo/Arpa-Putr = 5, Pipo/Ceve = 6 and Abgr/Pymy = 1).

(1) a letter (O, R, or T) designates the distribution of the species in relation to maximum tree influence as determined by Cole's index analysis in each of the communities, and (2) a letter (M) designates the possibility of a condition occurring within the community that fits the requirements of the species as determined by the hierarchial classification analysis and maximum density analysis. The area most compatible with the requirements of the species for a particular community may occur out in the open (designated by "OM"), underneath the tree (designated by "TM"), or out in the open and underneath the tree (designated by "RM"). Constancy data of the 63 understory species analyzed was similarly recorded on Table VIII in order to check the proposed model to see if it was similar to the situation found in nature. The denominator for constancy data was the number of plots for a particular community, while the numerator was the number of plots in which a species occurred. The letter codes "R," "O," and "T" are used in the model to designate where in the community the species will occur, but the species should not normally occur in this community. Finally, "M" indicates that the species is presently not found within the community but will probably invade, because there is an area compatible with the species' ecological requirements. Madia minima, located in the upper left corner of Table VIII, will probably occur in the open and remain (OM) in the Juniperus/Festuca community and will probably occur in the open and not remain

(O) in the Pinus/Purshia/Festuca and Pinus/Arctostaphylos-Purshia communities.

The species in the model were ordinated based upon the symbols "OM, RM, and TM." Those species which occurred only in the open (OM) were located at the top of the table. Those species which occurred only underneath trees (TM) were located at the bottom of the table. Those species which occurred both in the open and underneath the trees in some communities were located in the central part of the model. The community most compatible with species' requirements is suggested by the symbol "RM." These species could be considered characteristic species if the symbol "RM" occurred in only one community. Examples of characteristic species are Eriophyllum lanatum and Bromus tectorum for the Juniperus/Festuca community, Purshia tridentata and Collomia grandiflora for the Pinus/Purshia/Festuca community, Lomatium simplex for the Pinus/Arctostaphylos-Purshia community, Pteridium aquilinum and Campanula scouleri for the Pinus/Ceanothus community, and Chimaphila umbellata, Osmorhiza obtusa, and Rosa gymnocarpa for the Abies/Pachistima community. Some of the species occurred only out in the open (OM) and are usually widely distributed. These species are probably invading from more xeric communities. Other species occurred only underneath the trees and are also normally widely distributed. These species are probably invading from more mesic communities.

DISCUSSION

The pattern of plants and plant communities which occur across the landscape are the product of the environment arising from both the physical features (climate and soils) and the interaction between plants and other organisms (biotic factors). The environmental and vegetational gradient of concern in the study was divided for purposes of analysis into five communities: Abies/Pachistima, Pinus/Ceanothus, Pinus/Arctostaphylos-Purshia, Pinus/Purshia/Festuca, and Juniperus/Festuca.

Fire patterns of the area, especially before 1900, played an important role in shaping the composition of the communities along the gradient. In the more xeric part of the gradient where Pinus ponderosa is the dominant species, frequent light ground fires were prevalent prior to 1900 (Weaver, 1959; Soeriaatmadja, 1965). On the more mesic end of the gradient where Abies grandis is the dominant species, more destructive crown fires that occurred at less frequent intervals are in evidence (Soeriaatmadja, 1965).

Fire resistance of trees varies according to the type of fire, the size and age of the tree, its position along the gradient, and the frequency of fires. For example, young Libocedrus decurrens trees are readily killed by light ground fires, while mature trees of the species with thick bark and crown well above the ground surface are not

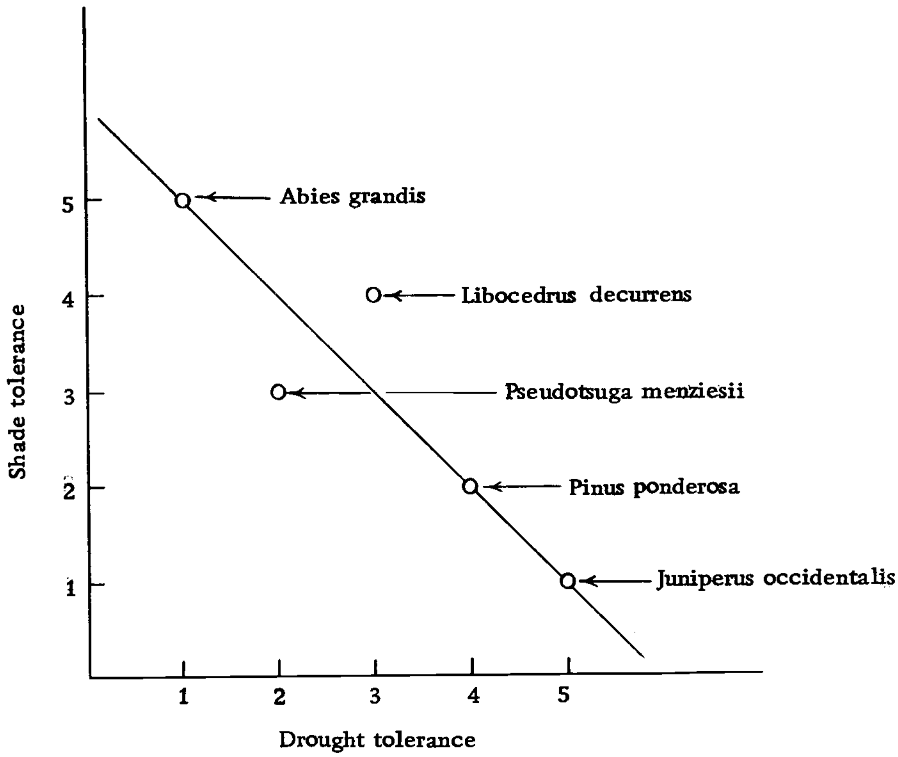

Figure 20. Relative shade and drought tolerance of selected conifers as interpreted from Fowells 1965 and Baker 1950.

damaged. Pinus ponderosa and Pseudotsuga menziesii are generally more resistant to fire than Libocedrus decurrens and Abies grandis (Starker, 1934). Under Pinus ponderosa, litter accumulation is usually light and the lower branches are self pruning. The mature trees are generously spaced and have thick, fire resistant bark. Unchecked light ground fires, by eliminating fire sensitive Abies grandis and Libocedrus decurrens, contribute to the formation of relatively pure stands of pine.

Two important aspects of the environment exerting a strong control over distribution of trees in the study area are relative drought and shade tolerance. In general, as shade tolerance increases, drought tolerance decreases (Figure 20). In the absence of fire or cutting, present trends indicate that Abies grandis, Libocedrus decurrens, and Pseudotsuga menziesii will extend down the gradient and invade the upper portions of the areas dominated by Pinus ponderosa. Evidence of this trend has been suggested for Pinus ponderosa forests of this area and in other regions by Weaver and Cooper (Weaver, 1943; Cooper, 1960).

In the absence of fire or cutting, the ensuing successional development of the forest canopy results in the increase of fire sensitive, shade tolerant species; and the decrease of fire resistant, shade intolerant species. Although tree layer succession involves long periods of time, (Pinus ponderosa lives up to 600 years), rapid development and short life spans of understory species lead to a more rapid adjustment of the understory layers. Although understory community adjustments are related to the rate of development and longevity of species, understory species with short life spans, limited seed dissemination, and narrow tolerance ranges may result in slower re-occupation of areas compatible with the ecological requirements of the species. This dependency upon the tree overstory and a relatively greater distance between suitable areas in terms of understory species dispersal capacity may result in a greater degree of lag in the successional development of the understory. Evidence of these phenomena is indicated in Appendix 1 and 2. Tree species show continuous distributional patterns from stand to stand along the gradient. However, the herbaceous species tend to show interrupted distributional patterns along the gradient (Appendix 1 and 2). Even when compatible environments occur, a long time may elapse before the species occupies the area. The theoretical model is based on existing vegetation, and although relatively stable, reflects some degree of lag from the ideal point of equilibrium (climax). This degree of lag may result in a less perfect model than would have been the case had the forest been in equilibrium with the environment.

The theoretical model with the above limitations, still should be a fairly accurate representation of what actually occurs in nature. In comparing the species' distribution as determined from the theoretical model (Table VIII) with the actual distribution of the species (constancy data from Table VIII and Appendix 1), some inconsistencies are apparent. (1) The species occur in the community, but the model indicates that the species should not be there. (2) The model indicates the species should be present in a community, but the species is not actually there. If the model is a true representation of the current species distributional pattern in nature, the average differences between the model and the constancy distribution of the species in nature should be zero (mean = 0). The hypothesis that on the average no difference exists between the actual species' distribution and the theoretical species' distribution as shown by the theoretical model ($\bar{y} = 0$) was tested by a T test of paired observations. Based on the data from which the model was made, when this difference was tested by a T test at the 1% level the hypothesis was accepted; but at the 2.5% level this hypothesis was rejected (T4 = 3.25). Thus, the distribution of the theoretical model was much wider than was actually found by constancy data, but may represent a reasonable first approximation. Examples of species which theoretically had wider distribution than was found by constancy data were Pyrola bracteata, Pyrola chlorantha, Silene douglasii, and Lupinus caudatus. This wider theoretical distribution may suggest irregularities related to a time lag in the complete occupation of all suitable habitats. However, compatible areas for some species exhibiting a wider theoretical distribution may be much narrower than presently defined by the model.

Much information was gained from this first approximation of hierarchial factor arrangement about the species. However, because the correct order of factor importance was not known, some factors which may be important did not appear significant and thus were not considered important in the distribution of the species. For example, were tree cover more important than plot location for a species, and were the small variance value for plot location divided by the large variance value for tree cover, plot location would not appear significant. However, if the large variance value for tree cover was divided by the small variance value for plot location, the tree cover F value would be greater than one and thus might appear significant. In addition, when plot location was divided by a factor less important than plot location, the resulting variance ratio (F statistic) would also be greater than one, and thus plot location could also be significant.

From this approximation, at least 28 different hierarchial arrangements for the species were noted by relating the importance of the factor to the statistics found in Figures 8 through 14. The most important hierarchial factor should be those with the highest statistic, while the least important would be those with the lowest statistic. In the second approximation, the factors should be arranged based on the highest to the lowest statistic, and thus almost every species would have its own hierarchial factor arrangement. Very few species would have identically the same arrangement. Thus, from this first approximation, a better assumption involving the hierarchial factor arrangement can be made for each species.

In addition to the problem of hierarchial factor arrangement, other factors not measured, probably had an influence on species' distribution. Those species in which the last factor measured in the hierarchial arrangement (factor H) did not have a variance ratio greater than one, indicate that there are other unmeasured factors that are more important than the last factor (H). A total of 23 species had variance ratio values (F values) less than one for factor H. Thirty species showed consistent distributional patterns to those factors which were found significant by the hierarchial classification analysis. Twenty-nine species showed inconsistent distributional patterns to those factors which were found significant by the hierarchial classification analysis. Thus, by using the species' hierarchial arrangement found in the first approximation, and increasing the number of factors measured in the field, more field data could be gathered and analyzed. A new model could then be constructed which should probably more closely resemble the actual distribution of the species found in nature. To help select points for taking additional data in the field, those species which showed a very narrow consistent distributional pattern in relation to their significant hierarchial factors (Appendix 4) and had F values for factor H greater than 1.00 may be used as species' indicators.

The gradient analysis emphasized the kinds and degrees of relationships between communities. One of the advantages of gradient analysis is that the population of species along a continuous environmental gradient form bell shaped curves with densities declining gradually on each side of the central peak (Whittaker, 1967). The central peak for each species is indicated in the theoretical model at the point along the gradient where understory species are distributed randomly within the stands (R). In gradient analysis, these bell shaped curves are distributed according to the species' response to environmental factors (Gleason, 1926). One use of this gradient analysis is in community coefficients (Jaccard, 1912). To avoid weighing species of low indicator values in the same way as species with high indicator values, frequency values, importance values, or density values are often used instead of presence data in calculating these community coefficients. Thus, data gathered on a gradient of stand structure may provide another approach to obtain some means of emphasizing certain species (Figure 21). Stands may be ordinated according to the central peaks (R value) of the bell shaped curves for the species' assemblage.

The separation of communities might be based on random distribution (R) of the characteristic species to tree layer influence.

	Juoc/ Feid	Pipo/Putr/Feid								Pipo/ Arpa-Putr				Pipo/Ceve						Abgr/ Pymy
	1	2	3	5	4	6	7	8	9	10	11	12	13	14	16	15	17	18	19	20
Erla*	O																			
Brte*	O																			
Copa*				O	O															
Chvi*			O	O	O															
Lipe*							O													
Clrh*							O													
Peci*							O	O												
Stla								O	O											
Cogr*			O	O	O	O	O													
Putr*			O	O	O	O	O	O	O											
Ange				O	O	O	O	O	O	O	O	O	O							
Acmi				O	O	O	O	O	O	O	O	O	O	O	O	O	O	O		
Lala							O	O	O	O	O			O	O	O				
Feid							O	O	O	O	O	O	O	O	O	O	O	O	O	
Liru													O	O	O	O				
Hial											O	O	O	O	O	O	O	O	O	
Apan*														O	O	O	O	O	O	
Ptaq*														O	O	O	O	O	O	
Epan*															O	O	O	O		
Cyoc*															O	O	O			
Baca*																		O	O	
Trla*																		O	O	
Casc*																		O		
Liwa*																			O	
Kega*																			O	
Frvi														O	O	O	O	O	O	O
Ruus																	O	O	O	O
Chum*																				O
Osob*																				O
Syal*																				O
Rogy*																				O

* Characteristic species

Figure 21. Ordination of stands based on the position within the gradient where understory species are distributed randomly (independent of tree influence within the stand)

In Figure 21, a circle was used every time condition "R" occurred within a stand for the species. Thus, Stand 9 was placed in the Pinus/Purshia/Festuca community, when the ordination based on the "R" value for the characteristic species. However, Stand 9 was placed in the Pinus/Arctostaphylos-Purshia community, when the ordination was based on the constancy, frequency, and density distribution for all the species. Furthermore, the ordination of Figure 21 suggests that Stand 2 is an ecotonal stand between the Juniperus/Festuca and the Pinus/Purshia/Festuca community, because no characteristic species of either community show a random correlation value to tree layer effect. Similarly, the ordination of Figure 21 indicates that the Pinus/Arctostaphylos-Purshia community is a transitional zone between areas dominated by Pinus ponderosa and areas dominated by Abies grandis; because there are no characteristic species found in the Pinus/Arctostaphylos-Purshia community which show a random Cole's index value (R) to tree effect. The species that do occur in this community also occur in both or either one of the two communities found on either side of the Pinus/Arctostaphylos-Purshia community.

Bailey (1966), in studying forest associations, used naturally occurring light and dark areas of the Coast forest of southern Oregon. By comparing the distribution of the species in light areas and dark areas, Bailey checked the validity of his phytosociological classification and likewise gained a better phytosociological understanding of understory species of the forest. This study goes further in that it determined if a correlation (random, positive, or negative) existed between the distribution of understory species, and light and dark areas. Besides determining whether or not a correlation existed between a species' distribution and dark and light areas, a more detailed analysis of the factors within these two main categories was undertaken. The influence of some of the factors affecting the distribution of understory species was determined by a hierarchial classification analysis.

Successional relationships of species within and between stands or communities may be suggested from a detailed analysis of the distributional patterns of understory species in relation to maximum and minimum tree influence. According to the theoretical model (Table VIII), those species which should not normally be present within a community but are present in areas of the maximum (T) or minimum (O) tree influence suggest that the vegetation is undergoing change. If this change is a result of the environment becoming more mesic, the mesic species (T) should invade as areas compatible with their ecological requirements become available underneath the trees. Eventually they will replace the more xeric species found only in the open (O). However, if the environment becomes more xeric, the xeric species (O) should invade as areas compatible with their ecological requirements become available in the open. Eventually they will replace more mesic species found only underneath the trees (T). The number of species in the open (O) or underneath trees (T) within and between stands or communities, suggest the relative stability of the vegetation. If no species fit either "O" or "T," this suggests that the vegetation may be relatively stable; but many species in either or both categories, suggest that the vegetation may be changing. Thus, the theoretical model suggests that the vegetation of the Juniperus/Festuca community is relatively stable, but that the vegetation of the other four communities may still be changing. For example, in the Pinus/Arctostaphylos-Purshia community, six species occur only in the open (O) and two occur only underneath trees (T). These eight species occur within the community, but the model indicates that these species should not normally be present. Past light frequent ground fires of this community suggest that species occurring only in the open (O) are likely to be replaced by more mesic species. If this is so, the effective environment will probably become more mesic, allowing the invasion of mesic species underneath the trees (T).

Further studies into successional changes of internal community structure may give additional information about future vegetation. By studying distributional patterns of species in relation to maximum and minimum tree influence at the same point along the gradient but with the vegetation at different stages of maturity, a better understanding of the significance of species occurring only under the trees or in the open might be gained. Thus, by noting the vegetational distribution within a stand, it is possible to locate several similar stands in vegetation with different maturity levels. For example, to find stands similar in gradient position to Stand 7, those stands in which Clarkia rhomboidea, Penstemon cinereus, Linum perenne, and the other six species of Stand 7 (Figure 21) showed random correlation values to maximum and minimum tree influence, would most likely have similar gradient positions. From this successional analysis several questions might be asked. (1) If the species occur underneath the trees in immature stands, does the species remain only underneath the trees in mature stands? (2) If the species show random Cole's index values to maximum and minimum tree influence in immature stands, does this species continue the same pattern in mature stands? And (3) if the species occur only in the open in immature stands, does this species remain in the open in mature stands?

Following the gain of some insight into the effect of succession upon the internal community structure along one gradient, other gradients could be analyzed in relation to elevation, parent materials, or different locations. From these analyses, questions might be answered about whether the structure of the community remained the same in different locations, on different parent materials, or in different types of gradients. Thus, with information about the geographical position and the successional effect upon internal community structure, theories could be derived for classification of landscapes for multipurpose land management.

CONCLUSION AND SUMMARY

Twenty sites of uniform topography and soil were selected in the montane forest found on the East flank of the Central Oregon Cascades. These sites were located along a vegetational gradient composed of five plant communities: Abies/Pachistima, Pinus/Ceanothus, Pinus/Arctostaphylos-Purshia, Pinus/Purshia/Festuca, and Juniperus/Festuca. An attempt was made to relate the distributional pattern of understory species to six aspects of tree influence (overhead cover, amount of shade, daily differences in shading, seasonal differences in shading, amount of litter deposit, and species of tree depositing the litter) understory species competition, and plot location. Cole's index and hierarchial classification analysis were statistical methods used to correlate the understory species' pattern to tree influence, understory species' competition, and plot location.

From frequency data of the 63 species analyzed by Cole's index, only two showed an inconsistent distributional pattern in relation to tree influence. Similarly, three distributional patterns were noted. (1) Species were distributed at random in the area of maximum tree influence regardless where the species occurred along the gradient. (2) Species were distributed at random in the area of minimum tree influence and were absent in the area of maximum tree influence regardless where the species occurred along the gradient. (3) Species at a point along the gradient were distributed at random in areas of maximum and minimum tree influence; but on more xeric plots the species were distributed similar to pattern 1, and on more mesic plots species were distributed similar to pattern 2. In pattern 3, the point along the gradient where the species were distributed at random to areas of maximum and minimum tree influence may suggest an optimum point along the gradient where the effect from tree layer influence is minimal. This point provides a basis for comparing the environmental tolerances of the species and ordinating the stands.

When the species' density data were analyzed by hierarchial classification to determine what factors of maximum and minimum tree influence effected the density distribution of the species, the following patterns were noted. Normally, species with highest densities in areas of maximum insolation or sparse litter were prominent on the xeric end of the gradient, and those species with maximum densities in areas of low insolation or deep litter were prominent on the mesic end of the gradient. Chamaephyte species sampled had highest densities in areas underneath the trees and usually near the mesic end of the gradient. Therophyte species sampled had highest densities in open areas usually near the xeric end of the gradient.

Thus, a theoretical model was constructed using data obtained from this structural analysis of internal distributional patterns of understory species. The distribution of the species is much wider according to the theoretical model than was actually found by constancy data, but the differences when statistically analyzed are not great enough to reject the model at the 1% significance level. The model suggests predictable patterns of species' distribution within the five community types and may reflect the relative stability of these species within the community types.

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APPENDICES

Appendix 1. Constancy[1] and Frequency[2] Distribution by Stands of Tree, Shrubs, and Herbs

Species	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo Ceve						Abgr Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP I																				
Pinus ponderosa	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.50
Carex complex	.06	.07	.08	.02	.02	.06	.04	.04	.01	.13	.06	.64	.02	.01	.03	T	T	T	T	.01
GROUP II																				
Achillea millefolium lanulosa	.03	T	.09	.21	.13	.13	.06	.28	.12	.08	.13	.17	T	.20	.21	.03	.22	T	.05	
Festuca idahoensis	.13	.17	.40	.48	.15	.18	.30	.46	.39	.28	.36	T	T	T	T	.09	.01	.09	.03	
Stipa complex	.14	.40	.15	.10	.02	.05	.09	.03	.18	.18	.40	.30	.26	.04	.05	.02	.02	.04	T	
Gayophytum nuttallii	.11	.13	.03	.09	.01	.12	.14	.02	.11	.01	.04	T	.01	T	T	.04	.03	T	.02	
Collinsia parviflora	.15	.61	.25	.40	.15	.22	.23	.08	.06					.01	.02	.01	T	.06	T	
Sitanion complex	.11	.17	.06	.10	.17	.02	.01	.06	.10	.07	.21	.21	.02	.05	T	T	.05		.01	
Collomia grandiflora	.01		.03	.05	.52	.03	.31	.06	T	T		T			T		T			
Microsteris gracilis	T		.03	.02		T	.07		.01			T		T			T			
Eriogonum umbellatum	.03		.01	.08	.01	T	.02	.03	T			T	.01	T						
GROUP III																				
Purshia tridentata	.09	.08	.41	.25	.60	.30	.25	.44	.23	.33	.25	.30	.01							
Madia minima	T	.03	.03	.17	.04	.02	.13	T	T	T	T	T								
Eriophyllum lanatum	.01		T	.05	T	.03	T	.02			T	.04								
Chrysothamnus viscidiflorus	.02		.01		.01	.04	.01				T									
Juniperus occidentalis	1.00	1.00	.50	T	1.00	T	1.00		.50		T									
Cryptantha ambigua	.08	.10	.02		T	.01	.03	T	T											
Scuttellaria nana	.04		T		T		T	T	T											
GROUP IV																				
Leucocrinum montanum	.05	T	T	T	.01	T	T	T												
Mimulus nanus	.06	.02	.01	.06	T	.10	T	T												
Linum perenne	T		T	.01		T	.02	T												
Bromus tectorum	.11	.20	.05	.05	T	.01		T												
Plectritis macrocera	.13	.13																		
GROUP V																				
Artemisia tridentata	.04																			
Erigeron filifolius	.08																			
Poa secunda	.05																			
Koeleria cristata	.01																			
Blepharipappus scaber	.21																			
Phacelia linearis	.12																			
GROUP VI																				
Hieracium albiflorum					T	T		T	T	.03	.06	.07	.03	.15	.05	.04	.07	.04	.05	.02
Chimaphila menziesii							T	T	T	T	T	T	T	T	T	T	.01	T	T	T
Pterospora andromedea							T	T	.01	T	T	T	T	T	.01	T	T	T		T
Chimaphila umbellata occidentalis								T	T	.01	T	T	T	.03	.01	.03	.05	.01	.01	.56
Fragaria virginiana platypetala								T	T	.14	.10	.60	.13	.09	.07	.26	.46	.03	.18	.10

Appendix 1 (continued).

Species	Juoc/Feid	Pipo/Putr/Feid						Pipo/Arpa-Putr					Pipo/Ceve						Abgr Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP VII																				
Viola purpurea		.01	.01		.02	.02	T	T	.01	T	T	T	T	T						
Lomatium simplex			.01			T		T		T				.02	.02	T	.01	T	T	
Lithospermum ruderale			.01	T		T	.02	.01	T	T	T		T	.01	T		T			
Lathyrus lanszwertii aridus			.16	.10		.10	.31	.29	.29	.14	.41	.13	.01	.38	.01	T	T			
Antennaria geyeri			.01	.01	T	.01	.01	.02	T	.02	T	.05	T	.01						
Clarkia rhomboidea				.02	.04	.01		.07	T	T				.01	T	T	.01	.01	T	
Stephanomeria lactucina				T	T			T	.01		.03	.05	.01	T	T	.01	.06	.03		
Haplopappus bloomeri				T		T	T			T	T	.01	.02	T	.02		.01			
Kelloggia galioides						T	T	T	T	.01	T	.02	.15	.01	T	T	T	T	.04	
Pyrola uliginosa								T	T	T	T	T	T	T	.01	.01	.01	.01	T	
GROUP VIII																				
Penstemon cinereus		T	.01	.03	.17	T	.03	.07	T	T	T		.01							
Aster canescens			T	.01		T	T	T	T	T		T								
Senecio canus			.01	T		T						T								
Silene douglasii			T	T		.01				T										
Lupinus caudatus				.07	.11			T	T	.03	.01									
Castilleja miniata						T	.02	.02	T											
Penstemon speciosus							T	T		T	T	T								
GROUP IX																				
Townsendia florifer		T	T	T		.01	T													
Cryptantha circumscissa		T	T	T		T	T													
Polygonum douglasii		T	T			T														
Chaenactis douglasii				T	T	.01	T													
Tragopogon dubius					.01															
Agropyron spicatum						T														
GROUP X																				
Abies grandis									.50	.50	.50	.50	.50	1.00	.50	1.00	1.00	.50	1.00	1.00
Symphoricarpos albus									T	T	T	T	.01	.01			T		.04	.52
Osmorhiza obtusa									T	T	T	T		T			T			.02
Bromus carinatus										.06	T	T								.05
Campanula scourleri											T		T		.02	.22	.07	.01	.03	.01
Pseudotsuga menziesii												.50		.50	1.00	1.00	.50	1.00	1.00	1.00
Pteridium aquilinum pubescens													T	.08	.09	.14	.01	.12	.23	.05
Apocynum androsaemifolium pumilum													.09	T	T	.03	.01	.07	T	.01
GROUP XI																				
Epilobium angustifolium										.06	T	T	.02	.08	.14	.05	.03	.02	.02	
Balsamorhiza careyana										T		T	T	T		T	.04	T	.04	
Ceanothus velutinus										.16	T	.12	.34	.15	.09	.06	.41	.28		
Horkelia fusca										.02	T	T			.02					

Appendix 1 (continued).

	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr/ Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP XI (continued)																				
Phacelia mutabilis											T			T						
Cynoglossum occidentale													T	.01	T	T	.04	T		
Prunus emarginata													.02		T	.01	.03			
Berberis nervosa													T			T	T	T	T	
GROUP XII																				
Arctostaphylos parryana pinetorum									T	.18	T	.02	.15							
Paeonia brownii									T			.01								
Lupinus lepidus										.01	T	T	T							
Madia gracilis											T									
GROUP XIII																				
Pyrola bracteata														T		T	T	T	T	.02
Rosa gymnocarpa														T			T	T	.02	.06
Rubus ursinus															T	.01	.05	T	.02	.16
Pyrola chlorantha															T	T			T	.02
Trientalis latifolia																.43	T	.28	.50	.26
Amelanchier alniflora semiintegrifolia																T	T	.05		T
Pinus monticola																	T			.50
Clintonia uniflora																		T	T	.38
Pachistima myrsinites																			T	.02
Goodyera oblongifolia																			T	.03
Smilacina racemosa amplexicaulis																			T	.12
Anemone piperi																			T	.07
GROUP XIV																				
Lilium washingtonianum														T	T	.01	.01	T	.01	
Cirsium centaureae														T	.01		.01		.01	
Castanopsis chrysophylla														T	.06	.05	.05			
Lupinus leucophyllus														T	T	T	T			
Montia perfoliata depressa															T	T			T	
Aquilegia formosa																T			T	
Libocedrus decurrens																.50	T	1.00		
Agoseris glauca																.02				
Equisetum hyemale																			.05	
GROUP XV																				
Linnaea borealis																				.46
Asarum caudatum																				.02
Adenocaulon bicolor																				.05
Corallorhiza maculata																				.01
Galium aparine																				.01
Acer circinatum																				.50

1 Trees = constancy data 2 Shrubs and herbs = frequency data T = trace

Appendix 2. Density Distribution by Stands of Trees, Shrubs, and Herbs

Species	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr/ Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP I																				
Pinus ponderosa	.0003	.001	.003	.005	.002	.004	.003	.007	.010	.010	.007	.063	.047	.026	.033	.032	.030	.012	.008	.0001
Carex complex	.05	.09	.08	.03	.06	.08	.10	.04	.01	.22	.20	1.28	.02	.02	.03	T	T	T	T	.01
GROUP II																				
Achillea millefolium lanulosa	.06	T	.16	.55	.29	.17	.07	.54	.17	.12	.28	.21	T	.28	.36	.03	.40	T	.05	
Festuca idahoensis	.15	.19	.47	.54	.17	.19	.38	.52	.47	.34	.50	T	T	T	T	.09	.01	.11	.04	
Stipa complex	.15	.53	.16	.10	.03	.05	.09	.03	.23	.25	.62	.41	.30	.04	.05	.02	.02	.04	T	
Gayophytum nuttallii	.16	.13	.03	.17	.01	.23	.15	.02	.24	.01	.04	T	.01	T	T	.06	.04	T	.06	
Collinsia parviflora	.26	2.48	.68	1.34	.33	.56	.42	.15	.06					.01	.02	.03	T	.15	T	
Sitanion complex	.12	.20	.06	.10	.22	.03	.01	.07	.11	.08	.26	.29	.02	.05	T	T	.07		.01	
Collomia grandiflora	.01		.04	.06	1.76	.03	.47	.10	T	T		T			T		T			
Microsteris gracilis	T		.04	.02	.02	T	.07		.01			T		T			T			
Eriogonum umbellatum	.04		.01	.09		T	.02	.03	T			T	.01	T						
GROUP III																				
Purshia tridentata	.06	.02	.12	.46	.43	.42	.16	.50	.23	.13	.15	.21	.01							
Madia minima	T	.03	.03	.39	.07	.03	.14	T	T	T	T	T								
Eriophyllum lanatum	.01		T	.06	T	.03	T	.02		T	T	.07								
Chrysothamnus viscidiflorus	.02		.01		.01	.04	.01				T									
Juniperus occidentalis	.005	.0008	.0001	T	.0008	T	.0002		.0001		T									
Cryptantha ambigua	.10	.12	.02	T	T	.02	.07	T	T											
Scutellaria nana	.04		T		T	T	T	T	T											
GROUP IV																				
Leucocrinum montanum	.06	T	T	T	T		T	T												
Mimulus nanus	.08	.03	.03	.06	T	.13	T	T												
Linum perenne	T		T	.01		T	.02	T												
Bromus tectorum	.25	.48	.13	.12	T	.01		T												
Plectritis macrocera	.45	.90																		
GROUP V																				
Artemisia tridentata	.04																			
Erigeron filifolius	.27																			
Poa secunda	.05																			
Koeleria cristata	.01																			
Blepharipappus scaber	.96																			
Phacelia linearis	.22																			
GROUP VI																				
Hieracium albiflorum					T	T			T	.03	.07	.07	.05	.16	.05	.04	.07	.04	.05	.02
Chimaphila menziesii							T	T	T	T	T	T	T	T	T	T	.01	T	T	T
Pterospora andromedea							T	T	.01	T	T	T	T	T	.01	T	T	T		T
Chimaphila umbellata occidentalis								T	T	.01	T	T	T	.04	.01	.03	.11	.01	.02	1.39
Fragaria virginiana platypetala								T	T	.19	.34	1.30	.34	.15	.14	.37	.80	.03	.21	.11

Appendix 2 (continued).

Species	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP VII																				
Viola purpurea		.01	.02		.02	.02	T	T	.01	T	T	T	T	T						
Lomatium simplex			.01			T		T		T				.02	.02	T	.01	T	T	
Lithospermum ruderale			.01	T		T	.02	.01	T	T	T		T	.01	T		T			
Lathyrus lanszwertii aridus			.32	.15		.18	.48	.41	.40	.18	.80	.15	.01	1.07	.01	T	T			
Antennaria geyeri			.01	.01	T	.01	.01	.02	T	.03	T	.12	T	.01						
Clarkia rhomboidea				.02	.08	.01		.10	T	T				.01	T	T	.01	.01	T	
Stephanomeria lactucina				T	T	T		T	.01		.03	.05	.01	T	T	.01	.11	.03		
Haplopappus bloomeri				T			T	T		T	T	.01	.02	T	.02		.01			
Kelloggia galioides						T	T	T	T	.03	T	.08	.29	.01	T	T	T	T	.14	
Pyrola uliginosa								T	T	T	T	T	T	T	.01	.01	.01	.01	T	
GROUP VIII																				
Penstemon cinereus		T	.08	.05	.17	T	.04	.07	T	T	T		.01							
Aster canescens			T	.01		T	T	T	T	T		T								
Senecio canus			.03	T		T						T								
Silene douglasii			T	T		.01				T										
Lupinus caudatus				.07	.12			T	T	.03	.01									
Castilleja miniata						T	.02	.02	T											
Penstemon speciosus							T	T		T	T	T								
GROUP IX																				
Townsendia florifer		T	T	T		.01	T													
Cryptantha circumscissa		T	T	T		T	T													
Polygonum douglasii		T	T			T														
Chaenactis douglasii				T	T	.01	T													
Tragopogon dubius					.01															
Agropyron spicatum						T														
GROUP X																				
Abies grandis									.0001	.0001	.0001	.0002	.0002	.0002	.0002	.0007	.0004	.0003	.002	.02
Symphoricarpos albus									T	T	T	T	.01	.01			T		.04	.54
Osmorhiza obtusa									T	T	T	T		T			T			.04
Bromus carinatus										.07	T	T								.05
Campanula scourleri											T		T			.91	.44	.01	.03	.02
Pseudotsuga menziesii												.0001		.0001	.0002	.0004	.0003	.0010	.0007	.0030
Pteridium aquilinum pubescens													T	.07	.12	.14	.01	.14	.26	.04
Apocynum androsaemifolium pumilum													.11	T	T	.03	.01	.07	T	.01
GROUP XI																				
Epilobium angustifolium										.07	T	T	.03	.08	.15	.05	.03	.03	.02	
Balsamorhiza careyana										T		T	T	T		T	.04	T	.04	
Ceanothus velutinus										.03	T	.05	.06	.02	.06	.02	.08	.03		
Horkelia fusca										.02	T	T			.02					

Appendix 2 (continued)

	Juoc/ Feid	Pipo/Putr/Feid							Pipo/Arpa-Putr					Pipo/Ceve						Abgr/ Pymy
	1	2	3	5	6	4	7	8	9	11	10	12	13	14	15	17	16	18	19	20
GROUP XI (continued)																				
Phacelia mutabilis											T			T						
Cynoglossum occidentale													T	.01	T	T	.04	T		
Prunus emarginata													.02		T	.01	.03			
Berberis nervosa													T			T	T	T	T	
GROUP XII																				
Arctostaphylos parryana pinetorum									T	.05	T	.01	.03							
Paeonia brownii									T			.01								
Lupinus lepidus										.01	T	T	T							
Madia gracilis											T									
GROUP XIII																				
Pyrola bracteata														T		T	T	T	T	.02
Rosa gymnocarpa														T			T	T	.02	.06
Rubus ursinus															T	.01	.06	T	.02	.12
Pyrola chlorantha															T	T			T	.02
Trientalis latifolia																1.16	T	.68	2.26	1.12
Amelanchier alniflora semintegrifolia																T	T	.05		T
Pinus monticola																	T			.0001
Clintonia uniflora																		T	T	1.68
Pachistima myrsinites																			T	.02
Goodyera oblongifolia																			T	.03
Smilacina racemosa amplexicaulis																			T	.15
Anemone piperi																			T	.09
GROUP XIV																				
Lilium washingtonianum														T	T	.02	.01	T	.01	
Cirsium centaureae														T	.01		.01		.01	
Castanopsis chrysophylla														T	.01	T	.02			
Lupinus leucophyllus														T	T	T	T			
Montia perfoliata depressa															.01	T			T	
Aquilegia formosa																T			T	
Libocedrus decurrens																.0001	T	.0024		
Agoseris glauca																.02				
Equisetum hyemale																			.05	
GROUP XV																				
Linnaea borealis																				.41
Asarum caudatum																				.02
Adenocaulon bicolor																				.45
Corallorhiza maculata																				.01
Galium aparine																				.01
Acer circinatum																				.0001

Appendix 3. Frequency Distribution of Microquadrats Within Plots[1] Along the Environmental Gradient According to Hierarchial Factor Conditions[2]

C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Competition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
												Open (B)													
95%	0"-	Juoc	P	B160	N1	.06																			
			N	B160	N1	.03																			
90%	0"-	Juoc	P	B160	N1	.13																			
			N	B160	N1	.04																			
	0"X	Pipo	P	B160	N1		.01																		
85%	0"-	Juoc	P	B160	N1	.13																			
			N	B160	N1	.07																			
			O	B160	N1	.004																			
		Pipo	P	B160	N1		.01		.01	.03															
80%	0"-	Pipo	P	B160	N1		.01	.01		.01															
			N	B160	N1					.004															
	0"X	Pipo	P	B160	N1		.01			.01															
	0"1	Pipo	P	B160	N1		.05																		
	0"2	Pipo	P	B160	N1			.01		.01															
			P	B160	N1			.03	.01																
	0"3	Pipo	N	B160	N1			.01																	
	0"4	Pipo	P	B160	N1		.01	.01																	
	0"5	Pipo	P	B160	N1		.01		.01																
			N	B160	N1				.004																
75%	0"-	Pipo	P	B160	N1		.03	.01																	
	0"X	Pipo	P	B160	N1		.02			.02															
			N	B160	N1		.004			.004															
	0"1	Pipo	P	B175	N1		.01																		
				B160	N1		.03																		
	0"2	Pipo	P	B160	N1			.01	.008																
			N	B160	N1				.008																
	0"3	Pipo	P	B160	N1			.02	.01																
			N	B160	N1			.01																	
	0"4	Pipo	P	B160	N1		.01	.03																	
	0"5	Pipo	P	B160	N1					.03															
	1/2"5	Pipo	P	B160	N1				.01																
70%	0"-	Pipo	P	B160	N1		.01	.008		.03	.03	.01													
			N	B160	N1			.008				.004													
	0"X	Pipo	P	B175	N1		.01																		
				B160	N1		.04	.01	.02	.04															
				B275	N2		.01																		
			N	B160	N1		.02		.03	.008															
	0"X	Pipo	O	B160	N1				.004																
	0"1	Pipo	P	B160	N1		.01																		
				B175	N1							.01													
	0"2	Pipo	P	B160	N1			.02				.004	.008												
				B250	N2			.01																	
			N	B160	N1			.008				.01	.008												
	0"3	Pipo	P	B160	N1		.01	.09																	
			N	B160	N1			.008																	
	0"4	Pipo	P	B175	N1		.03																		
				B160	N1			.02			.01		.01												
			N	B175	N1		.008																		
				B160	N1			.004					.004												
			O	B175	N1		.004																		
	0"5	Pipo	P	B160	N1		.01	.02		.01							.01								
				B175	N1			.04																	
			N	B175	N1			.004																	
			O	B160	N1			.004																	
	1/4"5	Pipo	P	B160	N1				.01																
65%	0"-	Pipo	P	B160	N1				.03	.008															
			N	B160	N1				.008	.004															
			O	B160	N1				.004	.004															
	0"X	Pipo	P	B160	N1				.05	.01	.01		.01												
				B250	N2				.02																
			N	B160	N1				.008		.004														
				B250	N2				.01																
			O	B250	N2				.004																
	0"1	Pipo	P	B160	N1				.008		.01														
			N	B160	N1				.004																
			O	B160	N1				.004																
	0"2	Pipo	P	B160	N1				.008				.01												
				B250	N2				.01																
			N	B160	N1				.008				.004												
	0"3	Pipo	P	B160	N1				.01	.01	.008		.01												
				B175	N1						.01														
			N	B160	N1						.008														
	0"4	Pipo	P	B175	N1				.01																
				B250	N2				.01																
				B160	N1						.008														
			N	B175	N1				.008																
				B160	N1						.004														
			O	B160	N1						.004														
	0"5	Pipo	P	B160	N1				.02																
				B175	N1					.01						.01									
			N	B160	N1				.02																
				B175	N1											.004									
60%	0"-	Pipo	P	B160	N1					.01		.06													
				B175	N1						.01	.01													
			N	B160	N1							.004													
				B175	N1							.004													
	0"X	Pipo	P	B275	N2					.008															
				B160	N1					.05	.01	.008													
				B175	N1							.01													
			N	B275	N2					.008															
				B160	N1							.004													
			O	B160	N1							.004													
	0"1	Pipo	P	B250	N2					.01															
	0"2	Pipo	P	B160	N1					.01															
	0"3	Pipo	P	B160	N1						.01						.01								
			N	B160	N1												.004								
	0"4	Pipo	P	B160	N1					.008	.01		.01												
			N	B160	N1					.008															
			O	B160	N1						.004														

C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Compe-tition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
60	0"5	Pipo	P	B160	N1					.02		.03													
				B275	N2					.01															
				B175	N1							.01		.01											
			N	B160	N1					.004		.01													
				B175	N1							.004													
	1/4"5	Pipo	P	B160	N1						.01														
55	0"-	Pipo	P	B175	N1						.01														
				B250	N2							.01													
				B160	N1							.01													
	0"X	Pipo	P	B175	N1						.01														
				B160	N1										.008										
			N	B175	N1						.004														
				B160	N1										.004										
			O	B160	N1										.004										
	0"1	Pipo	P	B160	N1						.01		.02												
			N	B160	N1								.004												
	0"2	Pipo	P	B175	N1							.004													
			N	B175	N1							.008													
			O	B175	N1							.004													
	0"3	Pipo	P	B250	N1							.01													
			N	B175	N1								.008												
			O	B175	N1								.008												
	0"4	Pipo	P	B175	N1								.004					.01							
				B160	N1								.01			.008									
				B250	N2									.008											
			N	B175	N1								.01												
				B160	N1											.004		.004							
				B250	N2									.008											
			O	B160	N1								.004			.004									
	0"5	Pipo	P	B160	N1												.02								
				B250	N1								.01												
			N	B160	N1							.01	.004				.008								
			O	B160	N1							.004													
	1/4"5	Pipo	P	B160	N1						.01														
			N	B160	N1						.01														
			O	B160	N1						.008														
	1/2"5	Pipo	P	B160	N1						.01		.01												
			N	B160	N1								.01												
			O	B160	N1						.004		.004												
	1"5	Pipo	N	B160	N1						.01														
50	0"-	Pipo	P	B160	N1							.01													
				B175	N1							.01	.008		.008										
			N	B160	N1							.004													
				B175	N1								.004		.004										
			O	B175	N1								.004		.004										
	0"X	Pipo	P	B275	N2						.02	.02		.008											
				B175	N1								.02												
				B160	N1						.01														
			N	B275	N2						.004	.01	.01	.008											
				B175	N1								.008												
	0"1	Pipo	P	B275	N2									.004		.01									
				B160	N1												.01								
			N	B275	N2									.01		.004									
				B160	N1												.004								
	0"2	Pipo	P	B250	N2							.004													
				B175	N1									.008											
				B275	N2											.01									
			N	B250	N2							.01													
				B175	N1									.004											
				B275	N2											.01									
			O	B175	N1									.004											
	0"3	Pipo	P	B250	N2						.02	.02					.01								
				B275	N2										.01										
			N	B160	N1								.008												
				B250	N2						.01														
			O	B250	N2							.004													
				B160	N1								.008												
	0"4	Pipo	P	B250	N2						.01						.01								
				B175	N1								.008												
			N	B250	N2						.004														
			O	B175	N1								.008												
	0"5	Pipo	P	B160	N1						.01			.01											
				B250	N2							.01		.02		.01	.01								
				B275	N2							.04		.01	.004										
				B175	N1									.01		.01	.01						.008		
			N	B275	N2							.004		.004	.008										
				B250	N2									.02											
				B175	N1									.01		.004			.008				.008		
				B160	N1									.004											
			O	B250	N2									.004		.004									
				B175	N1									.004					.008						
				B275	N2										.004										
	1/4"5	Pipo	P	B160	N1						.008														
			N	B160	N1						.008			.008											
			O	B160	N1									.008											
	1/2"5	Pipo	P	B160	N1						.01								.01						
				B175	N1						.01														
			N	B175	N1						.004														
	1"5	Pipo	P	B160	N1											.008									
			N	B160	N1											.004									
			O	B160	N1											.004									
45%	0"X	Pipo	P	B275	N2								.01												
	0"1	Pipo	P	B250	N2								.01			.008									
			N	B250	N2											.004									
			O	B250	N2								.004			.004									
	0"2	Pipo	P	B275	N2											.008									
				B250	N2												.03								
			N	B275	N2											.004									
			O	B275	N2											.004									
	0"3	Pipo	P	B350	M												.01								
	0"4	Pipo	P	B250	N2									.01	.008										
				B275	N2											.01									
			N	B250	N2									.004	.008										
				B275	N2											.004									

Appendix 3 (continued).

C	D	E	F	G	H	Plots (A)																			
Amt. of Insol.	Amt. of Litter	Type of Litter	Competition	Insol. Seas. Diff.	Insol. Daily Diff.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
45%	0"5	Pipo	P	B160	N1								.01												
				B275	N2									.02			.01	.008							
				B350	M												.01								
				B250	N2												.02								
				B175	N1														.008						
			N	B160	N1								.004												
				B275	N2									.004			.004	.004	.01						
				B350	M												.004								
				B250	N2												.01								
				B175	N1														.004						
			O	B275	N2													.004							
				B175	N1														.004						
	1/4"5	Pipo	P	B250	N2								.01												
	1/2"5	Pipo	P	B250	N2								.008												
			N	B250	N2								.004												
				B275	N2														.008						
			O	B250	N2								.004												
				B275	N2														.008						
40%	0"X	Pipo	P	B275	N2								.004												
				B250	N2									.008											
			N	B275	N2								.02												
				B250	N2									.008											
			O	B275	N2								.008												
	0"1	Pipo	P	B375	N2									.008											
				B275	N2									.01											
			N	B375	N2									.008											
				B275	N2									.004											
	0"2	Pipo	P	B250	N2									.008	.01										
				B275	N2								.01												
			N	B250	N2								.01	.008											
			O	B250	N2								.004												
	0"3	Pipo	P	B250	N2										.02	.01									
				B275	N2											.01		.01							
			N	B250	N2										.008										
	0"4	Pipo	P	B250	N2									.004	.01	.008	.01								
				B275	N2										.01		.01								
			N	B250	N2									.01			.004								
				B275	N2										.004										
			O	B250	N2											.008									
	0"5	Pipo	P	B350	N2									.01				.004	.008						
				B375	N2									.01			.008			.004					
				B275	N2									.05	.03		.008	.03	.004	.01		.004			
			N	B350	N2									.03	.03	.01	.008	.03	.01	.05			.01		
				B375	N2									.004			.008			.01					
				B275	N2									.01	.008		.008	.01	.01	.01		.008		.01	
				B250	N2									.01		.01	.008	.02		.008					
			O	B350	N2													.01	.004						
				B275	N2										.008			.004				.004			
				B250	N2											.004		.004							
	1/4"5	Pipo	P	B250	N2													.01		.01					
				B275	N2															.01			.004		
			N	B250	N2													.01							
				B275	N2																		.008		
			O	B250	N2													.004		.004					
				B275	N2																		.004		
	1/2"5	Pipo	P	B250	N2								.01												
				B350	N2																			.004	
			N	B250	N2								.004												
				B275	N2																			.01	
				B350	N2																			.004	
			O	B350	N2																			.008	
35%	0"-	Pipo	P	B375	N2										.01										
	0"X	Pipo	P	B250	N2											.008									
				B275	N2											.01									
			N	B250	N2											.008									
	0"1	Pipo	P	B275	N2											.02							.004		
			N	B275	N2											.02							.008		
			O	B275	N2											.004							.004		
	0"2	Pipo	P	B275	N2											.01									
	0"3	Pipo	P	B275	N2										.01										
				B375	N2											.004									
			N	B275	N2										.004										
				B375	N2										.008	.01									
			O	B375	N2										.008										
	0"4	Pipo	P	B350	N2										.01								.01		
				B250	N2										.01	.01									
				B275	N2										.04	.02	.008								
				B375	N2										.01										
			N	B350	N2										.004								.004		
				B275	N2										.008	.01	.008								
				B250	N2											.01									
				B375	N2												.008								
			O	B250	N2											.004									
				B375	N2												.008								
	0"5	Pipo	P	B375	N2										.05	.01	.004	.05	.01						
				B250	N2											.01	.01	.004	.04				.004	.01	
				B275	N2												.01	.05	.004			.02			
				B350	N2												.03	.008							
			N	B375	N2										.01	.004	.01	.01							
				B275	N2											.004	.004	.008	.01			.01			
				B250	N2												.004	.01	.03				.02		
				B350	N2												.01	.02							
			O	B275	N2											.01						.01			
				B375	N2													.01							
				B350	N2													.004							
				B250	N2														.02				.008		
	1/4"5	Pipo	P	B275	N2													.01		.04					
				B250	N2													.03		.01					
				B350	N2													.01							
				B375	N2														.004						
			N	B350	N2													.004							
				B375	N2														.01						
				B275	N2															.004			.008		
				B350	N2															.004					

Appendix 3 (continued).

C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Competition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
35%	1/4"S	Pipo	O	B275	N2																		.008		
	1 2"S	Pipo	P	B375	N2										.01			.008							
				B250	N2											.01						.008			
				B275	N2														.008						
			N	B375	N2													.008							
				B275	N2														.008						
				B250	N2																				
			O	B250	N2																	.008		.008	
	1"S	Pipo	P	B375	N2										.01									.008	
				B275	N2													.01							
				B350	N2													.01							
			N	B375	N2										.004										
				B350	N2																		.008		
30%	0"2	Pipo	P	B375	N2																		.01		
	0"S	Pipo	P	B275	N2														.03			.008			
				B250	N2														.004	.02			.01		
				B350	N2														.02	.004	.008	.02			
				B375	N2															.004					
			N	B275	N2														.008			.008			
				B250	N2														.004	.008	.008		.01		
				B350	N2														.03	.01					
				B375	N2															.01					
			O	B275	N2														.008						
				B250	N2														.008				.004		
				B350	N2														.004			.004			
	1/4"S	Pipo	P	B375	N2														.008	.008	.004				
				B350	N2														.008		.004	.008			
				B275	N2															.01					
			N	B375	N2														.004		.01				
				B350	N2														.008		.01	.004			
			O	B375	N2														.004	.008					
				B350	N2																	.004			
	1/2"S	Pipo	P	B250	N2															.01					
				B275	N2																	.004			
				B375	N2																	.008		.008	
				B350	N2																			.008	
			N	B275	N2																	.01			
				B375	N2																	.02		.004	
				B350	N2																			.008	
30%	1/2"S	Pipo	O	B375	N2																	.008		.004	
				B275	N2																	.004			
		Abgr	N	B350	N2																			.01	
			O	B350	N2																			.004	
	1"S	Pipo	P	B375	N2														.01						
			N	B375	N2														.02						
25%	0"2	Pipo	P	B350	N2																		.008		
			N	B350	N2																		.004		
			O	B350	N2																		.004		
	0"4	Pipo	P	B350	N2																		.008		
			N	B350	N2																		.008		
	0"S	Pipo	P	B350	N2															.01	.05	.02	.03	.01	
				B375	N2															.05	.10	.04			
					Nt																.01				
				B450	N2																.008				
			N	B350	N2															.004	.05	.02	.008		
				B375	N2																.03	.04		.02	
					Nt																.004				
				B450	N2																.008				
			O	B350	N2																.02	.004	.008		
				B375	N2																.03	.01		.008	
	1/4"S	Pipo	P	B350	N2															.06		.01			
					Nt																	.01			
				B350	N2															.06		.01			
				B450	Nt																.004				
			N	B375	N2															.01	.008				
					Nt																	.004			
				B350	N2															.01		.01			
				B450	Nt																.008				
			O	B375	N2																.008				
				B450	Nt																.004				
				B350	N2																	.008			
	1/2"S	Pipo	P	B350	N2															.01	.008	.01		.004	
				B375	N2																	.01		.02	
					M																			.004	
			N	B350	N2															.004	.008				
				B375	N2																			.008	
					M																			.008	
			O	B375	N2																			.004	
					M																			.004	
				B350	N2																			.01	
	1"S	Pipo	P	B375	N2															.01			.01	.02	
				B350	N2																.01	.01			
			N	B350	N2																	.004			
				B375	N2																		.004	.008	
			O	B350	N2																.004			.004	
	1-1/2"S	Pipo	P	B375	N2																			.008	
			N	B375	N2																			.004	
			O	B375	N2																			.004	
	2"S	Pipo	P	B375	N2																.01			.01	
				B350	N2																	.004			
			N	B375	N2																.004				
				B350	N2																.01	.004			
			O	B350	N2																	.008			
				B375	N2																			.004	
20%	0"S	Pipo	P	B375	N2																		.008		
					A																			.008	
				B350	Nt																		.004		
					N2																		.02		
				B450	Nt																		.008		
			N	B375	N2																		.008		
					A																			.004	

Appendix 3 (continued).

C	D	E	F	G	H	Plots (A)																			
Amt. of Insol.	Amt. of Litter	Type of Litter	Compe-tition	Insol. Seas. Diff.	Insol. Daily Diff,	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
20%	0"5	Pipo	N	B350	Nt																		.01		
					N2																		.008		
				B450	Nt																		.01		
			O	B350	Nt																		.004		
				B450	Nt																		.01		
				B375	N2																			.004	
	1/4"5	Pipo	P	B350	N2																		.01		
	1/2"5	Pipo	P	B375	Nt																		.008		
					N2																			.02	
				B350	Nt																		.004		
					N2																			.01	
				B475	Nt																		.008		
				B450	Nt																		.008		
				B4<50	Nt																		.008	.004	
			N	B375	Nt																		.008		
					N2																			.008	
				B350	Nt																		.01		
					N2																			.01	
				B475	Nt																		.008		
				B450	Nt																		.008		
				B4<50	Nt																		.004	.004	
			O	B375	N2																			.004	
				B4<50	Nt																		.004	.008	
	1"5	Pipo	P	B375	N2																			.008	
			N	B375	N2																			.01	
			O	B375	N2																			.01	
	2"5	Pipo	P	B375	N2																			.01	
			N	B375	N2																			.01	
			O	B375	N2																			.004	
		Abgr	N	B375	N2																			.008	
			O	B275	N2																			.008	
15%	0"3	Psme	P	B475	Nt																				.02
			N	B475	Nt																				.01
10%	0"3	Psme	P	B475	Mt																				.01
			N	B475	Mt																				.004
	0"5	Psme	P	B475	Nt																				.01
					Mt																				.01
					At																				.01
			N	B475	Nt																				.02
					Mt																				.004
					At																				.02
			O	B475	Nt																				.004
					At																				.008
	1/2"5	Psme	P	B475	Nt																				.02
				B450	At																				.004
			N	B475	Nt																				.008
				B450	At.																				.01
10%	1/2"5	Psme	O	B475	Nt																				.004
	1"5	Psme	P	A4	Nt																				.01
				B475	Nt																				.02
				B4<50	Nt																				.008
			N	A4	Nt																				.008
				B475	Nt																				.02
				B4<50	Nt																				.008
			O	A4	Nt																				.01
	1-1/2"5	Psme	P	B475	Nt																				.02
			N	B475	Nt																				.004
			O	B475	Nt																				.008
	2"5	Psme	P	A4	Nt																				.01
												Tree													
15%	1/4"5	Juoc	P	B450	Mt		.004																		
			N	B450	Mt		.008																		
			O	B450	Mt		.004																		
	1/2"5	Juoc	N	None	None	.01																			
	1"5	Juoc	P	A4	At	.01																			
				D4	At	.004																			
				B450	Mt		.01																		
			N	D4	At	.01																			
				B450	Mt		.004																		
		Pipo	P	B450	At		.008																		
					Nt						.01	.008													
				B475	Nt				.01		.01														
					Mt						.004														
				A4	Nt			.01																	
			N	B450	At		.008																		
					Nt						.01	.004													
				B475	Nt						.004														
					Mt						.004														
			O	B450	Nt						.008	.004													
				B475	Nt						.008														
	1-1/2"5	Pipo	P	B475	Nt				.004																
				B450	Nt					.008															
			N	B475	Nt				.004			.004													
				A4	Nt							.004													
			O	B475	Nt				.008			.01													
				B450	Nt					.008															
				A4	Nt							.008													
	2"5	Pipo	P	B475	Nt				.01	.004															
					Mt			.008																	
				B450	Nt					.008															
					Mt					.008															
			N	B475	Nt		.01			.004		.008													
					Mt			.008																	
				B450	Nt					.004															
					Mt					.004															
			O	B475	Nt		.004			.008		.008													
				B450	Nt					.004															
					Mt					.004															
10%	0"5	Pipo	P	B475	Nt			.004																	
			N	B475	Nt			.008																	
			O	B475	Nt			.004																	
	1/4"5	Juoc	N	A4	Nt	.01																			
		Pipo	P	B450	At		.008																		

Appendix 3 (continued).

C	D	E	F	G	H	Plots (A)																			
Amt. of Insol.	Amt. of Litter	Type of Litter	Compe-tition	Insol. Seas. Diff.	Insol. Daily Diff.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
10%	1/4"5	Pipo	N	B450	At		.008																		
	1/2"5	Juoc	P	A4	At	.01																			
				None	None	.02																			
			N	None	None	.008																			
		Pipo	P	A4	Nt								.08												
			N	B450	Nt		.01																		
				A4	Nt								.004												
			O	B450	Nt		.004																		
		Abgr	P	B450	Nt																				.01
	1"	Juoc	P	A4	At	.03																			
					Mt	.04																			
				B475	At	.01																			
				B375	At	.01																			
				None	None	.02																			
			N	B475	Mt		.01																		
				A4	Mt	.004																			
				None	None	.02																			
			O	None	None	.004																			
		Pipo	P	A4	Mt		.008																		
					Nt			.01																	
				B475	Nt		.008		.01	.004			.01												.02
				B450	Nt			.01			.01														
				B4<50	Nt			.008			.004														
			N	A4	Mt		.008																		
				B475	Nt		.008			.01			.004												.004
					At		.008																		
					Mt			.01																	
	1"5	Pipo	N	B4<50	Nt				.004		.01														
				B450	Nt						.01														
			O	B475	Mt			.004																	
					Nt		.008																		
				B4<50	Nt				.004																
		Abgr	P	B475	Nt																				.02
			N	B475	Nt																				.004
			O	B475	Nt																				.008
		Psme	P	A4	Mt																				.004
			N	A4	Mt																				.01
	1-1/2"5	Pipo	P	A4	Nt							.004		.01											
				B450	Nt				.02	.01															
					Mt						.01														
			N	A4	Nt							.008													
				B450	Nt				.01	.02															
			O	A4	Nt							.004													
	2"5	Pipo	P	A4	Mt								.004												
					Nt																				.008
				B475	Nt				.01	.004		.01	.008												
				B450	At				.01			.008													
					Nt			.01		.008	.01	.004													
					Mt								.01												
			N	A4	Nt				.01		.01														.008
					Mt						.01		.01												
					At							.01													
				B475	Nt					.01	.008	.004													
				B450	Nt			.01		.008		.008													
					At							.008													
			O	A4	At								.004												
					Nt				.004																
				B475	Nt						.008		.008												
				B450	Nt			.004				.004													
		Abgr	N	B475	Nt																				.008
			O	B475	Nt																				.008
5%	0"5	Pipo	P	A4	Nt														.01	.01					
					At												.004								
				B475	At										.01										
			N	A4	Nt							.01							.004						
					At												.01								
				B450	Mt											.008									
			O	A4	Nt							.01													
				B450	Mt											.008									
	1/4"5	Juoc	P	B450	Nt		.008																		
			N	B450	Nt		.008																		
	1/2"5	Juoc	P	B475	Mt	.01																			
				B450	At	.01																			
				B4<50	Nt	.01																			
					Mt		.004																		
			N	B4<50	Nt	.004																			
					Mt		.01																		
		Pipo	P	A4	At									.008				.01	.02						
					Mt					.01															
				B475	Nt				.008																
					At										.01										
			N	A4	At									.004					.008						
				B475	Nt				.008																
					At										.004										
			O	A4	At									.004											
	3/4"5	Pipo	N	None	None		.004																		
			O	None	None		.01																		
	1"5	Juoc	P	B450	Mt		.01																		
				B475	Nt	.01																			
				A4	At	.01																			
					Mt	.01																			
				None	None	.06	.01																		
			N	B450	Mt		.02																		
				None	None	.01																			
		Pipo	P	A4	Nt			.004	.01	.02	.004	.01													
					Mt								.01		.03										
				B475	At										.01										
					Mt										.008	.008	.008								
					Nt							.01				.008									

Appendix 3 (continued)

C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Competition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
5%	1"S	Pipo	P	B450	Mt											.01									
					Nt			.004			.004		.004												
				None	None										.01										
			N	A4	At							.008													
					Nt		.01	.01	.008	.01	.008	.004					.008								
					Mt								.004												
				B475	Mt			.01							.004	.008	.008								
					Nt							.004				.008									
				B450	Nt			.004			.008	.004	.004												
				None	None										.004										
			O	A4	Nt				.004				.004				.008								
					At							.008													
				B475	Mt			.004							.004										
				B450	Nt			.008			.004	.01	.008												
		Abgr	P	A4	Mt													.01							
			N	A4	Nt															.01					
			O	A4	Nt															.004					
	1-1/2"S	Juoc	P	A4	Nt		.004																		
			N	A4	Nt		.01																		
		Pipo	P	A4	At				.02					.02											
					Nt				.02	.004		.004													
				B475	Nt			.01		.01															
					Mt												.008								
				B450	Nt				.01	.01							.01								
					At				.008							.008									
			N	A4	Nt				.008	.008		.008													
					At				.008					.004											
				B475	Nt			.004		.004															
					Mt												.008								
				B450	Nt				.004							.01	.01								
					At				.008					.008		.008									
				None	None		.01																		
			O	A4	At				.004																
					Nt					.004		.004													
				B450	Nt					.004						.004	.008								
					At									.008											
		Abgr	P	A4	At													.01							
	2"S	Pipo	P	A4	Nt				.004			.008	.008					.004							
					At						.02		.01												
				B475	Nt							.01		.008											
					Mt						.01		.008												
					At								.01												
				B450	Nt				.004	.004			.004	.01	.01										
					At								.004												
					Mt			.01				.004	.004												
5%	2"S	Pipo	P	B4<50	Nt				.008																
					Mt								.004												
				None	None				.01																
			N	A4	Nt			.01	.01			.01	.004	.008				.01							
					Mt		.008																		
					At					.01	.01		.01												
				B475	Mt						.02		.008												
					Nt							.01	.008	.008											
				B450	At								.01												
					Nt				.01	.004			.01	.008											
					Mt			.01				.008	.02												
				B4<50	Nt				.008					.008											
					Mt								.01												
			O	A4	Nt			.01				.008	.004	.008											
					At				.004		.008		.004												
					Mt		.008																		
				B475	Mt						.01														
					Nt								.008												
				B450	Mt			.008				.004	.008												
					Nt					.008															
				B4<50	Nt																				
	2-1/2"S	Pipo	P	None	None									.01						.004					
			N	None	None															.01					
0%	0"S	Juoc	N	A4	Mt			.008																	
			O	A4	Mt			.04																	
		Pipo	P	A4	Mt														.01	.01					
					Nt																.01				
			N	A4	Mt															.004					
			O	A4	Nt																.004				
					Mt														.004						
		Psme	P	None	None															.01					
	1/2"S	Juoc	P	None	None	.008																			
			N	None	None	.008																			
		Pipo	P	A4	Mt													.01			.01				
					Nt										.04		.01								
				None	None					.004					.01			.01							
			N	A4	Nt									.01	.008										
				None	None					.01					.004			.004							
		Psme	P	None	None														.01						
		Abgr	P	None	None														.008	.008		.008			
			N																.004	.004				.01	
			O																.004	.004		.008			
	3/4"S	Pipo	P	A4	Nt													.01							
			N	B450	Mt		.01																		
	1"S	Juoc	N	B475	Mt	.01																			
				None	None		.01																		
		Pipo	P	A4	Mt			.008					.01			.02			.02	.01	.01		.008		
					Nt			.02				.004		.01		.008	.05	.01	.01				.01		
					At											.02									
				B450	Nt					.008					.01										
					At										.03										
				D4	Nt								.004												
				None	None		.01	.004	.008			.004		.004	.05	.05		.03	.004		.004				
			N	A4	Mt		.01	.004		.01			.01	.01		.008			.02				.03		

Appendix 3 (continued)

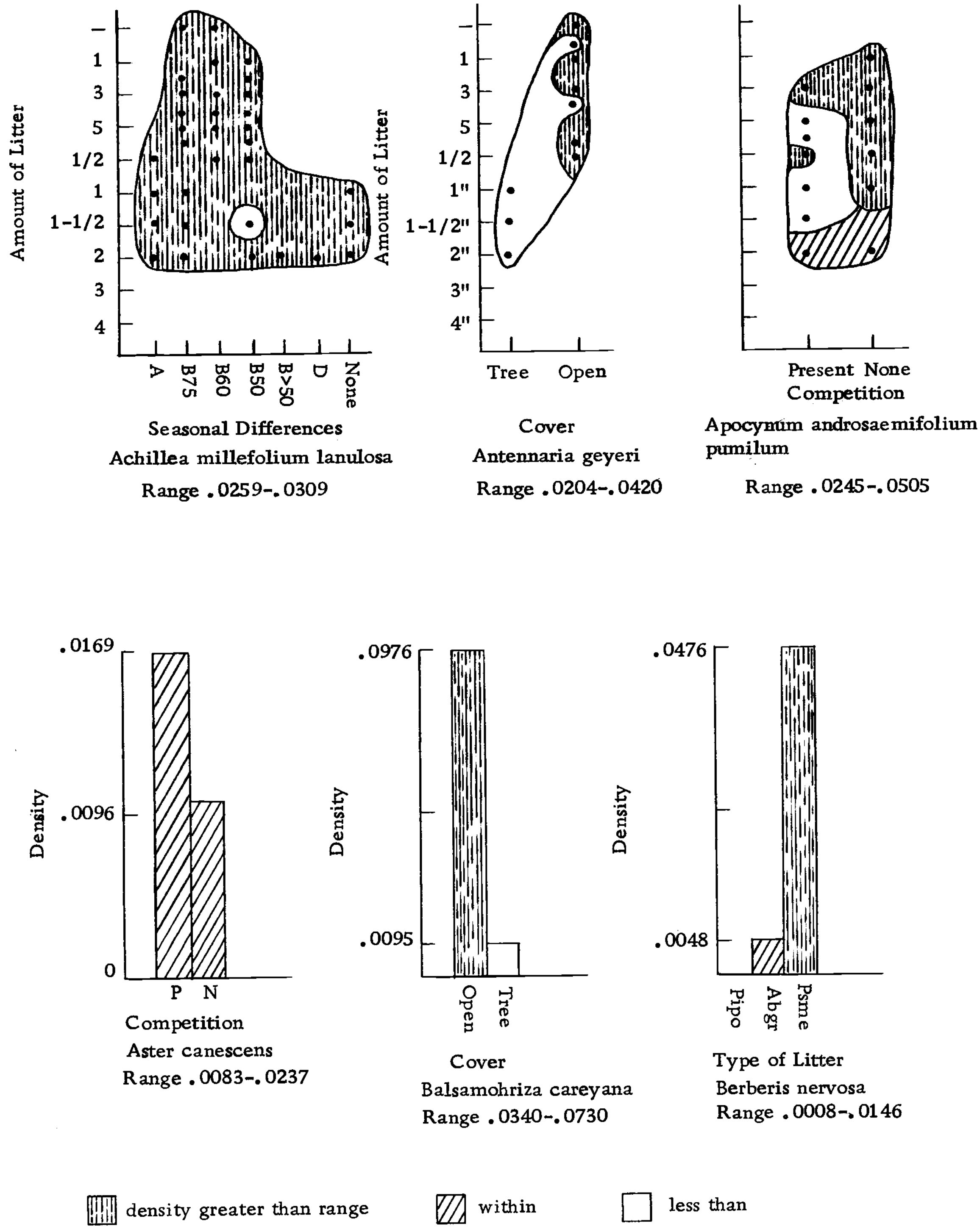
C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Compe- tition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0%	1"5	Pipo	N	A4	Nt			.01				.01				.01			.01						
					At											.01									
				B450	Nt					.008															
				D4	Nt								.008												
				None	None		.004	.008	.008			.008			.008	.01	.02		.01		.004		.01		
			O	A4	Mt		.004	.004					.004												
					Nt			.008						.004		.01							.004		
				D4	Nt								.004												
				None	None			.004				.004		.01	.008			.004			.008		.004		
		Cach	P	None	None																.01				
		Psme	P	A4	Mt														.01	.01			.01		
					At																	.01			
				B450	Nt															.004					
				None	None													.01	.01		.008	.05	.004		
			N	A4	Mt														.004				.01		
				B450	Nt															.004					
				None	None													.004			.008	.01	.008		
			O	B450	Nt															.008					
				None	None																		.004		
		Abgr	P	A4	Mt															.02				.01	
					At														.02	.01					
					Nt																.01				
				B450	Mt													.01							
				None	None												.01	.004		.05	.01	.02		.02	
			N	A4	Mt															.01	.004			.01	
					At														.008						
				None	None												.01	.008		.01	.004	.004		.004	.008
			O	A4	Mt																			.004	
				None	None												.008	.004		.008		.008			.008
	1-1/2"5	Juoc	N	A4	Nt		.01																		
		Pipo	P	A4	Mt					.004															
					Nt					.004		.004		.004		.02	.02				.008				
					At												.02								
				B475	Mt												.01								
				B450	At				.01								.01								
				None	None									.004	.02	.01	.01	.008							
			N	A4	Nt		.01	.008		.004		.008		.01		.02	.004				.01				
					At												.004								
					Mt					.01															
				B450	At				.004																
				None	None					.01				.004	.008	.01	.008	.008							
			O	A4	Nt			.008		.008		.004				.004				.004	.004				
				None	None									.008		.004	.008								
		Abgr	P	None	None												.02		.01		.008	.008			
			N	None	None												.02		.01		.008	.02			
			O	None	None												.02		.004						
		Psme	P	None	None																.004	.01			
			N	None	None																.01	.004			
	2"5	Juoc	N	None	None		.004																		
			O	None	None		.004																		
		Pipo	P	A4	Nt					.004	.01		.05	.05			.008				.01			.01	
					At					.008	.02	.004		.01											
					Mt		.004	.01	.01	.004		.004		.03	.01	.008	.008		.008					.01	
				B475	Mt						.008														
				B450	Mt				.004		.01														
					At						.008														
				D4	Mt								.008												
				None	None			.02	.004	.008		.02		.02	.09	.04	.01				.01		.01	.01	
			N	A4	At		.004	.01		.004	.01						.004								
					Nt			.008	.004	.02	.004	.01	.05	.02		.02					.004				
					Nt			.004		.004		.008				.004	.004		.02					.004	
				B475	Mt						.004														
				B450	Mt						.01		.01												
					At						.008														
				D4	Mt								.008												
				None	None		.008	.02	.02	.008	.008	.02		.02	.03	.02							.004		
			O	A4	At		.01	.004		.004	.008						.01								
					Mt		.01			.008				.01		.004	.004								
					Nt			.08	.01			.01	.01	.02		.02	.008								
				B475	Mt						.004														
				B450	Mt				.01		.004														
				None	None		.008	.01	.008	.01	.02	.008		.03	.004	.01									
		Psme	P	A4	At															.004				.01	
					Mt														.01				.02		
					Nt																		.01		
				None	None														.02		.02	.12	.12	.03	
			N	A4	At															.008				.004	
					Mt														.004				.02		
					Nt																		.004		
				None	None														.008		.03	.03	.10	.01	.004
			O	A4	Mt																		.004		
					At															.004					
				None	None														.004		.008	.004	.01		.01
		Abgr	P	A4	Nt																			.02	
					Mt															.01				.03	
				D4	At																.004				
				None	None												.004	.12	.04	.06	.06	.08	.008	.03	.01
			N	A4	Mt													.004							
					Nt																			.004	
					At																			.02	
				D4	At																.01				
				None	None												.01	.06	.05	.01	.07	.02	.01	.02	.09
			O	A4	Mt													.01							
					At																			.008	
				None	None												.01	.02	.01	.03	.01	.008	.008	.008	.07

Appendix 3 (continued).

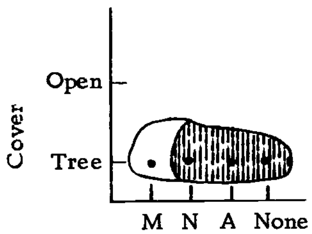
C Amt. of Insol.	D Amt. of Litter	E Type of Litter	F Competition	G Insol. Seas. Diff.	H Insol. Daily Diff.	Plots (A) 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0·.	2-1 '2"5	Abgr	P	None	None															.004					
			N	None	None															.03				.02	
			O	None	None															.01				.008	
		Pipo	N	A4	Mt																			.01	
	3"5	Abgr	P	A4	Mt																			.008	
				None	None																.008	.008		.004	.05
	3"	Abgr	N	A4	Mt																			.008	
					At																			.02	
				None	None															.004	.02	.02		.01	.09
			O	A4	At																			.01	
				None	None															.01	.004	.004		.01	.06

[1] 240 microquadrats sampled in the open and underneath the tree for each plot

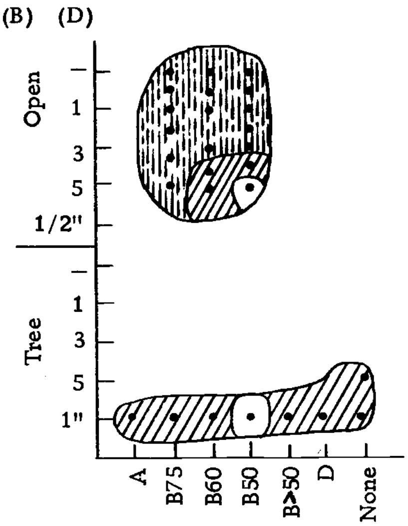
[2] Description of classes of hierarchial factors (tree cover, amount of insolation, amount of litter, type of litter, competition, seasonal differences in insolation and daily differences in insolation) are shown in Table II.



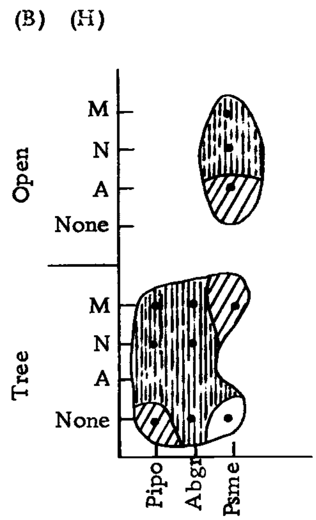
Appendix 4. Density Distribution of Understory Species in Relation to Factors which were Shown Significant by Hierarchial Classification Analysis. (Range = confidence interval for species density)



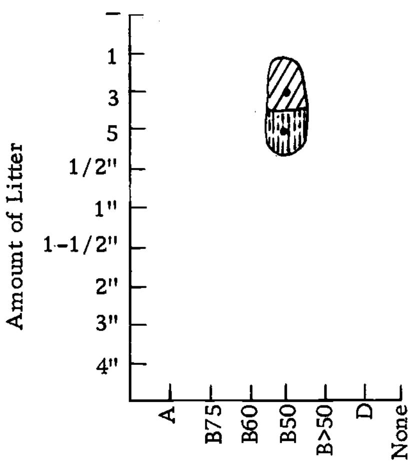
Daily Differences
Bromus carinatus
Range .0209-.0317



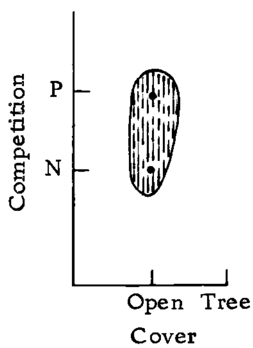
Seasonal Differences
Bromus tectorum
Range .1071-.1585



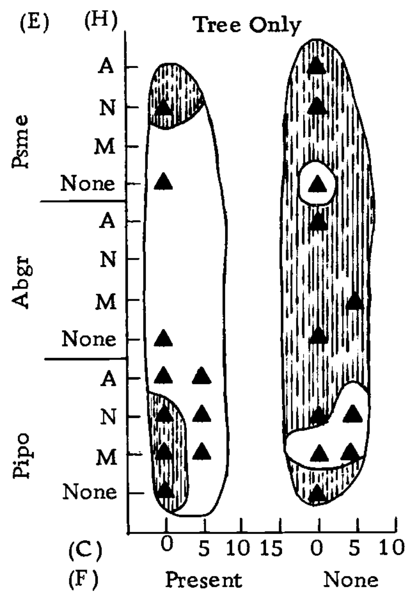
Type of Litter
Companula scouleri
Range .1827-.3423



Seasonal Differences
Castilleja miniata
Range .0000-.0146

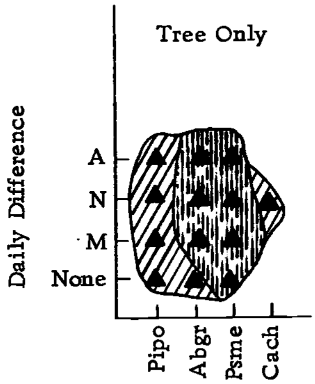


Chaenactis douglasii
Range .0116-.0404

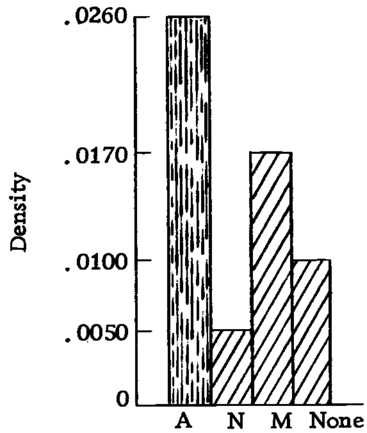


Chimaphila menziesii
Range .0454-.0736

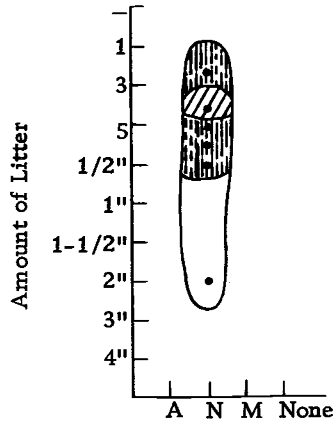
Appendix IV (continued)



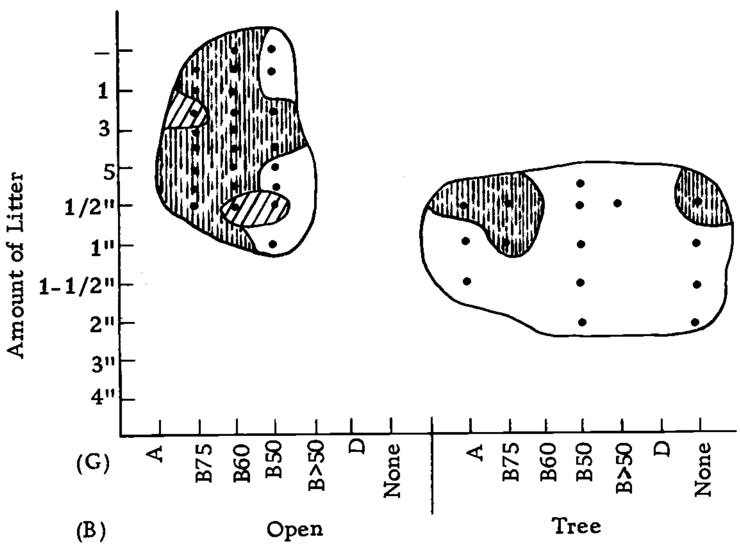
Type of Litter
Chimaphila umbellata
Range .0000-.3992



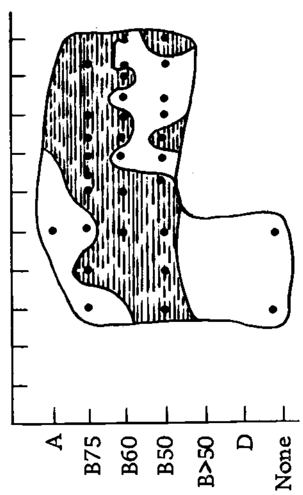
Daily Difference
Chrysothamnus viscidiflorus
Range .0015-.0170



Daily Difference
Clarkia rhomboidea
Range .0216-.0592

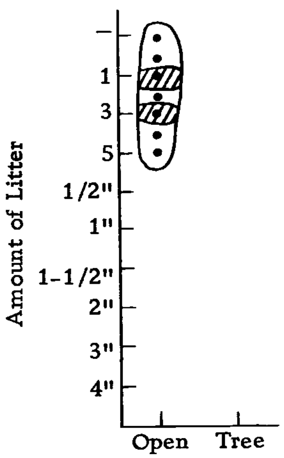


Collinsia parviflora
Range .4123-.5667

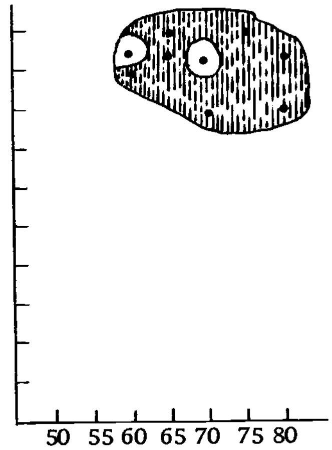


Seasonal Difference
Collomia grandiflora
Range .0625-.0867

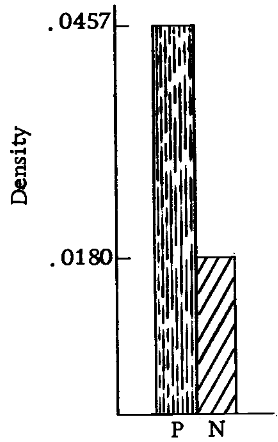
Appendix IV (continued)



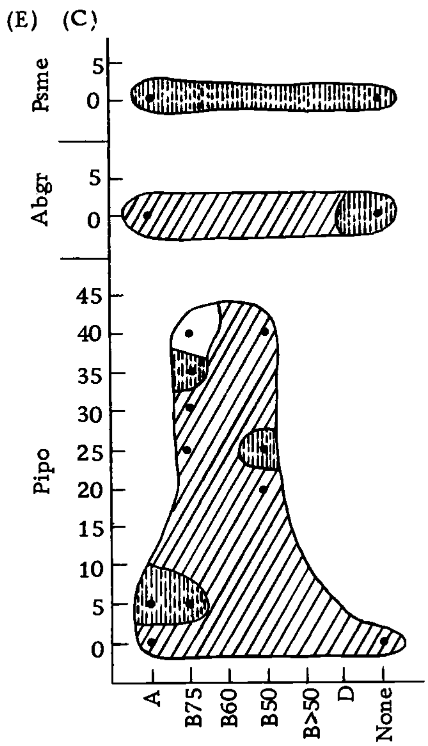
Cover
Cryptantha ambigua
Range .1831-.3321



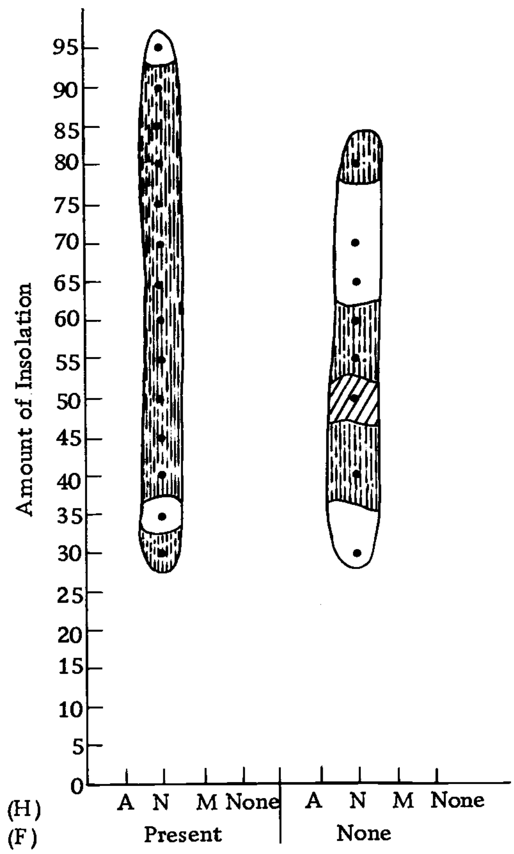
Amount of Insolation
Cryptantha circumscissa
Range .0218-.0450



Competition
Cynoglossum occidentale
Range .0068-.0222

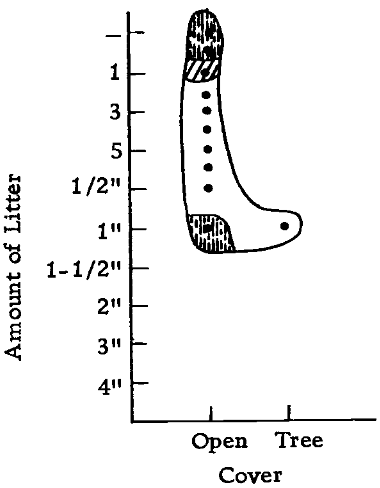


Seasonal Difference
Epilobium angustifolium
Range .0186-.0488

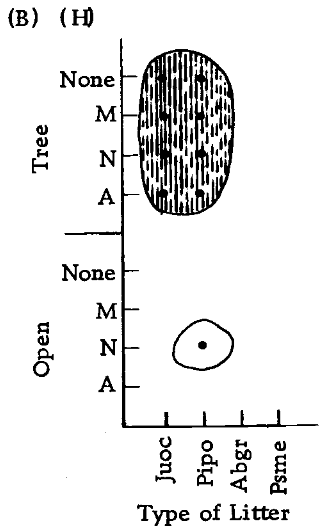


Eriogonum umbellatum
Range .0659-.0745

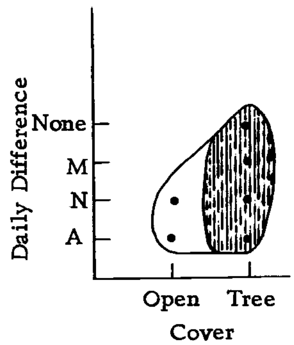
Appendix IV (continued)



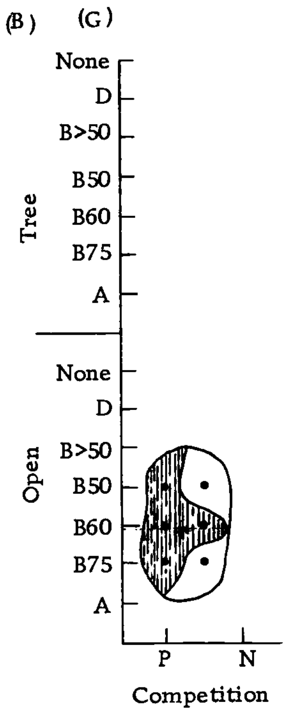
Eriophyllum lanatum
Range .0901-.1179



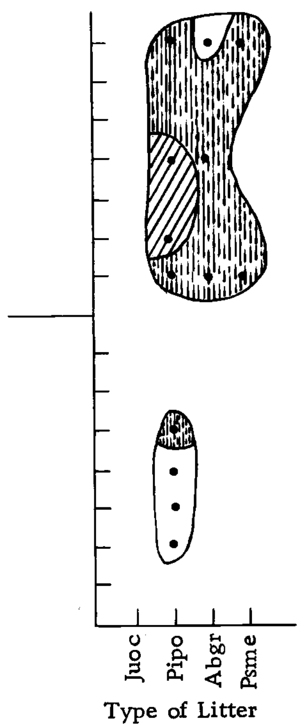
Festuca idahoensis
Range .2060-.2580



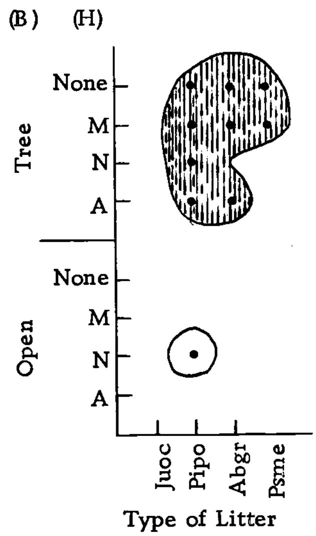
Fragaria virginiana
Range .3503-.4377



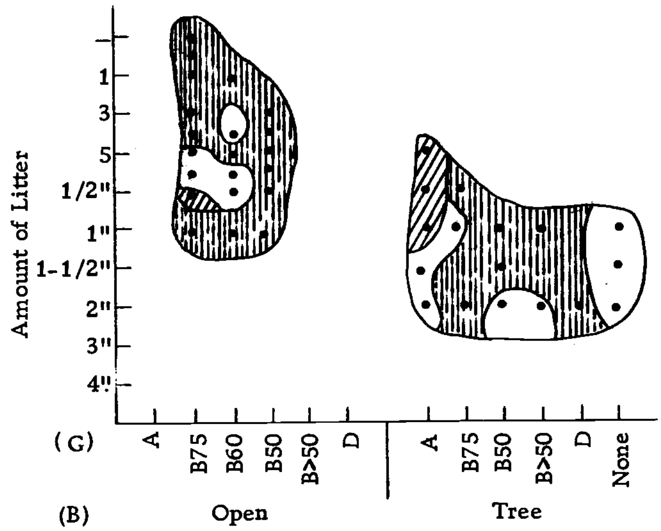
Gayophytum nuttallii
Range .1753-.2263



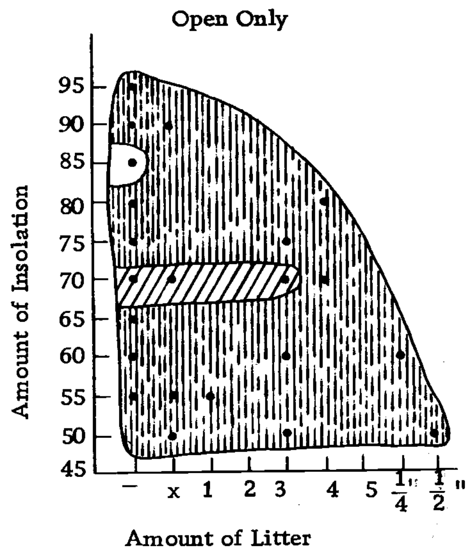
Hieracium albiflorum
Range .0307-.0501



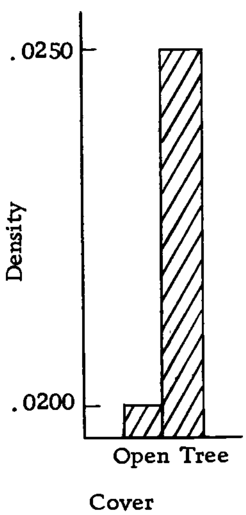
Kelloggia galioides
Range .1717-.1789



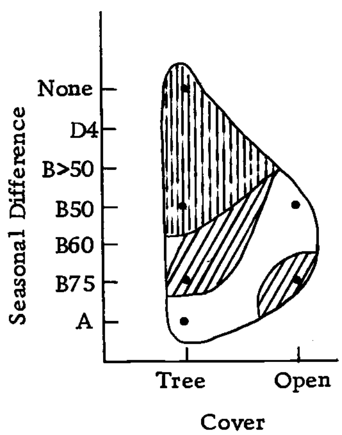
Lathyrus lanswertii aridus
Range .1591-.2311



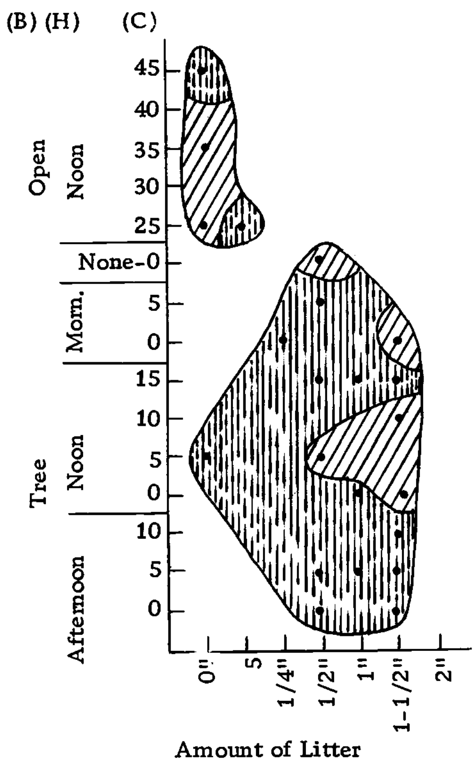
Leucocrinum montanum
Range .0000-.0515



Lilium washingtonianum
Range .0012-.0258

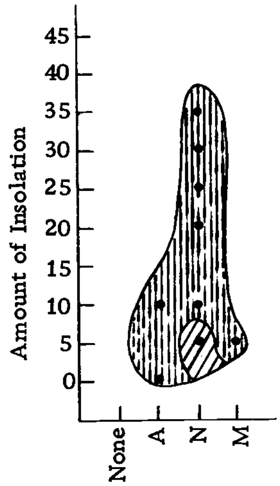


Linum perenne
Range .0207-.0293

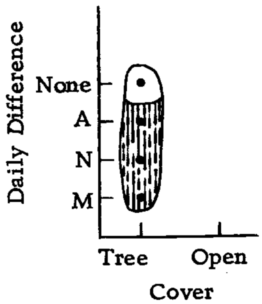


Lithospermum ruderale
Range .0077-.0385

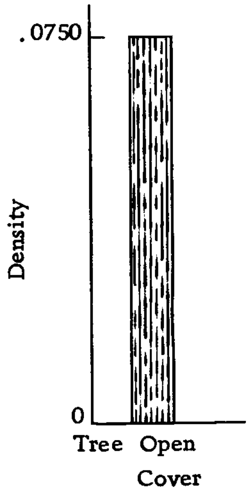
Appendix IV (continued)



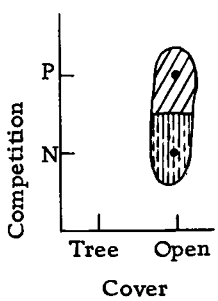
Daily Difference
Lomatium simplex
Range .0093-.0251



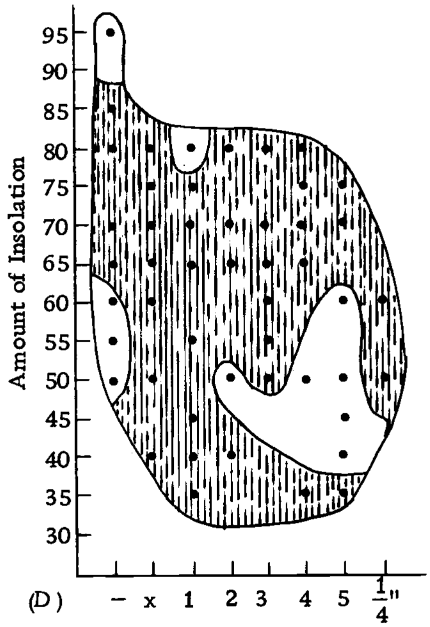
Lupinus caudatus
Range .0570-.0996



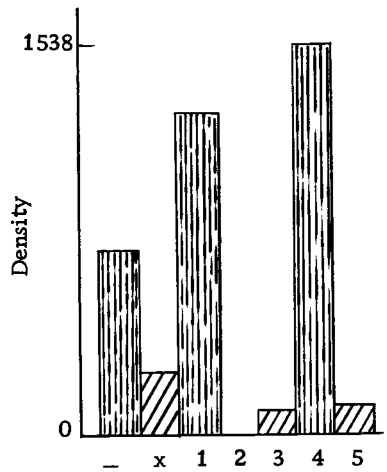
Lupinus lepidus
Range .0221-.0529



Lupinus leucophyllus
Range .0011-.0113

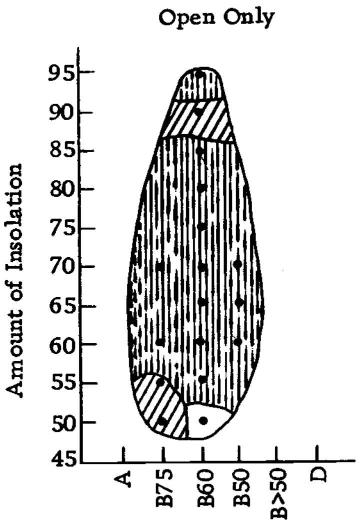


(B) Open Only
Madia Minima
Range .0861-.0993

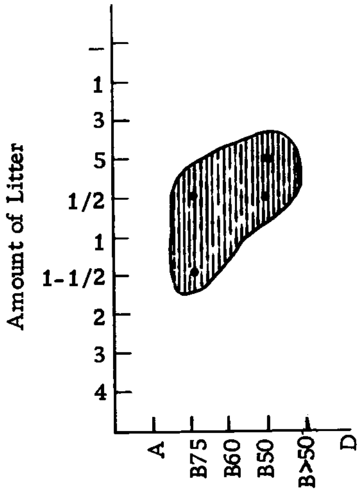


Amount of Litter
Microsteris gracilia
Range .0053-.0185

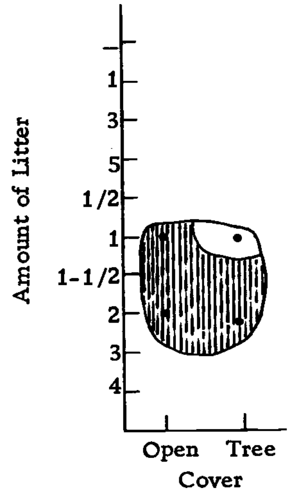
Appendix IV (continued)



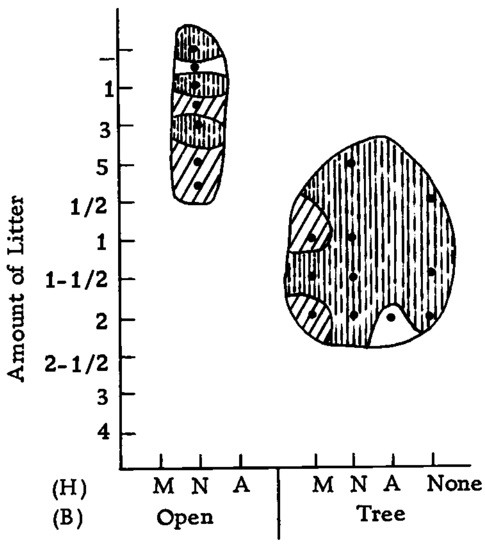
Seasonal Difference
Mimulus nanus
Range .2461-.3903



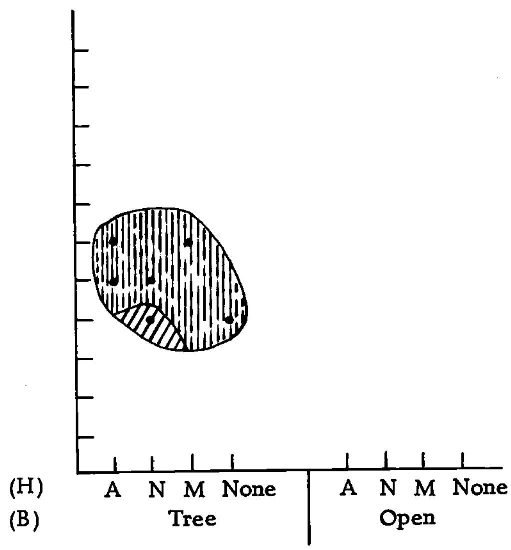
Seasonal Difference
Montia perfoliata
Range .0002-.0248



Osmorhiza obtusa
Range .0039-.0141

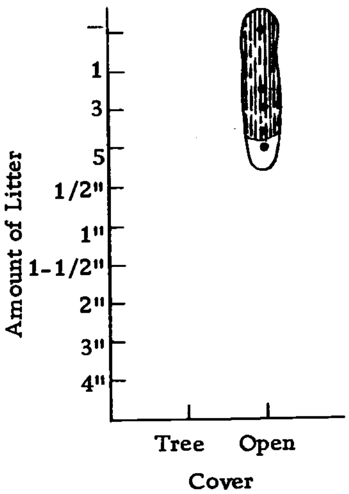


Penstemon cinereus
Range .0288-.0498

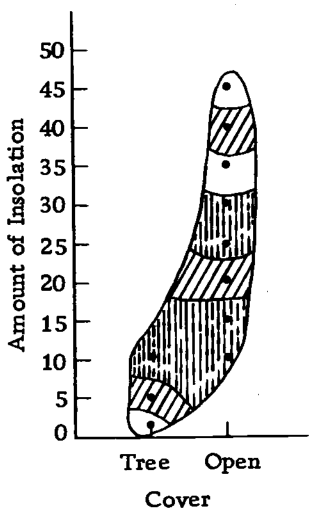


Penstemon speciosus
Range .0091-.0425

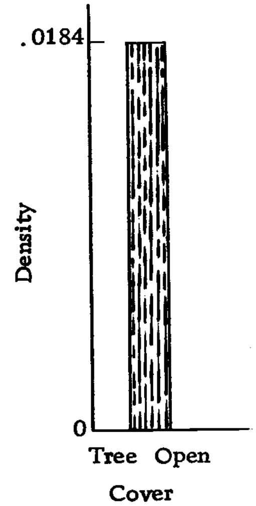
Appendix IV (continued)



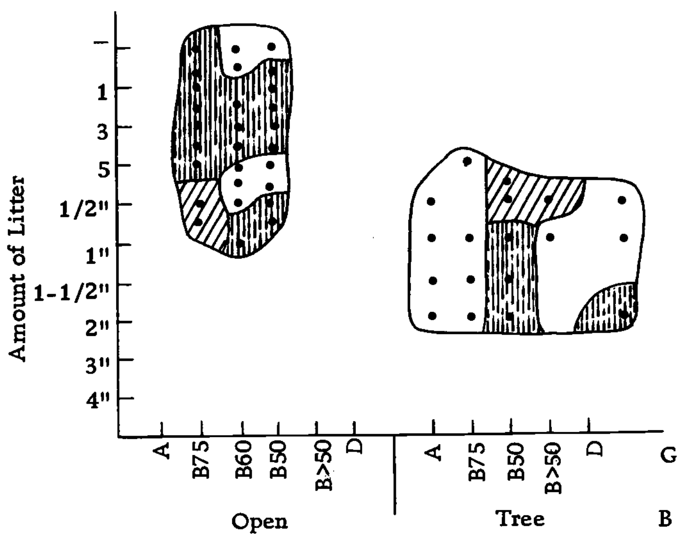
Polygonum douglasii
Range(.0018-.0342)



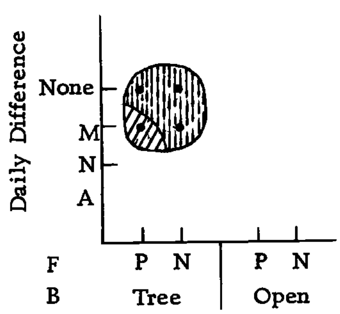
Pteridium aquilinum
Range .0950-.1434



Pterospora andromedea
Range .0040-.0140

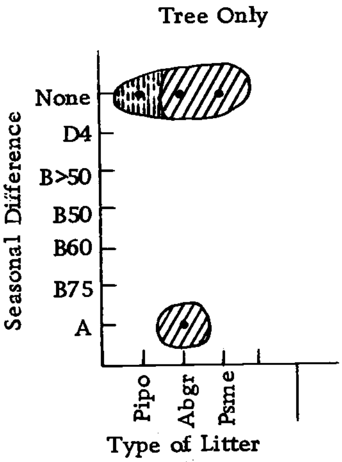


Purshia tridentata
Range .1587-.2719

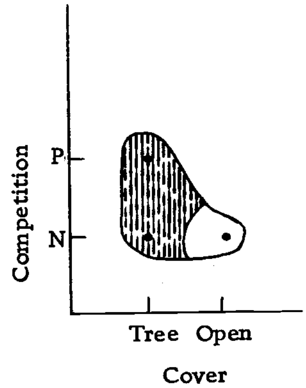


Pyrola braceteata
Range .0307-.0719

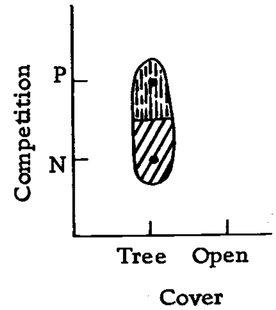
Appendix IV (continued)



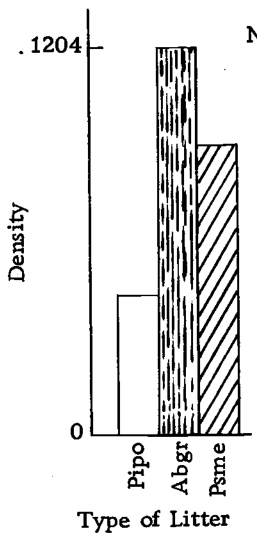
Pyrola chlorantha
Range .0053-.0259



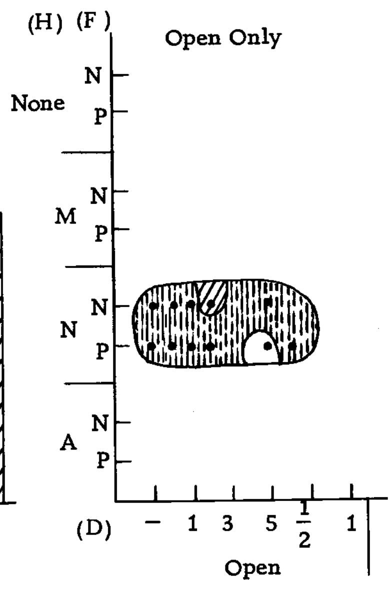
Pyrola uliginosa
Range .0397-.0653



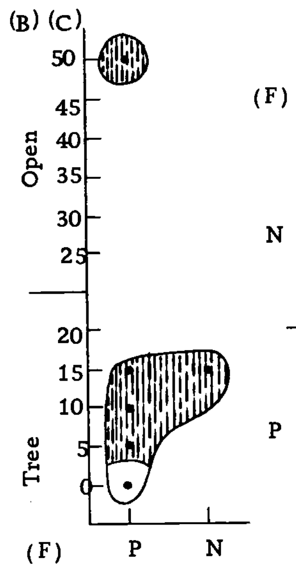
Rosa gymnocarpa
Range .0048-.0264



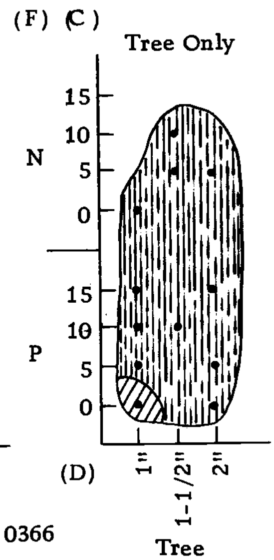
Rubus ursinus
Range .0566-.1022



Scutellaria nana
Range .1808-.3362

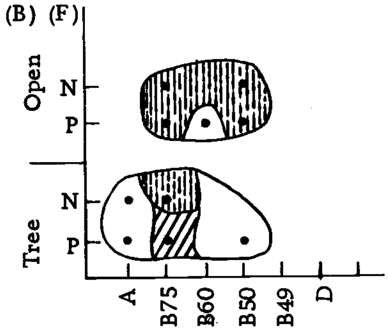


Senecio canus
Range .0346-.0366

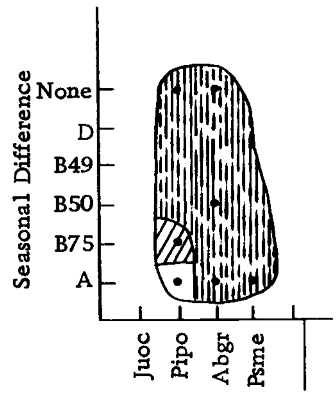


Silene douglasii
Range .0090-.0346

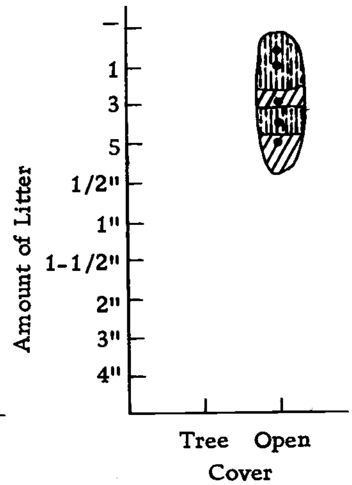
Appendis IV (continued)



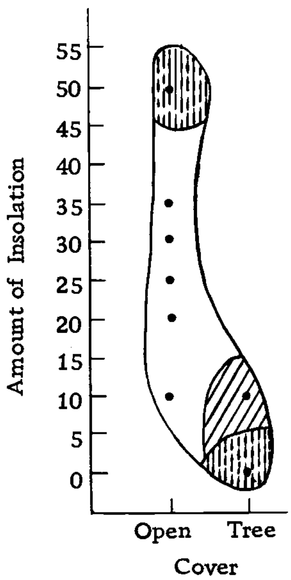
Seasonal Difference
Stephanomeria lactucina
Range .0214-.0368



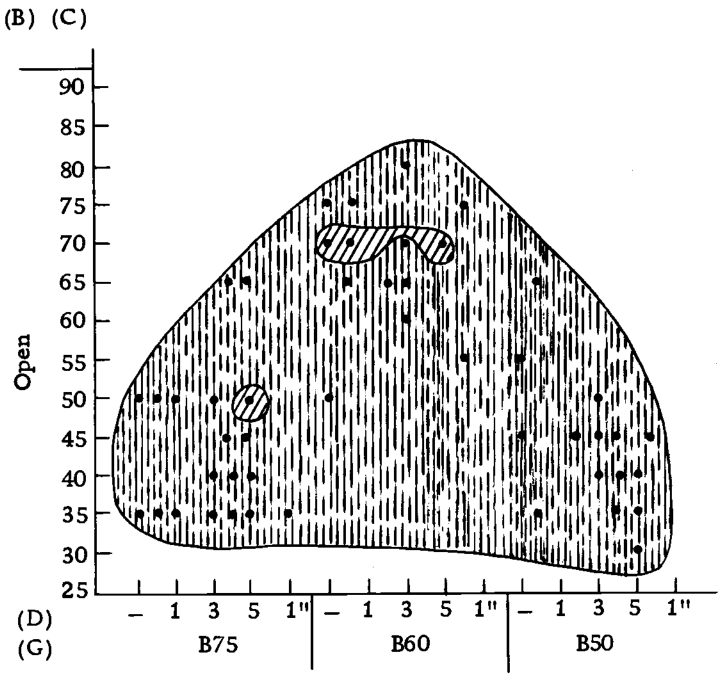
Type of Litter
Symphoricarpos albus
Range .0142-.0326



Townsendia florifer
Range .0086-.0280



Trientalis latifolia
Range .6237-.6463



Viola purpurea
Range .0389-.0645

Appendix IV (continued)

Appendix 5

Scientific names, authorities, abbreviations, and life forms of species and species groups cited in tables and text.

Life forms are modified from those defined by Raunkiaker (1934)

Symbol	Life Form Description
P	Phanerophytes: the perennating buds or shoot apices borne on aerial shoots.
C	Chamaephytes: Perennating buds or shoot apices borne very close to the ground.
H	Hemicryptophytes: Perennating buds at ground level, all above ground parts dying back at the onset of unfavorable conditions. Stolons may or may not be present. (a) Proto Hemicryptophytes. Lowermost leaves on stem less perfectly developed than the upper ones, the perennating buds arise at ground level. (b) Partial Rosette Plants. The best developed leaves form a rosette at the base of the aerial shoot, but some leaves are present on the aerial stems. (c) Rosette Plants. The leaves are restricted to a rosette at the base of the aerial shoot. (d) Grasslike Hemicryptophytes. Grasslike plants with perennating buds at ground level, all above ground parts dying back at the onset of unfavorable condition.
G	Geophytes: Rhizome, bulb or tuber geophytes, over-wintering by food stores under ground from which arise the buds to produce the next season's aerial shoots.
T	Therophytes: Annual species which complete a life history from seed to seed during the favorable season of the year.

Life Form Symbol	Species Abbreviation	Scientific Names and Authorities
P	Abgr	Abies grandis Lindl.
P	Acci	Acer circinatum Pursh
H	Acmi	Achillea millefolium L. var. lanulosa (Nutt.) Piper
H	Adbi	Adenocaulon bicolor Hook
G	Aggl	Agoseris glauca (Pursh) Raf.
H	Agsp	Agropyron spicatum (Pursh) Scribn. & Smith
P	Amal	Amelanchier alniflora Nutt. var. semintegrifolia (Hook) C. L. Hitchc.
G	Anpi	Anemone piperi Britt
C	Ange	Antennaria geyeri A. Gray
H	Apan	Apocynum androsaemifolium L. var. pumilum Gray
H	Aqfo	Aquilegia formosa Fisch.
P	Arpa	Arctostaphylos parryana Lem. Var. pinetorum (Rollins) Wiesl. & Schr.
P	Artr	Artemisia tridentata Nutt.
G	Ascau	Asarum caudatum Lindl.
H	Ascan	Aster canescens Pursh
H	Baca	Balsamorphiza careyana Gray
C	Bene	Berberis nervosa Pursh
T	Blsc	Blepharipappus scaber Hook.
H	Brca	Bromus carinatus H. & A.
T	Brte	Bromus tectorum L.
H	Casc	Campanula scouleri Hook.
H	Cain	Carex complex - composed of two species Carex inops Bailey & Carex sp.

Life Form Symbol	Abbreviation	Scientific Names and Authorities
P	Cach	Castanopsis chrysophylla (Dougl.) A. DC.
H	Cami	Castilleja miniata Dougl.
P	Ceve	Ceanothus velutinus Dougl.
H	Chdo	Chaenactis douglasii (Hook.) Hook. & Arn.
C	Chme	Chimaphila menziesii (R. Br.) Spreng
C	Chum	Chimaphila umbellata (L.) Nutt. var. occidentalis (Rydb.) Blake
P	Chvi	Chrysothamnus viscidiflorus (Hook.) Nutt.
H	Cice	Cirsium centaurea (Rydb.) Schum.
T	Clrh	Clarkia rhomboidea Dougl.
G	Clun	Clintonia uniflora (Schult.) Kunth.
T	Copa	Collinsia parviflora Dougl.
T	Cogr	Collomia grandiflora Dougl.
G	Coma	Corallorhiza maculata Raf.
T	Cram	Cryptantha ambigua (A. Gray) Greene
T	Crci	Cryptantha circumscissa (H. & A.) Johnst.
H	Cyoc	Cynoglossum occidentale A. Gray
H	Epan	Epilobium angustifolium L.
G	Eqhy	Equisetum hyemale L.
H	Erfi	Erigeron filifolius Nutt.
H	Erum	Eriogonum umbellatum Torr.
H	Erla	Eriophyllum lanatum (Pursh) Forbes
H	Feid	Festuca idahoensis Elmer
H	Frvi	Fragaria virginiana Druck ssp. platypetala (Rydb.) Staudt
T	Gaap	Galium aparine L.
T	Ganu	Gayophytum nuttallii T. & G.
H	Goob	Goodyera oblongifolia Raf.
P	Habl	Haplopappus bloomeri A. Gray
H	Hial	Hieracium albiflorum Hook.
H	Hofu	Horkelia fusca Lindl.
P	Juoc	Juniperus occidentalis Hook.
H	Kega	Kelloggia galioides Torr.
H	Kocr	Koeleria cristata (L.) Pers.
H	Lala	Lathyrus lanszwertii ssp. aridus (Piper) Brads.
G	Lemo	Leucocrinum montanum Nutt.
P	Lide	Libocedrus decurrens Torr.
G	Liwa	Lilium washingtonianum Kell.
C	Libo	Linnaea borealis L. var. americana (Forbes) Rehder
H	Lipe	Linum perenne L.
H	Liru	Lithospermum ruderale Dougl.
G	Losi	Lomatium simplex (Nutt.) J. F. Macbride
H	Luca	Lupinus caudatus Kell.
H	Lulep	Lupinus lepidus Dougl.
H	Luleu	Lupinus leucophyllus Dougl.
T	Magr	Madia gracilis (Smith) Keck
T	Mami	Madia minima (A. Gray) Keck
T	Migr	Microsteris gracilis Greene
T	Mina	Mimulus nanus H. & A.
T	Mope	Montia perfoliata (Donn.) Howell var. depressa (Gray) Jeps.
H	Osob	Osmorhiza obtusa (C. & R.) Fern.

Life Form Symbol	Species Abbreviation	Scientific Names and Authorities
C	Pamy	Pachistima myrsinites (Pursh) Raf.
H	Pabr	Paeonia brownii Dougl.
H	Peci	Penstemon cinereus Piper
H	Pesp	Penstemon speciosus Dougl.
T	Phli	Phacelia linearis (Pursh) Holz.
H	Phmu	Phacelia mutabilis Greene
P	Pimo	Pinus monticola Dougl.
P	Pipo	Pinus ponderosa Dougl.
T	Plma	Plectritis macrocera (T. & G.) Gray
H	Pose	Poa secunda Presl.
T	Podo	Polygonum douglasii Greene
P	Prem	Prunus emarginata (Dougl.) Walp.
P	Psme	Pseudotsuga menziesii (Mirb.) Franco
H	Ptaq	Pteridium aquilinum (L.) Kuhn. var. pubescens Underw.
G	Ptan	Pterospora andromedea Nutt.
P	Putr	Purshia tridentata (Pursh) DC.
H	Pybr	Pyrola bracteata Hook.
H	Pych	Pyrola chlorantha Smith
H	Pyul	Pyrola uliginosa Torr.
P	Rogy	Rosa gymnocarpa Nutt.
C	Ruur	Rubus ursinus Cham. & Schlecht.
H	Scna	Scutellaria nana Gray
H	Seca	Senecio canus Hook.
H	Sido	Silene douglasii Hook.
H	Sihy	Sitanion complex - composed of Sitanion hystrix (Nutt.) Smith-S. hanseni (Scribn.) Smith
H	Smra	Smilacina racemosa (L.) var. amplexicaulis (Nutt.) S. Watt.
H	Stla	Stephanomeria lactucina A. Gray
H	Stoc	Stipa complex - composed of Stipa occidentalis Thurb. - S. thurberiana Piper - S. elmeri Piper & Brodie
P	Syal	Symphoricarpos albus (L.) Blake
H	Tofl	Townsendia florifer (Hook.) Gray
H	Trdu	Tragopogon dubius Scop.
H	Trla	Trientalis latifolia Hook.
H	Vipu	Viola purpurea Kell.